

**LANDSCAPE LEVEL PATTERNS IN BREEDING
BIRD DISTRIBUTIONS IN THE WESTERN
OUACHITA MOUNTAINS**

By

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CHAPTER I

INTRODUCTION






In mountain regions such as the Ouachita Mountains, the elevational gradient plays an important role in shaping the characteristic landscape (Noss and Cooperrider 1994). There are other important environmental gradients. Because the orientation of the Ouachita Mountains is east/west, north-facing slopes receive less insolation than do south-facing slopes. In the areas of the Ouachita Mountains where there are higher elevations, there are higher annual averages of precipitation than in the rest of the region. Also, the processes of succession following disturbances such as logging, windstorms and fires form long-term temporal gradients. The characteristic natural landscape of the western Ouachita Mountain ecoregion emerges from the interplay of the environmental and temporal gradients which operate at the landscape level.

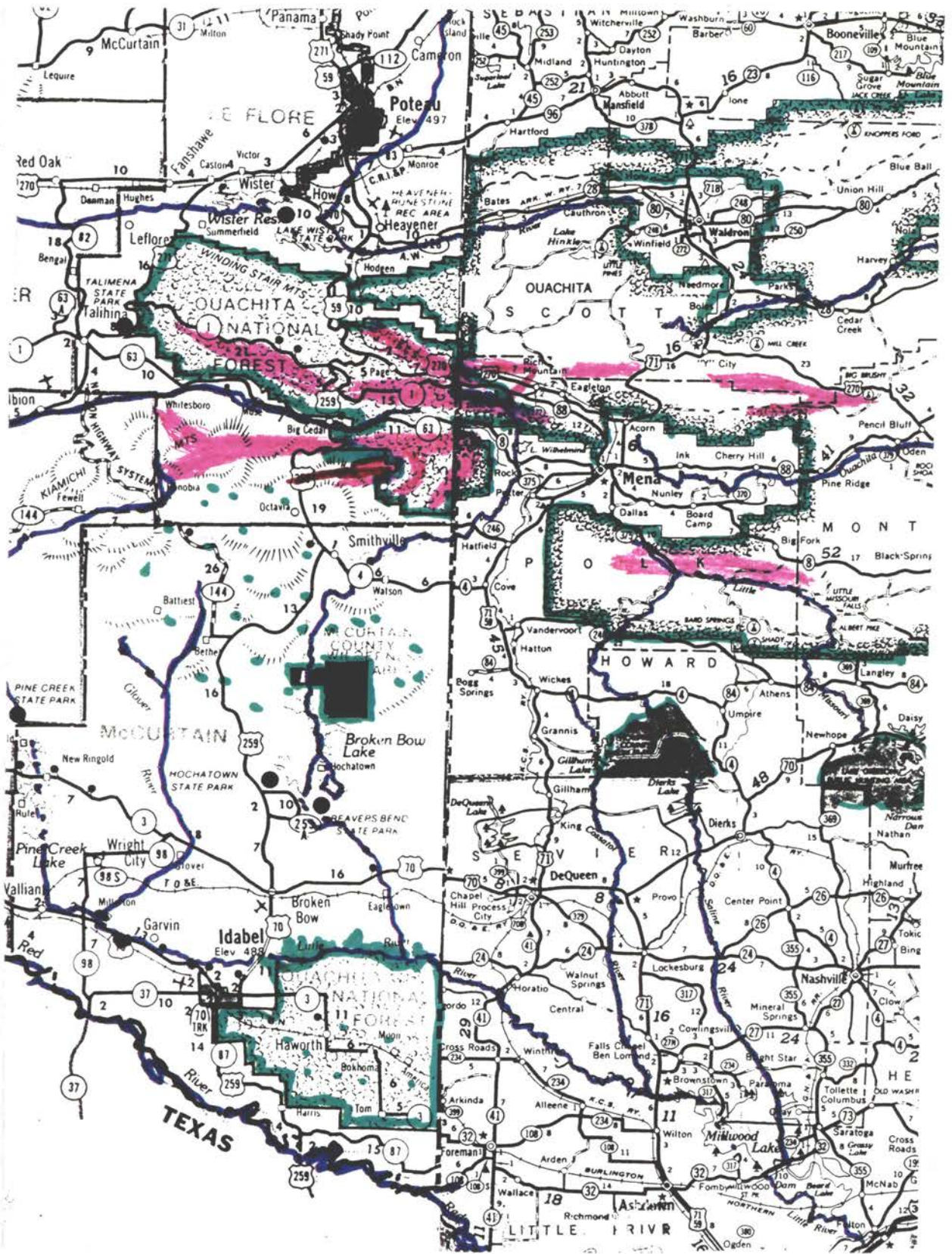
I studied the effect of these gradients on the distributions of breeding birds in the Cucumber Creek Preserve and adjacent area. There were also more basic questions addressed in this research. Not only was an initial inventory of breeding birds needed for the Cucumber Creek Preserve, but also there have been few studies of the breeding birds in the western Ouachita Mountains.

Cucumber Creek is one of many streams and rivers, including Mountain Fork River, Kiamichi River, Ouachita River, Poteau River, Little River and Glover River, which have headwaters in a geographic area straddling the Arkansas and Oklahoma borders. In this region the

Figure 1. Geographic map of the western Ouachita Mountains, showing approximate area of higher elevations, protected areas, the Cucumber Creek watershed and major rivers in the region.

Legend

-  Region of higher elevations (el. > 650 m, or 2000 ft.)
-  Boundaries of national forest and other protected areas
-  Rivers
-  Valley and lowlands of Cucumber Creek watershed
-  Area of proposed trade with Weyerhaeuser Company



Ouachita Mountains reach their highest elevations (see Figure 1). The highest mountains in the Cucumber Creek watershed are Kiamichi Mountain, Lynn Mountain and Blue Bouncer Mountain, all in excess of 700 m (2300 feet).

The watershed of Cucumber Creek encompasses about 7,280 ha (see Figure 2). Cucumber Creek is a headwater stream which flows into Big Eagle Creek, a tributary of Mountain Fork River. At a point about 9.5 kilometers (6 mi) from the confluence, Cucumber Creek splits into two tributaries, one of which flows to the north of Lynn Mountain and the other to the south. Between the confluence with Big Eagle Creek and the point where it splits into two tributaries, there are often several meandering branches of the creek which have formed a fairly wide valley.

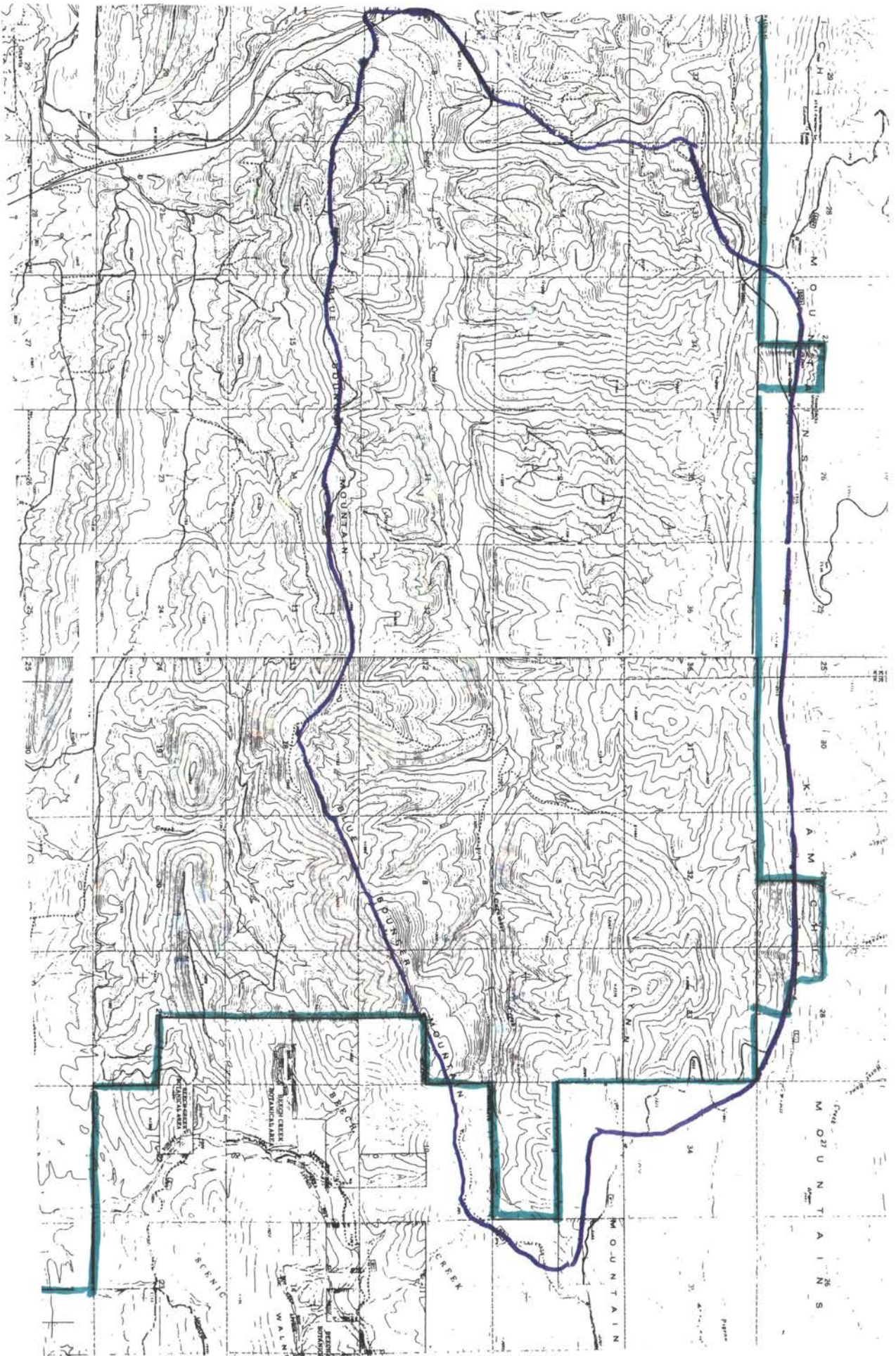
The Cucumber Creek Preserve is a cooperative project of The Nature Conservancy and the Ouachita National Forest. The Nature Conservancy began acquisition of land for the Cucumber Creek Preserve in 1990 and has acquired about 1,100 ha of the 7,285 watershed. The U.S. Forest Service has acquired about 2,000 ha. Approximately 1,500 ha of the eastern and northern part of the watershed was already part of the Ouachita National Forest, prior to the recent acquisitions. Both The Nature Conservancy and the Forest Service continue to acquire additional land. Cucumber Creek Preserve will be managed as a biodiversity preserve.

Cucumber Creek Preserve is a part of a much larger, contiguous natural area. The Ouachita National Forest adjoins the preserve on the east, and also includes the northern boundary of the watershed

Figure 2. Topographic of the Cucumber Creek watershed and adjacent area.

Legend

- National Forest boundary prior to recent acquisitions
- Approximate boundary of watershed



on Kiamichi Mountain. The Beech Creek National Scenic Area and Botanical area adjoins the Cucumber Creek watershed to the south. This area covers 3,250 ha and includes the valley along Beech Creek, the north-facing slope of Walnut Mountain, and the south-facing slopes of Blue Bouncer Mountain and Lynn Mountain. Also, an agreement is pending before Congress which would transfer approximately 40,000 additional hectares to the Forest Service from the Weyerhaeuser Company. This land is located to the south and west of the Cucumber Creek Preserve.

There are few human settlements and few paved roads in this large natural area. The connectivity, or lack of fragmentation, of the landscape means that there is a significant opportunity for conservation of birds, particularly neotropical migrants, as well as other forms of wildlife, not only in the Cucumber Creek Preserve, but also in the larger, adjacent natural area (Noss and Cooperrider 1994).

This study has three principal aims. The first is to sample the neotropical migrants and other breeding birds which are present in the Cucumber Creek watershed. The second is to investigate the distributions of breeding birds along environmental and temporal gradients, and to identify any characteristic associations of neotropical and other breeding birds at the landscape level in the Cucumber Creek watershed, and more generally in the region of higher elevations in the western Ouachita Mountains. The final aim is to design a strategy for representation of these particular associations of neotropical migrants and other birds for the

Cucumber Creek watershed, and for the region of higher elevations in the western Ouachita Mountain ecoregion.

In Chapter One, I discuss how the migratory strategy of neotropical migrants makes them particularly vulnerable to habitat fragmentation. Large natural areas such as that of the Cucumber Creek watershed and the adjacent natural area are indispensable for the conservation of many species of neotropical migrants.

In Chapter Two, I review Johnson's (1986) findings that there are certain forest community types across the landscape of the region, which are shaped by environmental gradients such as elevation and rate of insolation. Mesic oak (*Quercus* spp.) - hickory (*Carya* spp.) forests occur on upper north-facing slopes, but more xeric oak-pine (*Pinus* spp.) forests occur on south-facing slopes, and lower north-facing slopes. Dry oak-hickory forests occur on the ridgetops, but mesic mixed hardwood forests occur on floodplains.

Also, I review the multivariate statistical analysis which indicates that there are four different associations of breeding birds which occur in the Cucumber Creek watershed and probably across the landscape of the region of higher elevations. These associations are: an oak-pine association at sites on south-facing slopes, flats and valleys with high importance value for shortleaf pine; a higher elevation/north-facing slope association on upper north-facing slopes and ridgetops with patches of taller, denser shrubs in the undergrowth; a ridgetop association on ridgetops with sparse understories and upper south-facing slopes; and finally, a bottomland hardwood/riparian association in mixed hardwood forests

on bottomlands. The second and fourth association are particularly rich in neotropical migrants, including cerulean warbler (*Dendroica cerulea*), wood thrush (*Hylocichla mustelina*), Kentucky warbler (*Oporornis formosus*), hooded warbler (*Wilsonia citrina*), Louisiana waterthrush (*Seiurus motacilla*), ovenbird (*Seiurus aurocapillus*), Acadian flycatcher (*Empidonax virescens*) and scarlet tanager (*Piranga olivacea*).

In Chapter Three, I present a proposal for a landscape level strategy for representation of these important bird associations in the Cucumber Creek watershed and the surrounding large natural area. I also discuss other studies which have shown that there is another important bird association which is missing in the Cucumber Creek watershed and in most of the Ouachita Mountains, because of the disappearance of open wooded ecosystems, including pine and/or oak savanna and open woodlands.

These community types were widespread until fire suppression began about 50 years ago in the region, but have almost disappeared as dense stands of hardwoods have invaded the formerly open pine and/or oak (hereafter pine/oak) savannas and open woodlands, which were maintained by frequent ground fire. Birds of pine/oak savanna and open woodlands are red-cockaded woodpecker (*Picoides borealis*), brown-headed nuthatch (*Sitta pusilla*), red-headed woodpecker (*Melanerpes erythrocephalus*), Bachman's sparrow (*Aimophila aestivalis*), prairie warbler (*Dendroica discolor*), northern bobwhite (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*).

Under the new philosophy of ecosystem management, management

of the Ouachita National Forest, in the Cucumber Creek Preserve and elsewhere in the western Ouachita Mountain ecoregion has an historic opportunity to implement a landscape-level approach to management for the conservation of biodiversity. Already the Ouachita National Forest has proposed a plan for protection of the oak-hickory forests on ridgetops and north-facing slopes and of the hardwood forests on bottomlands (USDA 1993). Continued development of these forests toward uneven-aged, old growth status, which provides excellent habitat for many species of neotropical migrants and other birds, should be a conservation priority.

Under ecosystem management the Ouachita National Forest has also proposed a plan for the restoration of pine/oak savanna and open woodlands which have almost disappeared during the years of fire suppression (USDA 1993). Various methods of partial cutting in the oak-pine community, such as single-tree or group selection, shelterwood and seed tree, may conceivably both advance timber management objectives and restore these community types. After the forest is in effect thinned by one of these methods, periodic ground fire may be used to maintain the open structure of the forest and to prevent the growth of a hardwood midstory. Ongoing research may also eventually reveal how the forest may be regenerated under a regime of periodic ground fire.

CHAPTER II

THE MIGRATORY STRATEGY OF NEOTROPICAL MIGRANTS

THE LIFE HISTORY OF NEOTROPICAL MIGRANTS

Until the last two decades very little was known about the geographical distribution and the relative abundance of neotropical migrants in different habitats during the nonbreeding season. Recent surveys of habitat use have been made in western Mexico (Hutto 1992), the Yucatan Peninsula (Lynch 1992; Greenburg 1992), Vera Cruz, Mexico (Rappole et al. 1992), Costa Rica (Blake and Loiselle 1992), the Caribbean Islands (Robbins et al. 1992) and in other places in the neotropics. From these studies a general outline of the geographical distribution and the habitat preferences of many neotropical migrants during the nonbreeding season has begun to emerge.

Twenty years ago most ornithologists classified neotropical migrants as opportunistic species, as "weed-like opportunists that seasonally invade disturbed, fringe habitats of tropical and temperate communities" (Sherry et al. 1993). It was thought that because of competitive disadvantages, neotropical migrants were adapted to niches in the tropical and temperate communities not already claimed by the competitively superior resident species (Robinson et al. 1988; Hutto 1992). It is now understood that neotropical migrants are highly adaptive tropical species which have developed a migratory strategy for nesting.

The annual northward migration by these species is probably just an endpoint of a series of adaptations which began with

migrations within the tropics from one elevational zone to another in search of food resources such as fruit, nectar or insects (Levey and Stiles 1992). In the tropics these resources are often seasonally and sometimes temporally and spatially unpredictable. The annual migration to the temperate zone is an evolutionary strategy which allows the migrants to produce offspring during the northern spring when food resources are abundant and predictable (Levey and Stiles 1992). The status of neotropical migrants as highly adaptive neotropical species explains why they differ morphologically both from tropical residents and from temperate residents (Ricklefs 1992).

Neotropical migrants occur in every neotropical community and habitat during the nonbreeding season (Sherry and Holmes 1993). These birds choose ecologically separate niches to as great an extent as tropical residents. In fact, data from extensive point counts and mist netting on the Yucatan Peninsula show that neotropical migrants tend to occupy the same habitats as the permanently resident tropical species (Lynch 1992). There is a highly significant positive correlation between the occurrence rates of migrants and residents. If the traditional view of the migrants as opportunists were true, one would expect a negative correlation.

Also, during the nonbreeding season many species of neotropical migrants have preferred habitats, are territorial and exhibit site fidelity from year to year (Sherry and Holmes 1992; Holmes and Sherry 1993). In a study in Vera Cruz of sites in primary forest, second growth and scrub habitats, different species of neotropical migrants were found in different habitats. Wood thrush (*Hylocichla mustelina*),

worm-eating warbler (*Helmitheros vermivorus*), ovenbird (*Seiurus aurocapillus*) and Louisiana waterthrush (*Seiurus motacilla*) are primarily birds of the primary forest, but are occasionally found in second growth. Hooded warbler (*Wilsonia citrina*), white-eyed vireo (*Vireo griseus*), Kentucky warbler (*Oporornis formosus*), Wilson's warbler (*Wilsonia pusilla*) and magnolia warbler (*Dendroica magnolia*) were commonly found in both primary forest and second growth. A third group, including least flycatcher (*Empidonax minimus*), gray catbird (*Dumetella carolinensis*), yellow-breasted chat (*Icteria virens*), common yellowthroat (*Geothlypis trichas*), orange-crowned warbler (*Vermivora celata*) and indigo bunting (*Passerina cyanea*), was found in scrub and thickets. Recapture and resighting data indicated that these species remained in the same area during the nonbreeding season for periods of time ranging from three to seven months. And recaptures during succeeding years indicated that the same birds returned to the same nonbreeding territories year after year (Rappole et al. 1992).

In the Yucatan Peninsula neotropical migrants also occupy the full range of the successional gradient. Hooded Warbler, ovenbird, wood thrush, white-eyed vireo, black-and-white warbler (*Mniotilta varia*), Kentucky warbler and magnolia warbler occupy primary forest and mature second-growth. Some of the same species as well as others occupy early successional scrub known locally as *acahual*. These species include ovenbird, hooded warbler, magnolia warbler, black-and-white warbler, gray catbird, white-eyed vireo, common yellowthroat and indigo bunting. Still others prefer cleared and temporarily cultivated sites known locally as *milpas*, and fields and

pastures. Some of these species are common yellowthroat, least flycatcher and indigo bunting (Lynch 1992).

The distribution of neotropical species along the successional gradient during the nonbreeding season also is apparent in the Caribbean Islands. Late successional species, such as northern waterthrush (*Seiurus noveboracensis*), Louisiana waterthrush, ovenbird and Kentucky warbler, occupy primarily in undisturbed, primary forest. Early successional species occur in disturbed areas, such agricultural fields, plantations and orchards. The northern parula (*Parula americana*), American redstart (*Setophaga ruticilla*), black-and-white warbler and the magnolia warbler are common in citrus groves, cacao and coffee plantations and other agricultural habitats. The black-throated blue warbler (*Dendroica caerulescens*) was frequent in sun coffee plantations but rare in other agricultural habitats. Hooded warbler was frequent in pine plantations and cacao but rare in other agricultural habitats (Robbins et al. 1992).

HABITAT FRAGMENTATION: LIMITING THE POPULATIONS?

For at least one the species, wood thrush, the process of deforestation in the tropics may limit the population. In a study in excellent habitat in New Jersey, adult wood thrushes and fledglings were banded, and instances of nest predation and cowbird parasitism were recorded (Roth and Johnson, in press). In the habitat where the study was made, per capita reproduction remained constant and was adequate to maintain the population at the original, early level. The problem was that return rates of adult birds from the neotropics

declined steadily and significantly over the years. Other species which prefer habitat in primary forest are the waterthrushes, Kentucky warbler, ovenbird, Acadian flycatcher (*Empidonax virescens*) and yellow-bellied flycatcher (*Empidonax flaviventris*).

Most other species appear to be adapted at least to some extent to the anthropogenic landscapes which are being created in the neotropics. Declines in the populations of these species may be related to problems on the breeding grounds in the temperate zone, particularly to fragmentation of the habitat. A few species are faced with serious loss of habitat during both breeding and nonbreeding season: cerulean warbler is one of these (Robbins et al. 1992a).

The link of population declines of many species of neotropical migrants with fragmentation of breeding habitat was first brought to the attention of ornithologists in the seminal paper by Whitcomb et al. (1981). Field work revealed that few, if any, area-sensitive or forest-interior species were found during breeding season in smaller tracts of forest in eastern North America. Since publication of that paper, forest fragments under 10 ha in area have been found to be unsuitable for sustaining breeding populations of many forest-dwelling neotropical migrants, including veery (*Catharus fuscescens*), wood thrush, red-eyed vireo (*Vireo olivaceus*), black-throated blue warbler, cerulean warbler, hooded warbler, and ovenbird, just to name a few (Robbins et al. 1989). Only forested areas of at least 3000 ha may reasonably be expected to retain all of the forest-interior and area-sensitive species (Robbins et al. 1989).

Several factors have been suggested to explain the empirical

finding that area-sensitive and forest-interior species do not prefer to reproduce in small woodlots. First, reproductive success tends to be very low in small woodlots, because of increased rates of nest predation and nest parasitism. Nesting success in small woodlots and along edges is often less than 20% (Robinson 1992; Temple and Cary 1988). Many important nest predators, including bluejay (*Cyanocitta cristata*), American crow (*Corvus brachyrhynchos*), common grackle (*Quiscalus quiscula*), dogs, cats, rats, raccoons and squirrels have greatly elevated populations in anthropogenic landscapes where small woodlots are found (Ehrlich et al. 1988). Brown-headed cowbird (*Molothrus ater*) parasitism also increases to overwhelming levels with the proximity of nesting sites to cowbird feeding areas such as open fields and cattle pens (Temple and Cary 1988). Cowbirds may travel distances up to 7.5 km from feeding areas to breeding areas (Robinson et al. 1993).

Another factor is that neotropical migrants have developed breeding behaviors which key on breeding success in prior seasons. Successful breeding and high annual production of offspring in extensive forests imply that in subsequent years the migrants return to those areas where success has been achieved.

THE ROLE OF BEHAVIOR IN BREEDING SUCCESS

Several studies have investigated the kinds of breeding behavior which leads to high annual production of young. In a study of blackpoll warblers (*Dendroica striata*) in an extensive forest in Nova Scotia (Eliason 1986), females often showed strong site fidelity

to nesting sites in extensive forests. The females often arrived before their mates in the locations where they had successfully produced offspring in previous years. Rather than delay nesting, a high percentage of these females bred polygynously with early-arriving males. Any costs of these polygynous bonds to the females were apparently offset by reproductive success associated with early nesting. A female who bred with a polygynous male was able to begin raising young immediately on her territory, and she also had a better chance of successfully raising a second brood, often with a second male (Eliason 1986).

In a study of several species of neotropical migrants at Hubbard Brook (Holmes et al. 1992), a second growth forest in New Hampshire, black-throated blue warblers had high annual production of young: females laid an average of 6.6 eggs per season of which 5.2 hatched and 4.3 fledged. The high annual production was due to overall high nesting success (63%), low nest predation (22%), no brood parasitism, but most importantly to frequent multiple brooding (45%). Multiple brooding was significantly and positively related to age of the male parent. Two-year or older males were more likely to be mated to females that double brooded, and they were also more likely to mate polygynously. The older females were also more productive. Based on male singing activity and the occurrence of nests late in the season, black-throated green warbler (*Dendroica virens*), red-eyed vireo and scarlet tanager may also produce two broods at Hubbard Brook, at least in years when food is plentiful. American redstart, however, does not double brood at Hubbard Brook (Holmes et

al. 1992).

There is also evidence (Morton 1992) that some species of neotropical migrants begin breeding quite early, even before the migrants reach the nesting territories. This behavior probably produces fledglings of mixed parentage from the same nest. While exclusively monogamous behavior among birds is usually more adaptive (Morton 1992), This kind of mixed breeding behavior may also be conducive to high annual production of offspring by neotropical migrants.

Intraspecific competition among males for females and among females for territory tends to produce high annual production of offspring in high quality habitat. The migratory strategy creates a concentration in space and time of fertile females unequalled in tropical latitudes with a long breeding season (Morton 1992). Older males undoubtedly outcompete younger, less experienced males both for females and for the best breeding habitat, i.e., the habitat where high annual production of young has occurred in previous years, and the result is the selection of the more extensive tracts of forest by the females (Villard et al. 1993). On the other hand, more experienced females probably outcompete less experienced females for the best breeding territories in other species besides blackpoll warbler (Eliason 1986). The overall result is that the best breeding territories are won by the older and more experienced males and females, which are also the most successful at producing high numbers of offspring.

Further, the activity of older males in the best breeding

habitat during the early spring attracts yearling females and also yearling males. Yearling females are disproportionately recruited, but some yearling males may find acceptable territories as well (Cody 1985). Some younger birds may remain in the best territories as floaters.

In anthropogenic landscapes those yearling males which are outcompeted may finally seek mates in less desirable habitat, such as small woodlots. Because most of the females have selected older males which occupy more extensive forests, many of these younger males may be unpaired. This is the probable explanation for the continuous singing of male ovenbirds in woodlots in the Ozarks of Missouri: three-fourths of these birds were unpaired (Gibbs and Faaborg 1990). In contrast, 80% of male ovenbirds in extensive forests further east and north were paired (Villard et al. 1993). While the rate of successful breeding in these places is affected by high rates of nest predation and cowbird parasitism, the absence of older, more experienced individuals may be a contributing factor (Robinson 1992; Sherry and Holmes 1992). All of these factors reduce the rate of successful production of offspring to very low rates in these woodlots.

All of these factors emphasize the vital importance of high quality, unfragmented habitat for area-sensitive and forest-interior species of neotropical migrants. The key role in high annual production is played by older, experienced birds. High quality habitat attracts breeding birds of those particular species adapted to that habitat: older males and females return to these areas, because in

prior years high annual rates of offspring have been produced there. There is competition not only between males for breeding territories, but at least in some species, also between females for high quality habitat.

From this perspective it is also possible to begin to understand why the fragmentation of high quality habitat may disrupt the breeding activities of the older, more experienced birds and lead to declines of populations. Even these more experienced birds probably do not have time to search for alternate high quality habitat when they return to habitat which has been degraded by human activities and still produce high annual rates of offspring. The migratory strategy of neotropical migrants makes them dependent upon the continued availability of high quality habitat to which they have become accustomed in prior years.

NEOTROPICAL MIGRANTS IN THE WESTERN OUACHITA MOUNTAINS

According to data from Breeding Bird Surveys, eight neotropical species have declined significantly in the Ozark/Ouachita region since 1966. These species are Acadian flycatcher, wood thrush, cerulean warbler, ovenbird, gray catbird, painted bunting (*Passerina ciris*), orchard oriole (*Icterus spurius*) and prairie warbler (*Dendroica discolor*) (Hunter et al. 1993). Although the decline is not statistically significant, numerical declines have been noted in the Ozark/Ouachita region for nine other species, including eastern wood-peewee (*Contopus virens*), great crested flycatcher (*Myiarchus crinitus*), American redstart, worm-eating warbler, Louisiana

waterthrush, hooded warbler, Kentucky warbler, scarlet tanager and white-eyed vireo (Hunter et al. 1993). Some statistical methods indicate that these declines are steeper in the Ouachita Mountains, than in the Ozarks (James et al. 1996).

Several of the regionally declining species of neotropical migrants, such as cerulean warbler, Acadian flycatcher and Louisiana waterthrush, are forest interior or area sensitive species. The Cucumber Creek watershed and probably most of the region of higher elevations in western Ouachita Mountain ecoregion is just the kind of large natural area needed by the area-sensitive and forest interior species of neotropical migrants for successful breeding. Other declining species, such as prairie warbler, painted bunting and orchard oriole, are early successional species which prefer the early successional habitat of oak-pine savanna and open woodland.

CHAPTER III

LANDSCAPE LEVEL PATTERNS IN BREEDING BIRD DISTRIBUTIONS

INTRODUCTION

Biogeographical maps of the Ouachita Mountain ecoregion, such as Duck and Fletcher (1942), indicate that the vegetation of the region of higher elevations is a more or less homogeneous forest community type, usually called oak-pine or oak-hickory-pine. While this may be true at a coarse-grain level of resolution, this is not the case at a finer-grain level. There are fairly narrow, elevational zones with different forest community types (Johnson 1986; Stahle et al. 1985b). In this research I have investigated whether there are also distinct breeding bird associations within these different forest community types.

On the tops of the ridges, there is a dry oak-hickory forest, dominated by white oak (*Quercus alba*) and mockernut hickory (*Carya tomentosa*), usually only 5 to 7 m tall. The understory may be fairly open with patches of grass or in other places may have taller, dense patches of wild currant (*Ribes, spp.*) buckbrush (*Symphoricarpos orbiculatus*) and greenbriar (*Smilax, spp.*). On upper and middle north-facing slopes above about 600 m (1700 -1800 ft.), there is a mesic oak-hickory forest dominated by mockernut hickory but with many species typical of mesic forests, such as Carolina basswood (*Tilia caroliniana*), cucumber tree (*Magnolia acuminata*) and white ash (*Fraxinus americana*). There is a rich understory of tall shrubs along with grasses, herbs and ferns. A more typical oak-pine community

occurs on south-facing slopes with shortleaf pine (*Pinus echinata*) and xeric oaks such as black oak (*Quercus velutina*), post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*), and a scrubby, short understory of sugar huckleberry (*Vaccinium vacillans*). The community on the lower north-facing slopes is a mixture between oak-hickory and oak-pine, and individual stands are usually dominated by Shumard's oak (*Quercus shumardii*) or shortleaf pine. The valleys are usually tallgrass prairie, and in undisturbed bottomlands along the streams and rivers, there are forests with many different species of hardwoods and a rich understory.

A similar, but even more diverse, landscape may have existed before settlement by European immigrants. When Thomas Nuttall travelled through the area in 1819, he reported extensive prairies in the valleys and even a bison hunt in the Kiamichi River valley near the site of Talihina, Oklahoma (Nuttall, 1819). He observed pine-covered ridges on south-facing slopes, oak-covered ridges on north-facing slopes and stunted trees on the ridgetops. The floodplains and bottoms of the valleys were covered with stands of hardwoods and dense thickets of briars. But the lower slopes and valleys were characterized by savanna and open woodlands: during a tour of the eastern Ouachitas in the 1770's, du Pratz (1774) observed that "(t)he plains were intermixed with thickets...and interspersed with hills, running off in gentle declivities, and with valleys, thick set, and adorned with woods." In the second-growth forests of today, the suppression of fire has allowed the growth of hardwoods which have replaced the savanna and open woodlands.

The patterns of different forest community types across the landscape suggest "environmental sorting" (Gleason 1926) of the populations of the different species of plants occurs because of environmental and successional gradients. Some plant species prefer mesic habitats, for example, and others prefer more xeric, fire-prone ones. Some species prefer shaded habitats, others more open ones. Some species are fire-resistant, and others not.

Whittaker (1972) showed that "environmental sorting" occurs because species tend to be continuously distributed along environmental gradients, such as elevation, moisture, fire frequency and soil type. Over long periods of time, each species, or more generally, each population, has evolved into an individual niche. The niche of a species, or population, is the totality of the ways it relates to other species in a community and to the abiotic environment (Whittaker 1972).

Direct gradient analysis of many different communities along environmental gradients, such as elevation, by Whittaker and others has shown that the distributions of plant species along environmental gradients are usually unimodal (Gauch 1982). In a unimodal distribution the curve of the distribution of each species along such an environmental gradient is bell-shaped and has a maximum at some interval of the environmental variable. The series of bell-shaped curves along an environmental gradient is called a coenocline. In most cases the bell-shaped curves of the different species are scattered out along the gradient, but generally overlay one another to varying degrees (Whittaker 1972). Those species whose

distribution curves overlay one another are co-existing species. A group of plant species which co-exist form a community type; and birds and other animals which co-exist with or within a particular community type, form an assemblage, or association.

Traditional studies of avian habitat selection have focussed on the structure of the habitat. Rotenberry (1985) has proposed that habitat selection is a two-fold process: birds distinguish between broad habitat types according to vegetation structure, and that at a smaller scale, they distinguish specific habitat by floristic features. The underlying mechanism proposed by Rotenberry (1985) for habitat selection is food selection and foraging behavior: birds first select breeding territory with the desired food and foraging substrates broadly by vegetative structure and then more selectively by floristic features.

According to this model birds nest in territories which have the desired food and substrates for foraging. Each species selects a breeding territory which contains a preferred habitat structure for the nest and the substrate for foraging (Cody 1981). The term, habitat-niche, is often used to describe habitat which contains these essentials for breeding territory of a particular species (James 1971; Salwasser 1986).

Avian habitat-niches respond to large-scale environmental gradients, such as elevation, which cause differences in the structure of the vegetation, and also to small-scale gradients created by floristic variations in the composition of the plant community (Rotenberry 1985). Thus, bird assemblages or associations

are structured both at a large scale according to structural features of the vegetation and also at a smaller scale by floristic variations of the plant community. (Bersier and Meyer 1994).

ENVIRONMENTAL GRADIENTS IN THE OUACHITA MOUNTAINS

Topography. Differences in elevation in the Ouachita Mountains have developed over millions of years. A collision between two continental plates formed the Ouachita Mountains about 300 million years ago. That event created an uplift running east and west, and a pattern of complex folding and faulting of the predominantly sedimentary rocks in the area. Since the time of their formation long ago, the processes of erosion have worn away the Ouachita Mountains, and today broad valleys separate long east/west ridges. The tops of the ridges may be fairly wide and gently sloping, but are often very narrow and steeply sloping (Foti and Glenn 1991).

The climate of the Ouachita Mountain ecoregion is warm and humid during the summer and mild during the winter (Baker, 1994). Annual precipitation averages 110 cm (44") in the northern parts of the western Ouachita Mountains and as much as 135 cm (54") in the southern parts of the region (Baker, 1994). Periods of drought commonly occur in July, August and September.

Cucumber Creek Preserve is located in the southern part of the region where there are higher elevations: the ridges reach as high as 800 meters and the valleys lie at 300 meters (Baker, 1994). The high elevations produce an orographic effect which increases annual precipitation. Adiabatic cooling of humid air as it flows northward

over the Ouachitas from the Gulf of Mexico leads to condensation and increased precipitation in the immediate area. This area of higher elevations receives as much as 50% more annual precipitation than other areas in the region (Foti and Glenn 1991). Moreover, it is likely that the higher elevations along these ridges receive additional precipitation in the form of condensation during rather frequent occurrences of heavy fog during the fall and spring (pers. obs.).

Higher elevation causes another important microclimatic effect. Each 1000-m increase in elevation decreases air temperature by about 6 degrees Centigrade (Ricklefs 1993). This adiabatic cooling means that the highest ridges have an average temperature that is about 3 degrees centigrade cooler than that of the adjacent valleys. The lower average temperatures produce slower rates of evapotranspiration and moister soils at higher elevations.

Instead of the usual north/south orientation of mountains in North America, the ridges of the Ouachita Mountains are oriented east and west. South-facing slopes receive on average more direct insolation than do the north-facing slopes, where insolation is more oblique. Prevailing southwest winds also tend to make south-facing slopes drier (Johnson 1986). These factors produce warmer and drier microclimates on south-facing slopes, limiting vegetation to drought-resistant (xeric) forms. Vegetation on cooler, moister north-facing slopes tends to be more mesic, at least at higher elevations (Foti and Glenn 1991).

The distribution of soils is also related to differences in elevation. The soils of the region are derived from parent materials

of cherts, shales, slates, sandstones and novaculites and are not particularly fertile (Baker 1994). Soils of the ridgetops and upper slopes in the Cucumber Creek area are derived from shales (Carnasaw series) or sandstone (Pirum series). As is the case for most of the Ouachita Mountain ecoregion, these soil are usually shallow with a site index for shortleaf pine of about 50 feet at 50 years. Soils of middle to lower slopes are of the same series, and again like the rest of the ecoregion are deeper with a site index from about 50 to 90 feet at 50 years (Baker 1994; USDA 1983). Despite the general shallowness of the soil on the ridgetops and upper slopes, tree roots may penetrate to considerable depths at places where the parent material is inclined at steep angles to the surface due to geologic folding and faulting (Baker 1994).

Soils of the floodplains of the Cucumber Creek valley belong to the Neff-Kenn-Ceda series. They are moderately well drained loamy soils with a loamy or cobbly subsoil (USDA 1983). These floodplains have medium site potential for the growing of hardwoods and pines. In this study I describe the forests that grow on these soils as mixed hardwood forests on bottomlands.

The successional gradient and frequent ground fire. Early travelers in the Ouachita Mountain ecoregion commented on the fires which they observed in the area. Featherstonhaugh (1844) observed an "immense conflagration" between ridges in late November. Du Pratz had earlier observed that the grass were set on fire in the month of September (or perhaps later in the fall) and clouds of smoke are seen for "several days together to extend over a long track [sic] of

country." The fires made traveling easier across the "meadows", or prairie, and also produced verdant foliage after fall rains, which attracted abundant game and allowed travelers to find provisions (Foti and Glenn 1991). Prior to settlement these set fires must have played a vital role in the disturbance regime of the Ouachitas.

Undoubtedly wildfires also occurred prior to settlement. Climatic records indicate that present day wildfires started by lightning are most frequent in August, with high frequencies also in July and September (Foti and Glenn 1991).

Prior to settlement there was an almost continuous understory of grasses and forbs on south-facing slopes and in the valleys above the flood plains, which during dry periods of late summer and fall would have supported flashy, rapidly-moving fires that were not likely to seriously damage scattered dominant trees (USDA 1993). These growing season fires were probably frequent enough and hot enough to suppress most of the woody understory (USDA 1993, Waldrop et al. 1992, Engstrom et al. 1984).

The prairies, savannas and open woodlands reported by the early travelers were fire-maintained ecosystems. Since the initiation of the policy of fire suppression in the middle part of this century, the pine/oak savanna and open woodlands have almost disappeared. A few thousand acres of savanna and open woodland still remain in western Arkansas near Waldron (USDA 1993); but a considerable area of open woodland has disappeared from the McCurtain County Wilderness Area since 1955 (Kreiter et al. 1995b). Tallgrass prairie is still found in the larger valleys, where it is

grazed, but the absence of fire has allowed much of the area which was originally prairie to become woodland.

Fire may have also played an important role in shaping the composition of the vegetation across the landscape. Species of trees adapted to frequent fire such as shortleaf pine, post oak and blackjack oak have competitive advantages in fire-prone parts of the landscape such as south-facing slopes and valleys. Fire may also play a role in maintaining a diverse landscape consisting of patches of pines and oak or oak-hickory in savannas and open woodlands, rather than a more homogeneous landscape of pine-oak savanna or open woodlands (Kreiter et al. 1995b). In a regime of frequent fire, pines may tend to be associated with sandy soil, and hardwoods with clay (Foti 1974). Fire suppression in the brief time period from 1955 to 1990 in the McCurtain County Wilderness Area has allowed the emergence of a hardwood midstory in pine/oak savanna and open woodland (Kreiter et al. 1995b).

History of disturbance regime of present day forests. After a severe, large-scale disturbance such as clear-cutting, crown fire or tornado, there are four stages of succession (Oliver 1992). The stand-initiation stage begins as the seedlings and resprouts begin to grow after logging or severe disturbance. Ten or 20 years later as the trees grow taller, there is intense competition for light and other resources from the closely growing trees. This is called the stem-exclusion stage. The understory-reinitiation stage begins as an understory starts to grow beneath the canopy. After a long time uneven-aged stands of trees begin to emerge, with some very old

trees and a well-developed understory. This is the old growth stage.

Large-scale logging of old growth pine and oak began around the turn of the century in the Ouachitas. Six large sawmills began operation in 1908. This logging continued until the mid-1950's. Most of the virgin timber on private land was logged by the mid-1930's (USDA 1993). During the depression the Forest Service purchased large amounts of this cutover land, along with defunct farms. From 1919 to 1940, the Ouachita National Forest expanded from 625,000 acres to over 1.4 million acres.

After acquisition of these large areas, the Forest Service implemented a plan for second-growth forestry. One of the top priorities for second-growth forestry was cessation of continued burning of cutover land, which prevented development of the forest beyond the early stages. By about 1940 the Forest Service was finally able to control major fire outbreaks through fire prevention education programs, a road network built by the Civilian Conservation Corps and improved firefighting tactics and technology (USDA 1993).

The vast majority of these second-growth forests date from the logging boom, roughly 1900 to 1940. In fact, 69% of the stands are between 51 and 90 years old, and only 5% are older (USDA 1993). These are even-aged stands predominantly, because the regrowth occurred following a stand-level disturbance such as logging or fire. Because the policy of fire control has prevented low-intensity, frequent fires which occur naturally in the region, a vigorous hardwood midstory has become established throughout the Ouachita National Forest. The region has become predominantly pine-oak or oak-pine

forest, and the pine/oak savannas and open woodlands have all but disappeared.

The second-growth forests of today reflect the pattern of different forest community types which existed before settlement to some extent. Hardwoods dominate on moister, shadier north-facing slopes and on ridgetops. Shortleaf pine often dominates the canopy on south-facing slopes and on the flats along the streams. On better ground white oak and red oak (*Quercus rubra*) mix with pine and often form a substantial component of the overstory. On more xeric south-facing slopes, black hickory, blackjack oak and post oak occur in association with the pine (USDA 1993).

METHODS

SAMPLING METHODS

Sampling of the vegetation. In order to quantify important environmental variables which influence the distribution of breeding territories of birds, I made certain measurements of the vegetation and other environmental variables. I followed the method of measuring vegetation of James and Shugart (1970), but I used one to four subplots (11.3 m. radius circles) within each bird census plot. The first subplot was located in the center of each bird plot. In those count circles where time permitted, a second subplot was placed in a random direction, 30 m from the first subplot. The remaining subplots were placed 120 degrees and 240 degrees from the second subplot, and 30 m from the first.

All shrubs and saplings were counted by species within a 5m-

radius circle within the subplot. Shrubs were defined as woody plants with a diameter less than 2.5 cm and a height between .5 m and 2m. All larger woody plants were counted by species and stem diameter classes within a 11.3m-radius circle. I used the nomenclature of Waterfall, like Johnson (1985). Larger woody plants were classified by stem diameter using a Biltmore stick. Stems greater than 2.5 cm and less than 4 cm were classified as saplings. Stems greater than 4 cm but less than 8 cm were classified as poles. Larger stems were classified in three categories: 8-23 cm, 23-38 cm, and greater than 38 cm.

Direct measurements of slope and aspect were taken at the center of each count circle. Canopy height was estimated using a range finder. Percent canopy cover was measured using a convex densiometer. Elevation was taken from a topographic map. I also made rough estimates of the percent cover of the dominant tree species of the canopy, of percent cover of shrubs, of the percent cover of dominant shrub species, of percent ground cover and of percent cover of ground cover, including grasses.

Sampling of bird territories. I sampled the number of territories of breeding birds for the years 1994 and 1995 using the point count method. The point count method was developed in France by Ferry and Frochet (1970) as a method of rapidly obtaining indices of abundance, so that bird populations in different habitats might be compared during the breeding season (Robbins, 1978). Using this method as modified by Hutto et al.(1986), and Martin and Thill (1991), I stood for 8 minutes at the center of 40-m-radius circle, noting each

bird seen or heard within the plot and outside the plot. A count was made in each circle at least three times during the breeding season. The highest number of singing males, individual females or pairs of every species counted in each circle were used to compute the number of territories of each species detected per point count.

I selected fifty count circles, using a randomly stratified design, in the following manner. First, a set of 1000 randomly selected coordinate points was generated by a computer program for random numbers. Then, using topographic maps I divided the entire study area of 14 sections into 5 different stratifications: bottomland, upper north-facing slopes, ridgetops, lower north-facing slopes and south-facing slopes. Beginning with the first randomly selected coordinates, 12 regular sample points and 3-6 optional sample points were selected for each stratification. In the final selection of the point counts to be sampled, I selected optional sample points if a regular point was too inaccessible or isolated. All points were originally chosen a priori, however.

STATISTICAL METHODS

The environmental gradients which play important roles in affecting the environmental sorting of the various species of plants or birds across a landscape may be studied using multivariate statistical methods, such as ordination and multivariate direct gradient analysis (ter Braak and Prentice 1988; Bersier and Meyer 1994). These methods reduce the many factors or variables which characterize complex habitats to a few axes which explain most of the

complex variation (Cody 1981). These axes are useful in understanding the responses of the different species of birds to structure and composition of the vegetation (Rotenberry et al. 1981; Bersier et al. 1994).

Multivariate statistical methods perform either direct, or indirect, gradient analysis. In direct gradient analysis, the species and site data are related directly to the measured environmental variables which are to be tested. Canonical correspondence analysis (CCA) is a technique of multivariate direct gradient analysis. CCA combines ordination and multiple regression in the same algorithm, and identifies axes which are linear combinations of environmental variables and which explain the most variation in the data (ter Braak et al. 1988; Palmer 1994).

In indirect gradient analysis, the axes are determined by ordination of the site and species data. The most commonly used method of ordination for indirect gradient analysis is detrended correspondence analysis (DCA). DCA analyses the data by finding the axes which explain the most variation in the data. The relationship between the axes and the environmental variables may be found by a second step, such as the use of multiple regression to determine the relationship of a given axis to the environmental variables (ter Braak et al. 1988).

Both CCA and DCA are included in the computer package known as CANOCO (ter Braak 1987). I have used CANOCO for the analysis of the data here, as well as its companion graphics program, CANODRAW.

In order to test hypotheses regarding the distribution of

different species of trees or the breeding territories of birds across the landscape, Monte Carlo resampling may be used (Crowley, 1992), and CANOCO includes software for this in the package. Monte Carlo resampling involves pooling the data for all sites where point count were made, and then reassigning the environmental data randomly to the species data. The procedure is usually repeated at least 100 times, and the eigenvalues of the original data are compared with the eigenvalues generated randomly. This direct method of assessing the statistical significance of the data is an alternative to traditional statistical methods.

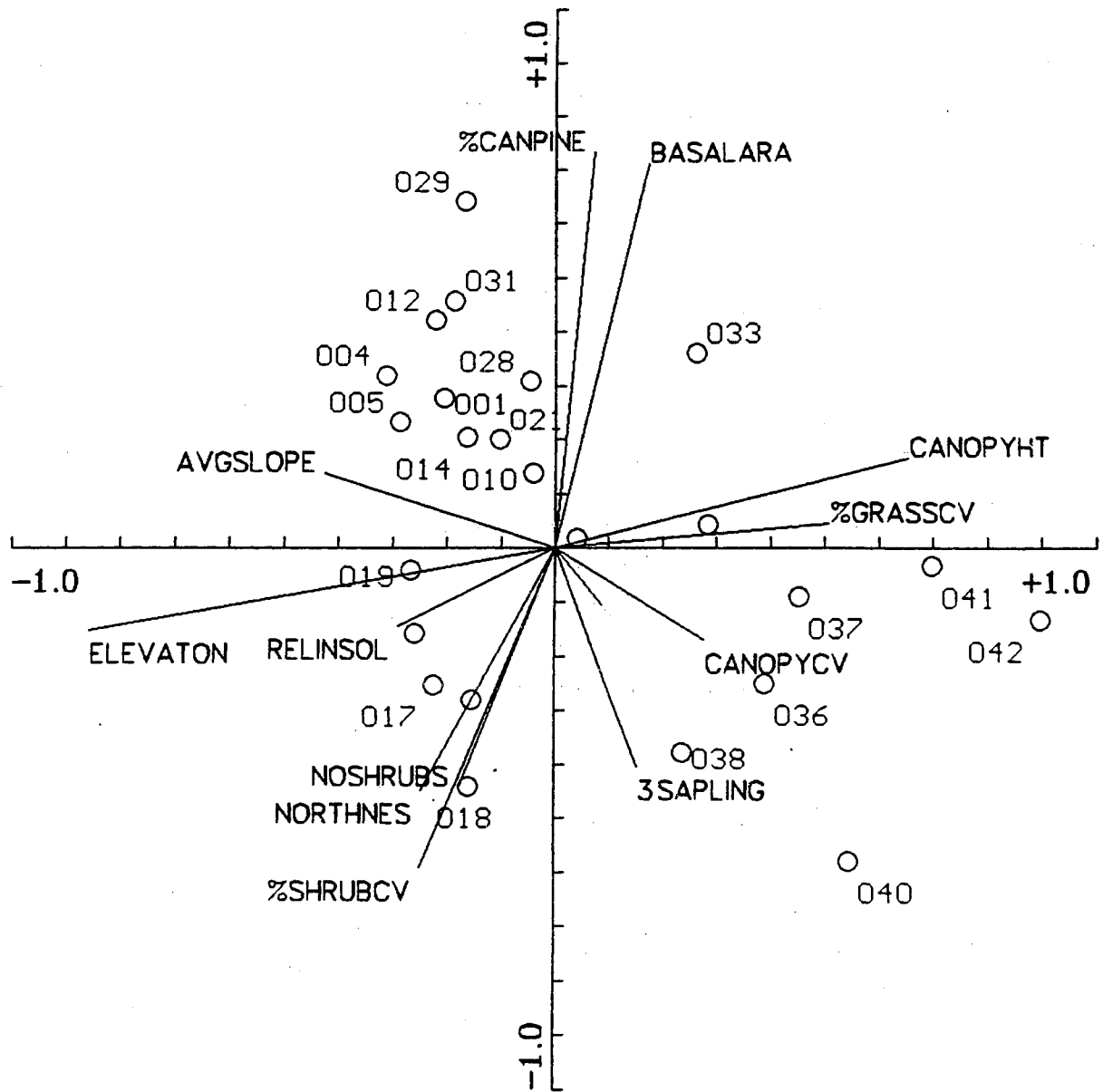
RESULTS

EXPLORATORY ANALYSIS

For all the statistical analyses discussed here, the species and site data for 1995 were used, along with 13 environmental variables: elevation, aspect, northness, eastness, biomass, relative shadiness, canopy height, canopy cover, number of saplings, percent pine in the canopy, percent shrub cover, percent grass cover and number of shrubs. Only 42 sites were included, because several of the sites on the east end of Cucumber Creek could not be reached during the 1995 season due to the presence of an aggressive female black bear, probably with cubs.

Initially, I ran a CCA with all the environmental variables included. Figure 3 is a biplot of the sites and the environmental variables for this analysis. Figure 3 indicates the location of the bird assemblage at the different sites in two-dimensional CCA

Figure 3. Biplot from the canonical correspondence analysis of 1995 bird data, showing sites and 13 environmental variables. Locations of sites on the biplot indicate where they lie in two-dimensional CCA space (ter Braak and Prentice 1988). For each of the environmental variables, arrows indicate the direction in which the variable increased, and the length of the arrow represents the strength of the correlation of the variable with the bird data.



space.

Next, in order to reduce the number of variables so that the key environmental gradients are easier to interpret, I ran a stepwise procedure known as forward selection in CANOCO. The stepwise procedure showed that four variables, elevation, number of shrubs, percent pine in the canopy and basal area, explained a considerable amount of the variation in the species data among sites. Figure 4 is a biplot of the sites and these four environmental variables, and Figure 5 shows a biplot of the bird species and these environmental variables.

The open circles on figures 3 and 4 represent sites; the points on figure 5 represent the approximate center of the distribution of the species of birds (ter Braak and Prentice 1988). The environmental variables in all figures are represented by arrows. The direction of the arrow indicates the direction of change in the environmental variable and the length of the arrow represents the correlation of the variable with the data (ter Braak and Prentice 1988).

Comparison of these figures with Figure 6 from detrended correspondence analysis (Figure 6) is interesting for two reasons. First, because the DCA axes exceed the range of 1.5 - 3 SD, ter Braak and Prentice (1988) recommend CCA for the analysis rather than PCA. Secondly, the two methods produced similar axes, although the y-axis is inverted in Figure 6. The inversion makes no difference in interpretation.

The first axis reflects variation in the bird assemblages produced by differences in elevation. Monte Carlo resampling showed

Figure 4. Biplot from the canonical correspondence analysis of 1995 bird data, showing sites and 4 key environmental variables. Locations of sites on the biplot indicate where they lie in two-dimensional CCA space (ter Braak and Prentice 1988). For each of the environmental variables, arrows indicate the direction in which the variable increased, and the length of the arrow represents the strength of the correlation coefficient of the variable. Biplot of 1995 bird data, showing sites and four environmental variables.

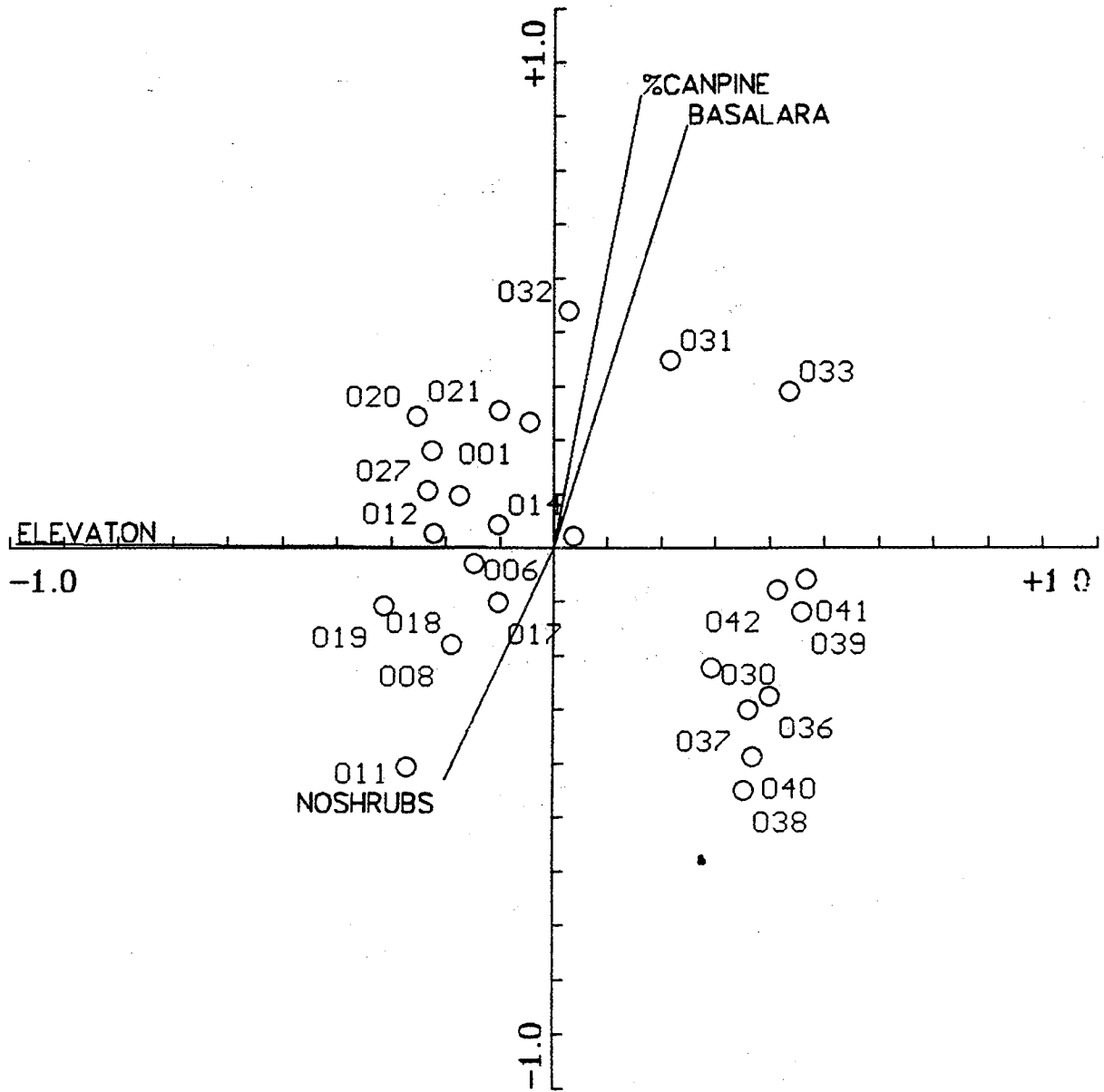
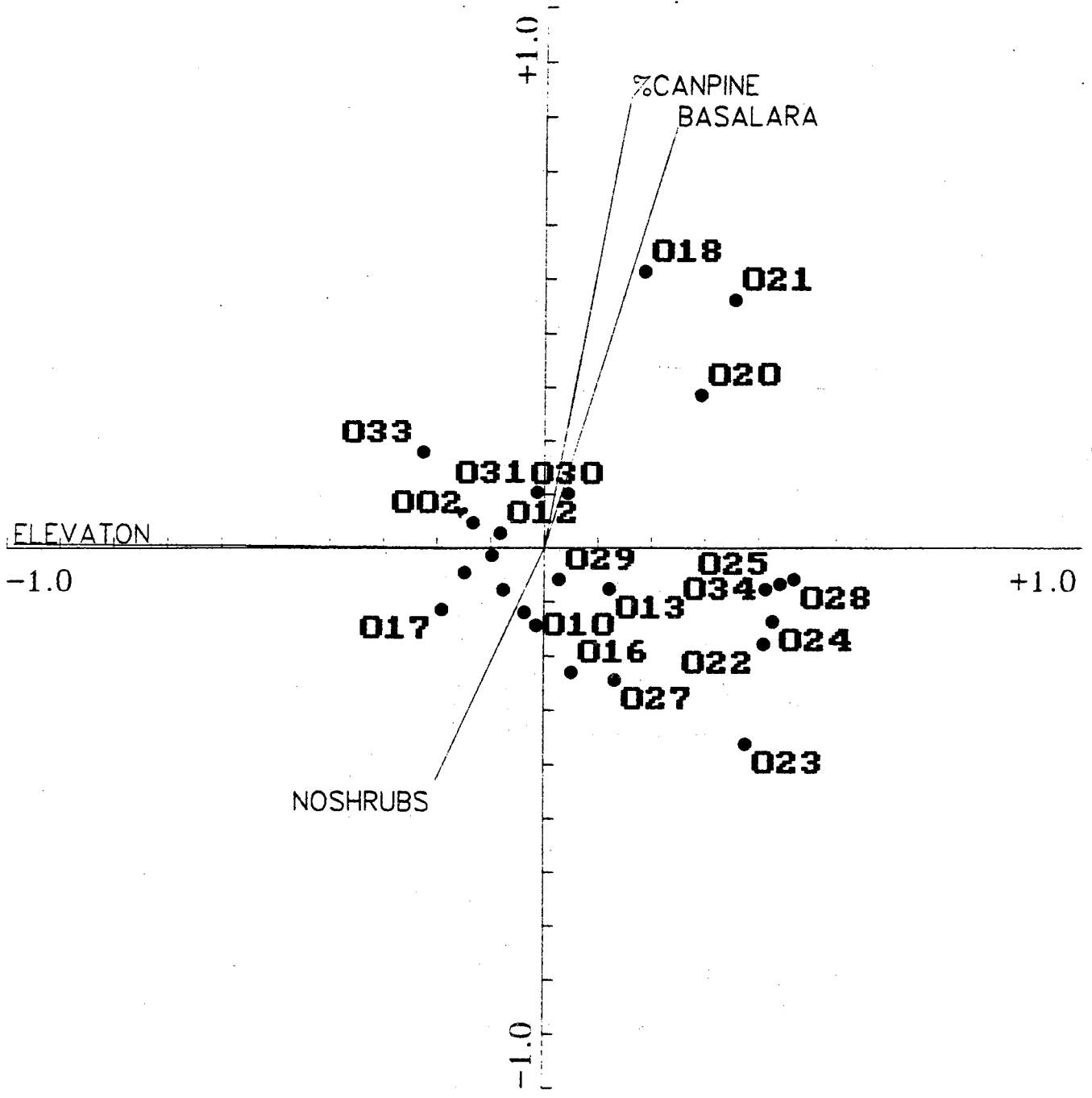


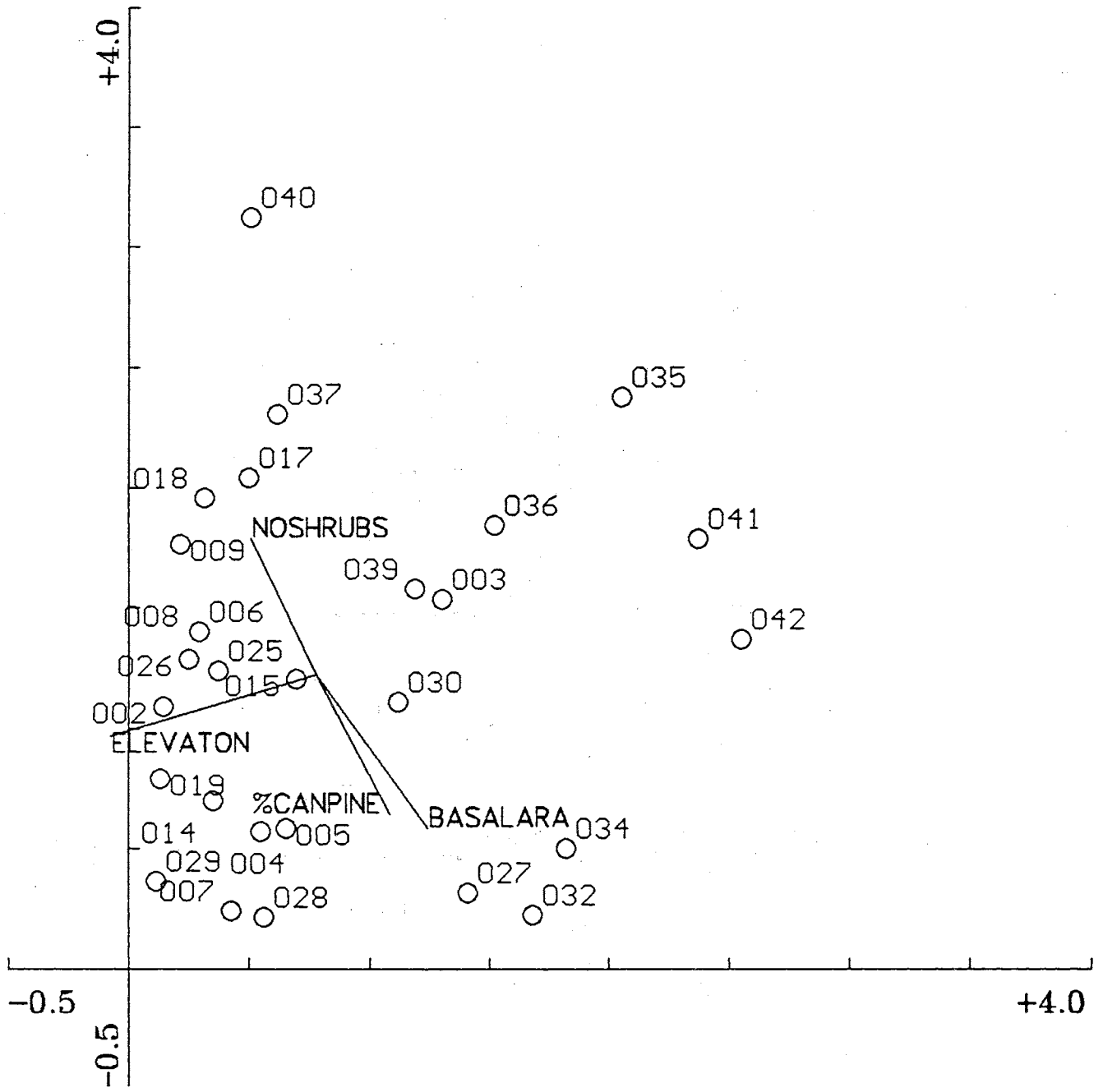
Figure 5. Biplot from the canonical correspondence analysis of 1995 bird data, showing species and 4 environmental variables. Locations of species on the biplot indicate where they were most abundant in two-dimensional CCA space (ter Braak and Prentice 1988). For each of the environmental variables, arrows indicate the direction in which the variable increased, and the length of the arrow represents the strength of the correlation of the variable with the data.



the relationship of the first axis to the bird data was significant ($p < 0.01$) in Figure 3 and Figure 4. The second axis reflects the variation in bird assemblages between mesic sites with mature hardwood stands and rich understories of grasses, forbs and shrubs, on the one hand, and dry sites with stands of mature pines and oaks and sparse understories, on the other hand.

Thus, the environmental variables in Figures 4 and 5 may be interpreted in the following way. Elevation is the longest arrow and is nearly parallel with the horizontal axis. Elevation is the most important factor in explaining the variation in the bird community. Basal area and percent pine in the canopy also strongly influence the data. The arrows for both these variables point in a positive direction along the vertical axis. The last variable, number of shrubs, is not as strongly correlated with the data and is not as long as the first three arrows (shrubs are defined as taller than .5m but less than 2 m). This arrow for number of shrubs points in a negative direction along the vertical axis. It makes good ecological sense that the number of shrubs and percent of pines in the canopy are inversely related, since pines dominate on xeric south-facing slopes and occasionally on lower north-facing slopes, both of which have very few shrubs. Thus, these latter three factors, which are related both to the structure and the composition of the vegetation, are next in importance to elevation in explaining the variation in the bird community. The four key environmental variables selected do provide confirmation of Rotenberry's (1985) hypothesis that habitat selection includes both structural and floristic features.

Figure 6. Biplot from the detrended correspondence analysis of 1995 bird data, showing sites and 4 environmental variables. Locations of sites on the biplot indicate where they are most likely in two-dimensional CCA space (ter Braak and Prentice 1988). For each of the environmental variables, arrows indicate the direction in which the variable increased, and the length of the arrow represents the strength of the correlation of the variable with the data.



Next, let us examine how the CCA biplots may be used to show how the ensemble of birds at different sites responds to the environmental variables. In Figure 4 the sites fall into three groups, one in the lower right quadrant, one in the upper right-hand quadrant and a large grouping in the upper- and lower- left quadrants. The presence of three different groups suggests that there are at least three different bird associations. The group in the lower right quadrant includes sites from hardwood forests in bottomlands and floodplains along Cucumber Creek and one site which is on a lower north-facing slope. The group in the upper right quadrant is horizontal and includes sites 031, 033, 029 and 032. (There is also another site, 016, which is located near the legend, %CANPINE, and which is not printed.) All of these sites are from south-facing slopes, or flatlands and stream bottoms along Beech Creek, and all have high importance values for shortleaf pine. To this group I have also added site 028, although it is on a lower north-facing slope and is borderline. It does have a high importance value for pines.

The last, and largest, grouping includes sites on upper north-facing slopes in the lower left quadrant and sites on ridgetops in the upper left quadrant. This large grouping actually comprises two sub-groups: sites in the upper quadrant are primarily from ridgetops and upper north-facing slopes and sites in the lower quadrant are from upper north-facing slopes. The transition between the two groups reflects the microclimatic changes as one proceeds from the mesic sites on the upper north-facing slopes upward to the ridgetop (lower right quadrant) and then on down the upper south-facing slopes

(upper right quadrant).

Sites on upper north-facing slopes usually have a large number of taller shrubs, such as buckeye (*Aesculus glabra*), St. John's wort (*Hypericum densiflorum*), paw-paw (*Asimina triloba*), wild currant (*Ribes* spp.), buckbrush, greenbriar and various tree species. The oak-hickory forest on these mesic slopes is dominated by mockernut hickory. On ridgetops the forest is dominated by white oak and mockernut hickory. Some sites on the tops of the highest ridges have taller, dense understories of wild currant, buckbrush and greenbriar. At other places on the ridgetops the understory is fairly open with widely scattered small shrubs and poverty grass. As one proceeds down the south-facing slope, the patches of brush and briar in the understory gradually become more scattered and are finally replaced by patches of sugar huckleberry less than .5 m in height. Initially the forest is mostly oak-hickory, but as one descends, the forest becomes a typical oak-pine forest (upper right quadrant).

Starting at the upper right quadrant, then, Figure 4 depicts sites where pines have high importance value on south-facing slopes, lower north-facing slopes, flatlands and along stream bottoms. The lower right quadrant depicts sites in mixed hardwood forests in bottomlands and sites on lower north-facing slopes without pines. The upper and lower left quadrants show sites on the higher slopes and ridgetops. The lower left quadrant depicts sites on upper north-facing slopes and sites on ridgetops with dense underbrush. Finally, the upper left quadrant depicts sites on ridgetops which have sparser understories.

Figure 4 does not show all the sites, because some are superimposed on others. The other sites which are not shown in Figure 4 are classified in the same manner for the purposes of comparing species richness and number of territories of neotropical migrants per point count among the different associations.

Distributions of bird species. Figure 5 indicates how the individual bird species respond to the important environmental variables. The horizontal axis is negatively correlated with elevation. The centers of distribution, or the species scores, of bottomland specialists such as Louisiana waterthrush (*Seiurus motacilla*), Acadian flycatcher (*Empidonax virescens*) and parula warbler (*Parula americana*), are shown to the right along the x-axis. The species scores of species found (at least in this data set) only at higher elevations, such as cerulean warbler (*Dendroica cerulea*), wood thrush (*Hylocichla mustelina*) and scarlet tanager (*Piranga olivacea*), are shown to the left.

The three variables that are the primary components of the vertical axis, percent pine in the canopy, basal area and number of shrubs (as defined), are different aspects of the structure and composition of the vegetation. Percent pine in the canopy and basal area are higher on lower south-facing slopes and flats, while number of shrubs is higher in mature or old growth forests on upper north-facing slopes and in bottomlands. Thus, the species scores of bird species found in pine-dominated sites, such as pine warbler (*Dendroica pinus*) and summer tanager (*Piranga rubra*), are represented at the top of the figure, while other species, such as Kentucky

warbler (*Oporornis formosus*) and white-eyed vireo (*Vireo griseus*), are represented toward the bottom.

Grouping of bird species in associations. Different species of birds co-exist in certain habitats because of their responses to food availability and foraging substrates (Rotenberry 1985). I have aggregated the species which the statistical analysis indicates are co-existing into associations in the following way.

Figure 5 shows the species scores of two bird species, pine warbler and summer tanager, in the upper right-hand corner, indicating that there is a high correlation between the occurrence of these species and those sites which have high importance value for shortleaf pine. The species score of another species, red-shouldered hawk (*Buteo lineatus*), is also displayed in the upper right quadrant. This species occurred in the 1995 data set at two sites: one a pine-dominated site in a flatland along Beech Creek and the other a deciduous bottomland along Cucumber Creek. The location of the center for this species appears to reflect its correlation with forests high in basal area and low in altitude, not particularly with shortleaf pines.

In addition to these species, other species which commonly occur in this oak-pine forest association are red-eyed vireo (*Vireo olivaceus*), ovenbird (*Seiurus aurocapillus*) and scarlet tanager. Red-eyed vireo is a habitat generalist and as such, its species score is near the center of figure 4. Ovenbird, as mentioned, occurs mostly on slopes and ridgetops and its score is somewhat to the left of the y-axis near the x-axis. Scarlet tanager has a similar distribution,

except that it is more common at the higher elevations. Another neotropical migrant listed in Table 1 -but not in Figure 4 - is the black-and-white warbler.

The lower right-hand quadrant of figure 4 depicts bird species in the bottomland hardwood/riparian association, which is composed of those species which coexist in mixed hardwood forests on bottomlands. The species scores for these birds occur in two different groups on biplot 3. The scores of the first group of species appear in the lower right-hand quadrant at some distance from either axis. This group includes Acadian flycatcher, yellow-throated vireo (*Vireo flavifrons*), red-bellied woodpecker (*Melanerpes carolinus*), blue-gray gnatcatcher (*Polioptila caerulea*) and northern flicker (*Colaptes auratus*). These species are positively correlated with high numbers of shrubs and with low altitudes. The scores of a second group of species are found in the lower right quadrant near the y-axis. This group includes Kentucky warbler, white-eyed vireo, barred owl (*Strix varia*), yellow-billed cuckoo (*Coccyzus americana*) and Carolina wren (*Thryothorus ludovicianus*). These species are found in both riparian areas and on upper north-facing slopes, and therefore are mapped at the center of their distribution between these habitats near the y-axis.

The lower left-hand quadrant of Figure 4 indicates the space of the higher elevation/north-facing slope association, which is composed bird species which are highly correlated with upper north-facing slopes and similar sites on ridgetops. There are three different groups of species scores which contribute to this

association. The first group is represented in the lower left quadrant. These are wood thrush and cerulean warbler. In this data set these species are found only on upper north-facing slopes, which are characterized by high elevations and high numbers of shrubs. (These species are also rare in the bottomland oak-hickory forest, but were not counted there during data collection in 1995.)

A second group of species scores are those species in the group below the x-axis but near the y-axis, which are also included in the bottomland hardwood/riparian association. This group includes Kentucky warbler, white-eyed vireo, barred owl, yellow-billed cuckoo and Carolina wren. A third group of species scores which straddles the x-axis between the upper and lower left quadrants is also included in this association. This group includes ovenbird, white-breasted nuthatch (*Sitta carolinensis*) and indigo bunting (*Passerina cyanea*). These species were found on upper north-facing slopes, on ridgetops and to a lesser extent on upper south-facing slopes in this data set (white-breasted nuthatch and indigo bunting also occur in bottomland hardwoods/riparian forests).

The last association of bird species are those which are associated with the upper left hand quadrant of Figure 4. This is the ridgetop association. This association includes bird species with a group of species scores which straddle the x-axis to the left of the y-axis, including ovenbird, indigo bunting and white-breasted nuthatch. This association also includes hooded warbler, scarlet tanager and red-eyed vireo.

Tables 1-4 list the mean number of territories of each species

of breeding bird counted on any point count during 1994 and 1995 for each of the four associations, and also those species which were noted as present in each association but which were not seen or heard during a point count. The total species richness of all breeding birds for the different associations is listed at the bottom of Tables 1-4. Species richness is lowest for the sites in the ridgetop association and highest for the bottomland hardwoods/riparian association. Considering only neotropical migrants, the same ranking occurs: ridgetops have the lowest number of species and mixed hardwoods/bottomlands have the highest number.

DENSITY OF TERRITORIES OF NEOTROPICAL MIGRANTS

The numbers of territories of neotropical migrants per point count is a rough approximation to density, and is thus of considerable interest for conservation. Table 2 shows that association 2 has high average numbers of territories per point count of several neotropical migrants, particularly red-eyed vireo, ovenbird and hooded warbler (*Wilsonia citrina*). Cerulean warbler, scarlet tanager and indigo bunting were also fairly common. An estimate of the number of territories per hectare may be made by dividing the number of territories per point count by 1.5, since the area in which I heard birds is a circle with a radius of about 70 m.

ANOVA indicates that the difference in number of territories of neotropical migrants per point count between the different associations is statistically significant ($p < 0.05$). Based on Table 5,

Table 1. Bird species in the oak-pine association. Mean territories per point count for each species for 1994 and 1995, with standard deviations in parentheses. Species present, but not counted during point counts, designated as +.

Species	1994	1995
Red-shouldered hawk		.14 (.37)
Wild turkey	+	
Yellow-billed cuckoo	.13 (.36)	
Whip-poor-will		+
Red-headed woodpecker		+
Downy woodpecker	.13 (.36)	.14 (.37)
Pileated woodpecker	.25 (.46)	+
Great crested flycatcher	.13 (.36)	
Eastern wood peewee		.29 (.49)
Blue jay	.13 (.36)	+
American crow	.13 (.36)	+
Carolina chickadee	.25 (.46)	.14 (.37)
Carolina wren	.37 (.52)	.29 (.49)
Wood thrush		+
Red-eyed vireo	1.63 (.72)	1.57 (.97)
Northern parula		.14 (.37)
Black-and-white warbler	.13 (.36)	.14 (.37)
Prairie warbler	+	
Pine warbler	.37 (.52)	.86 (.37)
Ovenbird	.87 (.36)	.43 (.53)
Northern cardinal	.13 (.36)	
Summer tanager	.50 (.54)	.43 (.53)
Total all species	16	17
Total neotropical migrants	5	7

Table 2. Bird species in the higher elevation/north-facing slope association. Mean territories per point count for each species for 1994 and 1995, with standard deviations in parentheses. Species not heard or seen at point counts are designated as +. Total number of all species and neotropical migrants.

Species	1994	1995
Wild turkey		.07 (.26)
Yellow-billed cuckoo	.45 (.52)	.13 (.35)
Barred owl	.09 (.30)	.13 (.35)
Downy woodpecker	.18 (.40)	.33 (.41)
Hairy woodpecker		.20 (.41)
Pileated woodpecker	.27 (.47)	
Eastern wood-peewee	.19 (.40)	.07 (.26)
American crow		.07 (.26)
Tufted titmouse	.09 (.30)	.13 (.35)
Carolina chickadee		.13 (.35)
Carolina wren	.36 (.50)	.13 (.35)
Wood thrush	.27 (.47)	.33 (.41)
Gray catbird		+
White-eyed vireo		.07 (.26)
Red-eyed vireo	2.36 (.50)	1.73 (.79)
Black-and-white warbler	.09 (.30)	.33 (.41)
Cerulean warbler	.54 (.52)	.27 (.46)
Kentucky warbler	.09 (.30)	.33 (.41)
Hooded warbler	.91 (.70)	1.07 (.88)
Worm-eating warbler		.07 (.26)
Ovenbird	1.72 (.91)	2.00 (.57)
Common yellowthroat	+	
Yellow-breasted chat		+
Northern cardinal	.09 (.30)	
Indigo bunting	.09 (.30)	.73 (.46)
Scarlet tanager	.55 (.69)	.56 (.52)

Total # of all species	18	23
Total # of neotropical migrants	11	15

Table 3. Bird species in the ridgetop association. Mean territories per point count for each species for 1994 and 1995, with standard deviations in parentheses. Additional species seen or heard away from point counts marked by +. Total numbers of all birds and neotropical migrants.

Species	1994	1995
Cooper's hawk		+
Red-tailed hawk	+	
Greater roadrunner		+
Yellow-billed cuckoo	.10 (.32)	
Whip-poor-will		+
Downy woodpecker		.18 (.40)
Hairy woodpecker		.09 (.30)
Pileated woodpecker	.20 (.42)	.09 (.30)
Great crested flycatcher	+	
Eastern phoebe		+
American crow		.09 (.30)
Tufted titmouse		.09 (.30)
Carolina chickadee		.09 (.30)
Carolina wren	.10 (.32)	.09 (.30)
Wood thrush	.20 (.42)	.18 (.40)
Yellow-throated vireo		+
Red-eyed vireo	2.20 (.79)	1.55 (.69)
Black-and-white warbler	.10 (.32)	
Hooded warbler	.50 (.71)	.36 (.50)
Ovenbird	1.50 (.71)	1.36 (.67)
Northern cardinal	.10 (.32)	
Indigo bunting	.40 (.71)	.55 (.50)
Scarlet tanager	.30 (.48)	.36 (.50)
Total # all species	13	18
Total # neotropical migrants	9	9

Table 4. Bird species in the bottomland hardwoods/riparian association. Mean territories per point count for each species for 1994 and 1995, with standard deviations in parentheses. Additional species seen or heard away from point counts marked by +. Total numbers of all species and of neotropical migrants.

Species	1994	1995
Red-shouldered hawk		.22 (.44)
Broad-winged hawk	.08 (.28)	
Mourning Dove	.08 (.28)	
Yellow-billed cuckoo	.08 (.28)	.11 (.33)
Barred owl		.11 (.33)
Northern flicker		.11 (.33)
Downy woodpecker		.11 (.33)
Pileated woodpecker	.23 (.44)	
Great crested flycatcher	.15 (.39)	.11 (.33)
Acadian flycatcher	.62 (.65)	.33 (.50)
Blue jay	.23 (.44)	
American crow	.62 (.51)	.11 (.33)
Tufted titmouse	.23 (.44)	.11 (.33)
Carolina chickadee	.15 (.37)	
White-breasted nuthatch	.08 (.28)	
Carolina wren	.38 (.51)	.55 (.53)
Blue-gray gnatcatcher	.38 (.51)	.22 (.44)
Wood thrush	+	
White-eyed vireo	.15 (.37)	
Yellow-throated vireo		.11 (.33)
Red-eyed vireo	2.20 (.80)	1.44 (.44)
Northern parula	.31 (.48)	.55 (.44)
Black-and-white warbler	.15 (.33)	
Cerulean warbler	.08 (.28)	
Kentucky warbler	.15 (.33)	.44 (.53)
Hooded warbler	.23 (.44)	.44 (.55)

Ovenbird	.62 (.87)	.11 (.33)
Louisiana waterthrush	.38 (.51)	.22 (.44)
Common yellowthroat		+
Yellow-breasted chat	.08 (.28)	+
American redstart		+
Indigo bunting	.08 (.28)	.33 (.50)
Scarlet tanager	.08 (.28)	.22 (.44)
Summer tanager	.08 (.28)	.33 (.50)
Total # all species	28	24
Total # neotropical migrants	18	17

Table 5. Mean territories per point count of neotropical migrants for each breeding bird association. Standard deviations in parentheses. ANOVA table and results of Student-Newman-Keuls test.

Associations	Mean territories/ point count
Oak-pine forest	3.29 (1.60)
Higher elevation/n-fac.slope	7.60 (1.64)
Ridgetop	4.00 (2.14)
Bottom.hardwood/riparian	5.22 (1.39)

Source	Sum of Squares	Degrees of freedom	Mean square	F
Between samples	125.70	3	41.9	14.25
Within samples	114.59	38	2.94	
Total	240.29	41		

1 3 4 2

we may properly reject the null hypotheses ($p < 0.05$). Further, the Student-Newman-Keuls test for determination of statistical significance between different means indicates that the mean number of territories of the sites found on upper north-facing slopes/ridgetops is significantly higher than the mean number of territories from any of the other three associations. There was also a significant difference using the 1994 data.

A cautionary comment is in order here, however. Selective cutting of trees in the last 20 years has taken place at six of the 12 sites along Cucumber Creek, and the average numbers of territories of neotropical migrants appears to be significantly higher in mature bottomland hardwood/riparian forests than in sites disturbed by clear-cutting or selective logging which are still in the stand-initiation stage or stem-exclusion stage. For these reasons, I have defined a fifth association, mature bottomland hardwoods/ riparian, in order to compare the other associations with that found in mature forests in the deciduous valley bottoms and floodplains. For this purpose I used the species and site data for 1995, with the 1994 data for the sites in mature bottomland which were not sampled in 1995 because of an aggressive black bear (*Ursus americanus*). With these changes the results of ANOVA are different (Table 6). Here, the S-N-K procedure shows that the means for the sites in association 2 are still significantly different from associations in sites where pines are important, in ridgetops and in disturbed bottomland, but not from mature bottomland sites (Table 6).

Table 6. Mean territories per point count of neotropical migrants for five bird associations. The first three as shown by Table 5, with the fourth as shown by that table divided into two: one for disturbed bottomland sites and one for mature hardwood forests on bottomlands. Variances shown in parenthesis. ANOVA table. Results of Student-Newman-Keuls procedure.

Association	Mean territories/ point count
Oak-pine forest	3.29 (1.60)
Higher elevation/n-fac. slope	7.60 (1.64)
Ridgetop	4.00 (2.14)
Disturb. bot.hardwood/riparian	4.86 (1.35)
Mature bot.hardwood/riparian	7.17 (1.60)

Source	Sum of Squares	Degrees of freedom	Mean square	F
Between samples	144.24	4	36.06	12.06
Within samples	122.59	41	2.99	
Totals	266.96	45		

1 3 4(dist.) 4(mature) 2

DISCUSSION

BIRD ASSOCIATIONS IN THE WESTERN OUACHITA MOUNTAINS

Three bird associations have been described in the western Ouachita Mountain ecoregion: 1. an association in pine/oak savanna and open woodlands; 2. an association in oak-pine or pine-oak forests and 3. a bottomland hardwood/riparian association. The first association is missing in the Cucumber Creek watershed and has almost disappeared entirely from the Ouachita Mountain ecoregion due to fire suppression.

Savanna and open woodlands are fire-maintained ecosystems and in the absence of fire a dense hardwood midstory develops and the savanna and open woodlands change to a closed forest. A remnant of pine-oak savanna and open woodland still exists in the Ouachita National Forest near Waldron, Arkansas, and the characteristic bird association consists of red-cockaded woodpecker (*Picoides borealis*), red-headed woodpecker (*Melanerpes erythrocephalus*), Bachman's sparrow (*Aimophila aestivalis*), brown-headed nuthatch (*Sitta pusilla*), eastern wood-peewee, northern bobwhite (*Colinus virginianus*), prairie warbler (*Dendroica discolor*), chipping sparrow (*Spizella passerina*), as well as generalist species (Wilson et al. 1995). This appears to be the same association which Carter (1965) described as the upland association in the McCurtain County Wilderness area, although fire had been suppressed for about 10 years at the time of the study and some savanna and open woodland species, such as orchard oriole (*Icterus spurius*), may have begun to drop out (Engstrom et al. 1984).

The association of birds in oak-pine and pine-oak forests has been reported in three recent studies. In a survey of the breeding birds of late-rotational stands of oak-pine on south-facing slopes within the Ouachita National Forest in Arkansas, Martin (1992) reported that the most common species were pine warbler (*Dendroica pinus*) and red-eyed vireo, and also that black-and-white warbler (*Mniotilta varia*) and summer tanager were common. Secondly, in the areas of mature pine-oak forest near the pine-oak savanna remnant in Arkansas, the most common species were pine warbler, black-and-white warbler, Carolina chickadee (*Parus carolinensis*), red-eyed vireo, tufted titmouse (*Parus bicolor*) and summer tanager (Wilson et al. 1995). Finally, in a study of late-rotation pine-hardwood stands made as part of the Ecosystem Management Research project in the Ouachita National Forest in Arkansas and Oklahoma, the most common birds were again pine warbler, red-eyed vireo, summer tanager and black-and-white warbler (Petit et al. 1993).

The association of bird species in bottomland hardwoods/riparian is very similar to that reported by two other sources. The first source is Carter (1965), who studied the breeding birds in old growth, bottomland hardwood forest along the Mountain Fork River in the McCurtain County Wilderness Area, prior to the inundation of the area by the Broken Bow Reservoir. Carter (1965) reported 36 different species in this association. The most common resident species were barred owl, Carolina chickadee, white-breasted nuthatch and Carolina wren. The most common neotropical migrants were hooded warbler, northern parula, Kentucky warbler, American redstart

(*Setophaga ruticilla*) and Acadian flycatcher. A very similar association of species is listed for bottomland hardwoods/riparian by the Southeast Management Group for Partners in Flight (Hunter et al. 1993).

Although the occurrences of individual species at higher elevations has been noted in the literature, the higher elevation/north-facing slope association and the ridgetop association have not mentioned in the literature for the region. Identification of these associations is important in the development of a landscape-level conservation plan. These associations are similar to the association found in hardwood forests in bottomlands, and apparently include nearly all species found in that association with the exception of the bottomland specialists, such as Acadian flycatcher, parula warbler, blue-gray gnatcatcher, Louisiana waterthrush and red-shouldered hawk. The most common birds listed in Table 1 for the higher elevation/north-facing slope association are red-eyed vireo, ovenbird and hooded warbler. Several other species are fairly common in the Cucumber Creek watershed: cerulean warbler, wood thrush, yellow-billed cuckoo, and scarlet tanager. The ridgetop association is similar, but lacks several of the species found in the richer higher elevation/north-facing slope association.

POPULATIONS OF NEOTROPICAL MIGRANTS

According to data from Breeding Bird Surveys, eight neotropical species have declined significantly in the Ozark/Ouachita region since 1966. These species are Acadian flycatcher, wood thrush, cerulean warbler, ovenbird, gray catbird (*Dumetella carolinensis*),

painted bunting (*Passerina ciris*), orchard oriole (*Icterus spurius*) and prairie warbler (*Dendroica discolor*) (Hunter et al. 1993). Although the decline is nonsignificant, numerical declines have been noted in the Ozark/Ouachita region for nine other species, including eastern wood-peewee, great crested flycatcher (*Myiarchus crinitus*), American redstart, worm-eating warbler (*Helminthos vermivorus*), Louisiana waterthrush, hooded warbler, Kentucky warbler, scarlet tanager and white-eyed vireo (Hunter et al. 1993).

Several of the species of neotropical migrants which are declining in the Ozark/Ouachita region are forest interior or area sensitive species. The link of population declines of many species of neotropical migrants with fragmentation of breeding habitat was first brought to the attention of ornithologists in the seminal paper by Whitcomb et al. (1981). Very few area-sensitive or forest-interior species were found during breeding season in smaller tracts of forest in eastern North America. Subsequent research has shown that forest fragments under 10 ha are unsuitable for sustaining breeding populations of many forest-dwelling neotropical migrants, including veery (*Catharus fuscescens*), wood thrush, red-eyed vireo, black-throated blue warbler (*Mniotilta varia*), cerulean warbler, hooded warbler, and ovenbird, just to name a few (Robbins et al. 1989). Only natural areas of at least 3,000 ha may reasonably be expected to retain all of the forest-interior and area-sensitive species (Robbins et al. 1989).

The Cucumber Creek area and probably most of the western Ouachita Mountain ecoregion is just the kind of large natural area

needed by the area-sensitive and forest interior species of neotropical migrants. Only two of the declining species which nest in the Ozark/Ouachita region, orchard oriole and painted bunting, were not found during 3 breeding seasons in the study area.

Five of the declining species primarily breed in sites on higher elevation/north-facing slopes and sites on ridgetops with dense undergrowth. These are scarlet tanager, cerulean warbler, wood thrush, gray catbird and worm-eating warbler. The first three of these species were also counted in bottomland hardwood/ riparian habitat but are much rarer there. Gray catbird and worm-eating warbler were each counted only once: in both cases on higher elevation/upper north-facing slopes.

Two species primarily breed on slopes, both on higher elevation/north-facing slopes, on ridgetops and on lower slopes. These are ovenbird and eastern wood-peewee. (It should be noted that while ovenbird was counted in deciduous valley bottom and floodplain habitat, the valley bottom is very narrow at some places and adjacent to slopes, from which the ovenbirds may be heard.)

Two other species are relatively common both in bottomland hardwood/riparian forests and higher elevation/north-facing slopes. These are hooded warbler and Kentucky warbler. Finally, four species primarily breed in bottomland hardwood/riparian forests: Acadian flycatcher, great crested flycatcher, Louisiana waterthrush and white-eyed vireo. White-eyed vireo and great crested flycatcher are much rarer on higher elevation/north-facing slopes.

It is surprising that the number of territories of neotropical

migrants per point count is at least as high for the higher elevation/north-facing slope association as for mature sites of the bottomland hardwood/riparian association. Initially I assumed that the bottomland hardwood/riparian association would have the highest density of neotropical migrants. This unexpected result adds to the importance of conserving habitat on upper north-facing slopes and ridgetops.

There is a possible explanation for the high densities of territories of neotropical migrants on upper north-facing slopes and ridgetops, in addition to the numerical increase in layers of vegetation due to the rich understories with an abundance of shrubs used for nesting by several species (MacArthur et al.1961). These places may also provide a rich supply of food resources, particularly insects. A rich supply of insect food resources was the explanation offered by Terborgh (1977) for a mid-elevational "hot-spot" of avian density in the Andes Mountains. Terborgh speculated that the increase in food resources at these elevations was due to an increase in the primary productivity of plants. Janzen (1973) suggested that primary productivity increases where cooler temperatures at night decrease transpiration rates.

The Ouachita Mountains, of course, are vastly dissimilar from the Andes: even the highest elevations do not reach the mid-elevational range of 1400 - 1800 m which Terborgh (1977) described in the Andes. But microclimatic factors do combine at the higher elevations in the Ouachita Mountains to produce more mesic environments there, particularly on north-facing slopes. Here also

night-time temperatures are decreased during the spring breeding bird season compared to the lower elevations of the valley bottoms. Further anecdotal evidence of high primary productivity of plants at these higher elevations is the abundance of butterflies along the ridgetops during March and April.

As expected, species richness of all birds, and of neotropical migrants in particular, was highest in the mature, bottomland hardwood forests. All of the species of neotropical migrants found on upper north-facing slopes and ridgetops with thick undergrowth are also found in bottomlands. However, the numbers of some species of particular interest, such as cerulean warbler and wood thrush, are very low in the bottomlands compared to the upper north-facing slopes.

While large areas of bottomland hardwoods along Cucumber Creek have obviously been disturbed by selective cutting during the recent past, other areas may not have been disturbed since the turn of the century. These areas have reached the understory-reinitiation stage (Devall et al. 1991). The oak-hickory forests on most of the upper north-facing slopes have also reached the understory-reinitiation stage, or in some case may actually be old growth (Stahle et al. 1985b).

CONCLUSION

Environmental and successional gradients produce landscape level patterns of community forest types and bird associations in the Cucumber Creek watershed and probably throughout the region of

higher elevations in the western Ouachita Mountains. Breeding populations of most species of declining neotropical migrants are concentrated in mature forests on upper north-facing slopes and ridgetops, and mixed hardwood forests on bottomlands. The same landscape level patterns probably hold in the entire region of higher elevations in the western Ouachita Mountains. These forests have high conservation priority which clearly justifies the Cucumber Creek Preserve and demonstrates a need for conservation management at the landscape level in the region of higher elevations of the western Ouachita Mountains.

CHAPTER IV

A LANDSCAPE LEVEL APPROACH TO CONSERVATION

INTRODUCTION

The scale of the large natural area which includes the study area and most of the western part of the Ouachita Mountain ecoregion is on the order of thousands of square kilometers (Figure 1). At this scale management at the landscape level becomes necessary (Petit et al. 1995; Noss and Cooperrider 1994). Management at the landscape level means that goals for managing at the local or stand level should be determined at the regional or landscape level (Petit et al. 1995).

The primary goal for conservation of birds and other wildlife at the landscape level is the representation of all natural communities at the ecoregion and landscape scale (Noss and Cooperrider 1984). This includes preservation or restoration of source habitats of individual species that support dispersal of individuals within the region (Pulliam 1988). Source habitats for many area-sensitive and forest-interior species of neotropical migrants and other birds occur in large natural areas. These areas constitute a larger search area for predators and cowbirds (*Molothrus ater*) and decrease their efficiency in locating nests (Martin 1992). Nesting success is higher in extensive natural areas than in fragment, anthropogenic landscapes (Holmes et al. 1992; Wilcove 1985), and nesting territories are more dense in the natural areas. For example, nesting territories of ovenbirds are twice as dense in unfragmented forests as in small woodlots (Villard et al. 1993).

Many of the factors which have been offered to explain decreased rates of breeding success of neotropical species and other birds in fragmented, anthropogenic landscapes are notably absent in the study area and in much of the Ouachita Mountain ecoregion. Except in the valleys, there are few human habitations, and there are few anthropogenic changes to the natural landscape, except those successional changes due to fire suppression. Remarkably, brown-headed cowbird (*Molothrus ater*) was recorded only once in the study area during the three seasons of field work. Cowbirds may travel distances of up to 7.5 km (about 4 miles) from feeding areas in cow pastures and feedlots to breeding territories in forest openings (Robinson et al. 1993). Also, I saw very few small mammalian predators, such as striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*), in the study area, and there were very few tracks of these animals found during the 3 seasons of field work. This may possibly be explained by the presence of larger predators in the area, including bobcats (*Lynx rufus*) and in my opinion, mountain lions (*Felis concolor*). Also, populations of avian nest predators, such as crows (*Corvus brachyrhynchos*) and bluejays (*Cyanocitta cristata*), were not elevated (Tables 1-4).

LANDSCAPE LEVEL MANAGEMENT

Management for conservation of birds at the landscape level should be based upon the different ecological potentialities of the different forest community types across the landscape. The best habitat for many neotropical migrants and other species are the oak-

hickory forests along the ridgetops and upper north-facing slopes and the mixed hardwood forests in bottomlands. At the landscape level these mostly linear communities form region-wide networks of interconnected communities. These networks of hardwoods are interwoven through a matrix of second-growth oak-pine and pine-oak forests on south-facing slopes, flats, lower north-facing slopes and along streams. Timber is extensively managed in these oak-pine and pine-oak forests in Ouachita National Forest and on private lands in the region.

Ecosystem management is the new philosophy for the management of the National Forests (Pell 1994; Robertson 1992). Ecosystem management means that the needs of people, such as needs for timber, recreation and grazing, are balanced with ecological principles in such a way that "the National Forests and Grasslands represent diverse, healthy, productive and sustainable ecosystems" (Robertson 1992). Ecosystem management strives to work "within the ecological potential of sites and landscapes, maintain native diversity, and employ nature's processes to the greatest degree possible" (Robertson 1992).

Under the aegis of ecosystem management the Ouachita National Forest is moving toward landscape level management. Under phase III of its plan for ecosystem management, timber management will begin to be carried out at the ecosystem or watershed level as well as the stand level (Baker 1994). The template for such management should be the patterns of forest community types which occur at the landscape level. Ridgetops and upper north-facing slopes would be allowed to

continue to develop toward old growth. Hardwood forests in bottomlands should also be allowed to continue to develop in this manner. At the landscape level the ridgetops, upper north-facing slopes and bottomland hardwood/riparian forests would form a network of hardwood communities in the oak-pine and pine-oak matrix. Ecosystem management of the extensive second-growth oak-pine and pine-oak forests is much more challenging, and would involve restoration of an ecological process, frequent ground fire, which has been absent for many years.

OAK-HICKORY FORESTS ON UPPER NORTH-FACING SLOPES AND RIDGETOPS

Mature forests on ridgetops and upper north-facing slopes are particularly important habitat for neotropical migrants and other species of birds. The higher elevation/ north-facing slope bird association has the highest number of territories of neotropical migrants per point count of any of the forest community types. These forests provide habitat for several declining neotropical migrants, including hooded warbler (*Wilsonia citrina*), ovenbird (*Seiurus aurocapillus*), cerulean warbler (*Dendroica cerulea*), wood thrush (*Hylocichla mustelina*), and scarlet tanager (*Piranga olivacea*). For purposes of management, it would not be practical to manage these places differently from the other places where the undergrowth is more xeric (ridgetop association), and the ridgetops and upper north-facing slopes should be managed as a unit for the development of old growth.

Restoration of old growth on ridgetops and upper north-facing

slopes requires little active management. These hardwood stands are now approaching maturity throughout the Ouachita National Forest - 84% are between 51 and 90 years old, and 6% are even older (USDA 1993). In many of these sites on the higher ridgetops and upper-north-facing slopes, the structure of the forest has reached the understory-initiation stage, or in some cases, may still be virgin old growth.

Major disturbances such as large-scale windstorms, destructive ice storms, severe drought and intense fire, are relatively uncommon. Regeneration and renewal of the forest occurs primarily through small scale disturbances such as damage from lightning and high wind in local thunderstorms and disease (USDA 1993). All of these small scale disturbances, singularly or in combination, regenerate and renew the forest by the creation of treefall gaps. Fire rarely enters these mesic areas, but there, it is reasonable to conclude, periodic low-intensity ground fires have been important in maintaining the dominance of oaks, particularly red oak and post oak, over maple, elm and other less fire-tolerant species (USDA 1993).

Because of the steepness of the slopes, the relative shortness of the trees and the low site indices of the ridgetops and upper north-facing slopes, the stands of hardwoods on the ridgetops and upper north-facing slopes have probably never had high commercial value as timber. Forest Service records indicate the upper north-facing slope north of Forest Service Road 6026 between the top of Blue Bouncer Mountain and the top of Lynn Mountain has not

been timbered for many years. Most areas were last cut in 1915, but two areas were last cut in the 1860s. Although no information on timbering of the area is available because it is on private property, most of the ridgetop and upper north-facing slope of Lynn Mountain has uneven-aged oak-hickory forests which look very much like the areas where the Forest Service records show that the forest is very old, or possibly old growth.

The uneven-aged oak-hickory forests in these areas have woody understories and irregular canopies, both of which are the mark of old growth forests (Oliver 1992). In these areas the canopy is irregular because of the presence of very old oaks with large diameters but with nearly all the branches above the trunk dead or dying. One of the characteristics of old growth oak-hickory forests is the presence of such large diameter oaks with dead or dying upper branches (Stahle et al. 1985b). Of course, as these trees finally die completely, openings in the canopy grow even larger and younger trees are released. Snags and downed logs are also common in these areas.

While the study area included only Kiamichi Mountain, Lynn Mountain and Blue Bouncer Mountain, there is every reason to think that similar older forests on the highest mountains are also important throughout the western part of the Ouachita Mountain ecoregion. Limited field work on Rich Mountain during 1995 showed tentatively that the same associations of birds occur there. Additional research is needed in other areas in the upper Ouachita Mountain ecoregion.

The higher elevations in the Ouachita Mountains extend to the west and the east from the Cucumber Creek area (Figure 1). Many of the areas of higher elevation are within the boundaries of the Ouachita National Forest. In its proposed plan for ecosystem management the Forest Service has wisely set aside these oak-hickory forests for the continuing development of uneven-aged stands and ultimately old growth (USDA 1993).

BOTTOMLAND FORESTS/RIPARIAN AREAS

The association of birds in bottomland forests/riparian areas has the highest species richness of any of the four associations. Carter (1965) listed 36 different species in this association, many of which are declining neotropical migrants and other species. These forests are of course vital for the bottomland specialists such as Acadian flycatcher, Louisiana waterthrush, blue-gray gnatcatcher and American redstart.

Mature stands of mixed hardwood forests on bottomlands are rare in the Ouachita National Forest (USDA 1993). Most of the land in the valleys remains in private ownership, and most of the bottomland forests have been logged. Prior to logging operations, the bottomland forests probably resembled the virgin bottomland forests in the McCurtain County Wilderness Area, as reported by Carter (1965). Carter reported that the bottomland forest in that area was dominated by three species, American holly (*Ilex opaca*), white oak (*Quercus alba*), and sweet gum (*Liquidambar styraciflua*) (importance values of almost 20%). Baldcypress (*Taxodium distichum*), mockernut

hickory (*Carya tomentosa*) and blackgum (*Nyssa sylvatica*) were also important (importance value greater than 5%).

The Cucumber Creek valley has bottomland soils for about 9 km (6 mi.) above the confluence with Big Eagle Creek (USDA 1983). The valley is fairly wide and multiple streams meander through the valley. Tree species that are important today include sugar maple (*Acer saccharum*), bitternut hickory (*Carya cordiformis*), sweet gum, ironwood (*Ostrya virginiana*), Shumard's oak (*Quercus shumardii*), white oak and shagbark hickory (*Carya ovata*). Prior to settlement an extensive forest undoubtedly occupied the valley. Like other bottomland forests in the region, however, this forest has been subjected to selective cutting of the most valuable timber. At the present time the forest is composed of a wide spectrum of stands ranging from the stand-initiation stage and stem-exclusion stage to the understory-reinitiation stage. One area in the eastern end of the valley, south of Lynn Mountain, however, has apparently not been cut since the turn of the century. An understory of buckeye (*Aesculus glabra*), papaw (*Asimila triloba*) and other taller shrubs has regrown there.

Management of these bottomland forests, like management of the oak-hickory forest on upper north-facing slopes and ridgetops, requires little active management, while the forest develops toward the understory-reinitiation and old growth stages. The disturbance regime here is more complex, because in addition to dynamics of tree-fall gaps, there is also disturbance from flooding. During peak flooding events, such as occurred in the spring of 1995, flooding may suddenly alter the course of a stream and trees along the former

bank may be uprooted. These events also create oxbows and early successional habitat where the stream has abandoned its former course.

The ecological potential of the Cucumber Creek valley for the development of a bottomland forest is crucial for a regional conservation plan due to the scarcity of similar areas in the western part of the Ouachita Mountain ecoregion. Parts of the upper Kiamichi River valley are within the National Forest and could also be managed for the development of bottomland forest. Additional areas of bottomland forest along the Mountain Fork River and the Glover River will be incorporated into the Ouachita National Forest as part of the trade of land with the Weyerhaeuser Company now pending in Congress. Other areas of bottomland forest include two areas on the Little River which are federal wildlife refuges and one state wildlife management area on Fourche Maline Creek.

OAK-PINE AND PINE-OAK FORESTS

Ecosystem management. The Ouachita National Forest classifies the stands of timber in the forest according to the predominant trees of the upper canopy. According to the "Continuous Inventory of Stand Conditions", a computer-based inventory, pines dominate the canopy on 59 percent of the forests, hardwoods dominate on 23 percent and a mix of pines and hardwoods occurs on the remaining 18 percent (USDA 1993). The pine-dominated stands are usually mixed: hardwoods may occupy up to 30 percent of the canopy in these stands, and usually dominate the midstory and smaller size classes of trees (USDA 1993).

Thus, roughly speaking, 75% of the forest is either pine or mixed pine and oak.

Until the last 5 years, logging in the oak-pine and pine-oak forests was primarily by clearcutting, followed by mechanical and/or chemical site preparation and planting of pine plantations. Pine plantations have been established on about 16 percent of the Ouachita National Forest (USDA 1993). In most of these plantations, however, hardwood sprouts are abundant and compete vigorously with the pines. In a few plantations acquired from Weyerhaeuser, hardwoods were almost eradicated by intensive site preparation.

Under ecosystem management, clearcutting has been phased out and has been replaced by single-tree and group selection (uneven-aged management) and modified seedtree and shelterwood management (two-aged systems) (Baker 1994). Under phase III of ecosystem management, timber management at the watershed level could be planned not only to reflect the patterns of forest community types at the landscape level, but also to restore the pine/oak savannas and open woodlands. Prior to the turn of the century these communities may have encompassed most of the area which is now oak-pine and pine-oak.

Landscape-level management of the pine-oak and oak-pine forests to achieve both of these goals is feasible using the information technology of today. Under such management the phase II silvicultural operations would be directed toward a target distribution of stand structures for timber management purposes (Oliver 1992). By integrating these silvicultural methods and the

periodic use of ground fire, the existing oak-pine and pine-oak forests could be thinned by logging of some timber and then managed as fire-maintained forests by periodic ground fire. This form of timber management would begin to restore the native pine/oak savannas and open woodlands, benefitting birds and other wildlife.

Pine/oak savanna and open woodlands. A recent study of historical oak barrens in Illinois has re-introduced the idea that these open woodlands (which the author calls savannas) are a distinct association, as different from prairie and from forest as these associations are from each other (Packard 1988). There is continuing confusion concerning how to define these open woodlands (or savanna), because it intergrades both with prairie and with hardwood forests. In Oklahoma, at least, savanna should be defined as a permanent, more or less continuous ground cover of grasses and forbs, containing scattered distinct trees or scattered small groves, where the tree cover < 50% (Penfound 1962; Eiten 1982). Open woodland would then be defined as a community with greater than 50% tree canopy cover but < 80%.

Historical accounts of the Ouachita Mountains prior to the turn of the century, such as that of Smith (1986), recount a landscape of savannas or open woodlands of pine and oak. The pine/oak savanna and open woodland was a fire-maintained ecosystem which was "characterized by open stands of old, large, and often widely-spaced pines and hardwoods, occurring in patches and clumps" with a grassy understory (USDA 1993). Woody patches with near canopy closure were intermingled with open meadows. Pines probably tended to

dominate on sandy soils and oaks and hickories on clay (Foti 1974). It is possible that the pine/oak savanna and open woodland was an ecotone between the pine savannas and woodlands extending south to the coastal plain and the oak and oak-hickory savannas and woodlands extending west and north (Rice et al. 1959).

Canopy trees in pine/oak savanna and open woodlands were large on good sites, smaller on poorer sites, but all had a "flat-topped" appearance (USDA 1993). Midstory trees were uncommon, and a great deal of light reached the forest floor, permitting a species-rich understory of grasses, forbs and low shrubs such as sugar huckleberry and blackberry (USDA 1993).

Moderately intense ground fires occurred frequently in pine/oak savanna and open woodlands, usually in the summer and fall during dry periods (USDA 1993). Studies of fire scars on old growth pine trees in the McCurtain County Wilderness Area have shown that fire return intervals were probably about 3.5-5.6 years (Masters et al. 1994). The continuous understory of grass in this habitat type supported flashy, rapidly-moving fires that did not damage overstory trees, but which set back the midstory (USDA 1993). Fire suppression has changed the nature of the available fuels, and fires are today much more intense and more damaging to dominant trees (USDA 1993).

Since the advent of fire control in the 1930's in the Ouachita National Forest, a vigorous hardwood midstory has become established throughout nearly all of the Ouachita Mountains. The pine/oak savanna and open woodlands, which depended on frequent fire, has been nearly completely replaced by pine-oak or oak-pine

forests (Kreiter, 1995b). One example of how this may be happening in the Ouachita Mountain ecoregion comes from a recent study in the McCurtain County Wilderness Area. In 1955 there were still stands of open woodland in the McCurtain County Wilderness Area, but in 1990, after 35 years of fire suppression, there was a complete transition to hardwood forest on these same sites (Kreiter 1995b). Original survey notes from the McCurtain County Wilderness Area suggest that at the time of the survey in 1896 the oaks were dominant at most survey points; that the average tree was larger in diameter than at present; and there were roughly 70 trees per hectare, far fewer than at present (Kreiter 1995a). True pine/oak savanna and open woodland occurs today in the Ouachita National Forest on only a few thousand acres in the Poteau Ranger District. These have been deliberately maintained to support the red-cockaded woodpecker (*Picoides borealis*).

The bird association in pine/oak savanna and open woodlands. A recent study of the breeding birds in the Ouachita Mountains in western Arkansas has shown that there is a characteristic association of birds in the pine/oak savanna and open woodlands. This association includes red-cockaded woodpecker, Bachman's sparrow (*Aimophila aestivalis*), brown-headed nuthatch (*Sitta pusilla*), eastern wood-peewee (*Contopus virens*), northern bobwhite (*Colinus virginianus*), prairie warbler (*Dendroica discolor*), chipping sparrow (*Spizella passerina*) and red-headed woodpecker (*Melanerpes erythrocephalus*), as well as the generalist species (Wilson et al. 1995). This is probably the same association which Carter (1965)

reported in upland forests in the McCurtain County Wilderness Area, although fire had been suppressed in the Wilderness Area for about 10 years at that time. Even in that period of time, savanna species may have begun to drop out (Engstrom et al. 1984), and some species of the understory such as wood thrush may have begun to appear. Carter reported, for example, that orchard oriole (*Icterus spurius*) nested in the disturbed, open area around the headquarters area, but not elsewhere.

Restoration of pine-oak savanna and open woodland. The Forest Service has proposed an action plan for restoration of the pine/oak savanna and open woodland. About 50,000 acres of pine stands currently classified as suitable for timber production, well distributed across the national forest, will be included in "Pine Old Growth Restoration Units" (POGRU's). Each unit will include a core area of at least 10% of the total pine acreage. The core area will not be harvested. The remainder of the POGRU will be managed on a very long rotation (160 years) to provide a sustainable presence of old growth. When a core area is lost to catastrophe or old age, it will be regenerated and reenter the cycle as a replacement stand. The oldest replacement stand in the POGRU will then be designated as the new core area (USDA 1993).

Both the core and the replacement stands will be managed for the development of pine/oak savanna and open woodland by thinning and removal of midstory trees and by regular prescribed burning, particularly during late summer and fall. Seed tree harvesting (with high residual BA) and shelterwood harvests are permitted in

replacement stands on a 160 year rotation.

Restoration of pine/oak savanna and open woodland will create significant additional habitat for the association of bird species found in that community type, including the endangered red-cockaded woodpecker. Early-successional habitat for certain neotropical migrants, such as prairie warbler and yellow-breasted chat (*Icteria virens*), also will be created because of the effects of thinning and fire. Good numbers of prairie warblers and yellow-breasted chats also occur in clear-cuts and also in stands where alternative methods of forestry, such as seed tree and shelterbelt, have been introduced under the new philosophy of ecosystem management (Marian Lichtler, pers. comm.).

Restoration of oak and oak-hickory savanna and open woodlands. According to Rice and Penfound (1959), oak and oak-hickory savanna probably ranged to the west and north of the region of higher elevations in the Ouachita Mountains in Oklahoma at the time of settlement. However, these savannas may have occurred on less favorable sites such as upper, south-facing slopes and ridgetops within the latter region (Rice et al. 1959). In most of the Ouachita Mountains greater amounts of annual precipitation produced denser stands of oaks or oaks and hickories with grasses and forbs in the understory, which I describe as open woodlands (Kreiter 1995b).

As early as 1959, Rice and Penfound (1959) described how the savannas were disappearing in most of Oklahoma, due to overgrazing and fire suppression. Kreiter (1995b) has described how the open woodlands in the McCurtain County Wilderness area have also been

invaded by denser stands of hardwoods, and that the formerly open woodlands are now hardwood forests.

Active management is undoubtedly required for the restoration of oak and oak-hickory savanna and open woodlands, just as it will be required to restore pine/oak savanna and open woodlands. There may be an entire assemblage of plants and animals which are associated with oak and oak-hickory savanna and open woodlands in Oklahoma, as a recent study of hickory in Illinois has identified for the oak barrens there. Underneath the big old oaks with spreading branches still surviving in a few places in Illinois, the understory of native herbs changes as the canopy becomes more closed. In the most open places (10-30% canopy), there are prairie herbs. Distinctive savanna species appear where the light is intermediate (30-70% canopy), and oak barren species are found as the canopy closes (70-90% canopy) (Packard 1988). The seeds of the distinctively savanna species and oak barren species are sticky and pulpy - not dry like the prairie species. These plants depended not on wind to disperse seed, but on animals, probably the turkeys, deer, squirrels, doves and other species known to have been abundant in the old oak barrens (Packard 1988).

In order to restore the understories of oak barrens in Illinois, it was necessary to gather seeds of the plants and replant them. In the absence of such restoration of oak barrens, many of the animals that depended them (Packard 1988). Many of the species that once inhabited oak barrens subsequently done fairly well for a time in artificial, anthropogenic habitats such as woodlot edges, orchards,

grain fields or even backyards. But these habitats are also subject to disappearance - and with them would go the animals associated with oak barrens (Packard 1988).

Further research is clearly needed in Oklahoma to test the hypothesis that oak and oak-hickory savanna/open woodlands may form ecologically important associations in the Ouachita Mountain region (and elsewhere in eastern Oklahoma) with a distinct assemblage of plants and animals. Such research would help to answer several intriguing questions. For example, is the recent decline of several game species in the western Ouachitas, including deer, turkey and northern bobwhite, related to the disappearance of these savannas and open woodlands? Are certain declining species of neotropical migrants, such as orchard oriole and painted bunting, also declining because they are associated with them?

Unless some extensive areas of oak savanna or oak-hickory savanna or open woodland can be located in the ecoregion, perhaps these questions are best addressed by restoration of oak and oak-hickory savanna/open woodlands in the Ouachita Mountain ecoregion, at least on a small scale, in addition to the proposed restoration of pine/oak savanna and open woodlands. A thinning and burning approach to the restoration of oak and oak/hickory savanna and open woodlands could be practiced similar to that for the restoration of pine/oak savanna and open woodlands. The Forest Service does intend to carry out such a pilot project on several small tracts of hardwoods near the headwaters of the Mountain Fork river on lower north-facing slopes of Phillips Mountain (Marian Lichtler, pers. comm.), but a

larger, interconnected area is probably essential.

SUMMARY

A landscape level approach to conservation of breeding birds in the western Ouachita Mountains means that goals for management at the local or stand level are determined at the landscape level. Local decisions are directed toward maintenance or restoration of the natural, presettlement, landscape level patterns of vegetative community types and bird associations. These communities and associations are complex assemblages of species which have evolved over the ages (Packard 1993).

Very productive habitats for many declining species of neotropical migrants are the oak-hickory forests along the ridgetops and upper north-facing slopes and the bottomland hardwood/riparian forests. On a regional scale these linear communities form networks of interconnected communities in the present-day matrix of second-growth pine-oak forests. These communities provide habitat for several declining neotropical migrants, including hooded warbler, ovenbird, cerulean warbler, wood thrush, scarlet tanager, Louisiana waterthrush (*Seiurus motacilla*) and Acadian flycatcher (*Empidonax virescens*).

Restoration of pine/oak savannas and open woodlands should also be managed at the landscape level. Thinning of the stands and use of periodic ground fire should be planned so that the resulting patches of pine/oak savanna and open woodlands are interconnected. Ecosystem management is appropriate for this goal. This community

type provides habitat for a large assemblage of birds, including the endangered red-cockaded woodpecker, a declining short distance migrant, Bachman's sparrow and a significantly declining neotropical migrant, prairie warbler.

Experimental scale efforts should also be made to restore oak and oak-hickory savanna and open woodlands. This community may provide habitat for another assemblage of birds, possibly including the declining neotropical migrants orchard oriole and painted bunting.

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