HABITAT AND BEHAVIOR OF THE AMERICAN WOODCOCK IN NORTHCENTRAL OKLAHOMA

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HABITAT AND BEHAVIOR OF THE AMERICAN WOODCOCK

IN NORTHCENTRAL OKLAHOMA

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PREFACE

I studied the ecological relationships of a very habitat-specific bird, the American woodcock (Philohela minor, Gmelin), in northcentral Oklahoma, on the southwestern fringe of its range in North America. The primary objective was to evaluate relationships between woodcock and their habitat by analyzing their breeding behavior, observing their response to habitat manipulation, determining their seasonal numbers and distribution, and by attempting to identify factors responsible for scarcity of woodcock in summer months.

The project was funded by the Rob and Bessie Welder Wildlife Foundation, Sinton, Texas. I express sincere gratitude to my major adviser, Dr. John Barclay, Associate Professor, Oklahoma State University, for his patience, understanding, and assistance in the completion of this study. Other members of my graduate committee who deserve praise are: Dr. William Warde, Associate Professor of Statistics, for his untiring work on the statistical analyses; Dr. James McPherson, Associate Professor of Botany and Plant Pathology, for his help in mowing plots on my study area and for his assistance in vegetative analysis; Dr. James Lewis, former Assistant Leader, Oklahoma Cooperative Wildlife Research Unit, for his invaluable editorial assistance.

I thank the Oklahoma Cooperative Wildlife Research Unit for the use of vehicles and other equipment. Especially, I thank Dr. John Morrison, former Unit Leader, who edited my quarterly reports, and Gay Williams,

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I am very grateful to many undergraduate and graduate students whose names I cannot mention for lack of space. Without their help there would have been many gaps in my data, and the study would not have been as interesting.

There were some trying moments in the course of my research, but they were made bearable by special friends and their presence in time of need. John Barclay and his family, Jerry Brabander and his family, and Rod Smith were very special friends to me, and I thank them for making my study enjoyable.

Most importantly, I wish to thank my family for their love and support throughout this study.

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INTRODUCTION

Oklahoma has been undergoing extensive land use changes with respect to reservoir construction and agricultural practices. Between 1948 and 1975, more than 16,647 ha of detention reservoirs were built by the United States Department of Agriculture (USDA). Since 1952, some 68,826 ha of farm ponds were built by the Soil Conservation Service (SCS) (personal communications with Alvin Clements, Oklahoma SCS, 1973). Several hundred thousand hectares of lakes were created by the United States Army Corps of Engineers (USCOE) and the Bureau of Reclamation (BR) for flood control and water supply.

Among the changes in agricultural land use has been an increase in pasture and a decrease in cropland. In 1932, 1,037,296 and 4,996,900 ha of land in Oklahoma were used for pasture and cropland respectively. By 1969, those figures had changed to 1,985,425 ha of pasture and 3,346,068 ha of cropland (Oklahoma Agricultural Census 1972).

One of the basic tenets of ecology is that animal species adjust their ranges according to the availability of suitable habitat. Land use changes such as fire control, impoundments, land clearing, and cultivation alter both the amount and availability of suitable wildlife habitat.

The land use changes in Oklahoma have affected the status of many wildlife species. One of them, the American woodcock (Philohela minor,

Gmelin), is the subject of this study.

The status of the woodcock in Oklahoma had not previously been studied because Oklahoma had traditionally been classified as peripheral to the principal wintering and breeding range of woodcock (Robbins et al. 1966; Sheldon 1967). However, Barclay (personal communication, 1973) noted that the bird was being observed in greater numbers and farther westward than previously.

Little was known about the woodcock's importance in the "hunter's bag" because the questionnaire annually mailed to a sample of Oklahoma's hunters, by the Oklahoma Department of Conservation, did not include questions about woodcock until 1976. Oklahoma had been largely ignored in annual Woodcock Wing Collection Surveys conducted by the United States Fish and Wildlife Service (USFWS). Clark (1974) listed two, four, and two cooperators (hunters) for Oklahoma in the Woodcock Wing Collection Surveys for 1970-71, 1971-72, and 1972-73, respectively. Yet, in our files we had reports of many hunters killing woodcock as an "incidental" while hunting turkey or quail. A considerable number of woodcock may be taken each fall in Oklahoma. As Clark (1971:7) remarked:

> . . . the woodcock is increasing in popularity as a game bird. Although interest in the species is still greatly in northern states, and adjacent Canadian provinces, more U.S. hunters in central latitudes and the South [emphasis added] are turning to woodcock.

Three years later Clark (1974:1) again stated:

> . . . the American woodcock has become a popular game bird with increasing numbers of hunters over a wider portion of its range [emphasis added] during the past decade. The woodcock-to-waterfowl ratio has narrowed to 1:3 or less in several northern states. Although state harvest surveys and the Bureau's waterfowl hunter mail survey show considerable variations in annual woodcock harvests, the general trend is upwards. Thus, the species had advanced from a 'specialty' game bird highly regarded by a few hunters to a broader based source of recreation.

Virtually no conclusive data were available on the migration of woodcock as they pass through Oklahoma. Williams (1969) noted that of 14,438 woodcock banded in Louisiana from 1965-66, 412 band recoveries were reported to the Bird Banding Laboratory at Patuxant, Maryland. Only two of these birds were from Texas and none were from Oklahoma.

Woodcock had not been known to perform courtship displays in Oklahoma nor to breed as far west as Payne County, Oklahoma, before 1970. It was then that Barclay (personal communication, 1973) observed displaying woodcock on the 62.3 ha Oklahoma State University (OSU) Ecology Preserve 14.5 Km west of Stillwater.

In 1973, Barclay discovered a brood of woodcock on the Preserve on 7 April.

It is in the context of the previously mentioned land use changes in Oklahoma, of the changing habits of people, and of the woodcock's status as affected by these changes that the need for woodcock research in Oklahoma became obvious. It would be necessary to understand more clearly the habitat requirements, seasonal numbers and distribution, population composition, courtship, nesting and brooding behavior, and migration patterns of woodcock should this bird become more popular as a game species in the state.

Much of the significance of this study was to depend on the small size of the woodcock population under observation and its location in "atypical" habitat on the western fringe of its range in North America. As Leopold (1933) implied, the periphery of a species' range is where valuable insights about biological tolerance and habitat requirements may be obtained. It was anticipated that many questions about woodcock

left unanswered in previous work elsewhere would be clarified in this study.

Therefore, the purpose of this research was to evaluate the major ecological relationships of woodcock and their habitat in northcentral Oklahoma through pursuit of the following objectives:

1. To analyze breeding behavior of woodcock on the OSU Ecology Preserve in relation to behavior, meteorological, and seasonal factors.

2. To observe the response of a small breeding population of woodcock to manipulation of habitat on the Ecology Preserve.

3. To determine seasonal numbers and distribution of woodcock populations and their major habitat requirements in Oklahoma with particular emphasis on northcentral Oklahoma.

4. To identify the major factors limiting the seasonal distribution of woodcock in northcentral Oklahoma.

CHAPTER II

LITERATURE REVIEW

Previous Work in Oklahoma

Records of woodcock observations in Oklahoma date back to 1853 when Woodhouse (see Sutton 1967:181) stated that "this bird only came under my observation whilst in Indian Territory, and it was there quite rare." Force (1929:68) called it a "rare transient" in Tulsa County. Nice (1931:88) called it a "rare transient in Eastern Oklahoma, probably a breeder." Baumgartner and Howell (1948:51) called it a "rare Fall visitant" in Payne County. Letson (see Sutton 1967:181) classified it as an "occasional winter resident" in the Tulsa area. It has been known to be a rare transient visitor on the Salt Plains National Wildlife Refuge (Sutton 1967). Sutton remarked that all seasons occurrence depends on availability of mud in which food may be obtained through probing. Mendall and Aldous (1943:39) classified it as "casual in summer --not believed to breed--uncommon migrant and winter resident, chiefly in the southeastern part of the state." Formerly, woodcock nested as far west as eastern North Dakota and eastern Oklahoma, but Mendall and Aldous (1943) reported no breeding records in the previous 25 years.

Fletcher and Temple (unpublished report for Oklahoma Game and Fish Department, 1942:1), two biologists for the state of Oklahoma, said: "The woodcock never has been or never will be an important game bird in

Oklahoma. . . . These birds are found only in the flood plain and cover type of the extreme eastern part of the state." They cited two reasons for the "demise" of the woodcock in many parts of Oklahoma: first, the best woodcock habitat, which was formerly rich marshy soil along streams supporting a heavy growth of flood plain timber, had been converted to some of the most productive farmland in the state; second, excessive shooting had led to the woodcock's decline.

Very little is known about the distribution and seasonal numbers of woodcock throughout Oklahoma. Barclay (personal communication, 1973) noticed that woodcock in northcentral Oklahoma were conspicuously scarce in mid-summer through early fall. Sutton (1967) also documented this and mentioned that where woodcock were present, they depended on soft mud to probe for earthworms. The dry, hot summer conditions in north-central Oklahoma may force invertebrates deep into the soil and make them unavailable to woodcock, thereby forcing woodcock northward or eastward to better habitat. Sheldon (1967) mentioned that the westward distribution of woodcock is undoubtedly limited by moisture and availability of foods.

Sutton (1967) believes that the peaks of the fall and spring migration of woodcock in Oklahoma are from 15 October to 20 November and from 10 March to 20 April respectively.

Although Mendall and Aldous (1943) concluded that no woodcock nesting occurred in Oklahoma, Sutton (1967; 1974) cites mid-summer records from 1 June to 17 August for Tulsa, Lincoln, Oklahoma, Kay, and Alfalfa Counties, suggesting that the species may breed rather widely throughout the state. Barclay (personal communication, 1973) confirmed they nested

in northcentral Oklahoma when he banded a young woodcock chick 14 km west of Stillwater in April, 1973.

Previous Work in Other States

General Habitat Requirements

Little was known about woodcock habitat in Oklahoma, particularly in northcentral sections. Fletcher and Temple (unpublished report for Oklahoma Game and Fish Department, 1942) mentioned that woodcock were found on bottomlands, but made no mention of specific habitat requirements. Yet, Liscinsky (1965) and Sheldon (1969) stressed the importance of inventorying vegetation, physiographic features, and soil characteristics to acquire basic information needed for woodcock management.

The influence of species composition on the use of cover by woodcock was studied by Liscinsky (1965) in Pennsylvania. He found that in summer and fall, very few species of vegetation occurred more than 15 percent of the time in habitat used by woodcock. Of these species, alder (see the Appendix for common and scientific names of plants) was the preferred cover, but in localized areas aspen was also important.

Alder was also the most important species in the understory of woodcock habitat in Maine (Dunford 1971). Ground cover consisted of grasses, ferns, and other species typical of moist areas.

Cover requirements of woodcock are more stringent than those of most game birds and the pattern of vegetation and in good woodcock habitat varies greatly in different areas. Very subtle differences sometimes determine the suitability of woodcock habitat. For example, an aspen-birch cover type may seem ideal, but upon closer examination, one may find a layer of moss (which is unattractive to woodcock) scattered over

the forest floor. Scattered evergreens in the understory seemed to increase the carrying capacity of coverts in Massachusetts and Vermont (Sheldon 1967).

Seasonal cover preferences by woodcock have been confirmed by previous studies. In New Brunswick, though summer and fall habitats were similar, sparser cover was used by woodcock in the fall. Studies in Maine indicated that in early spring, during brood rearing, denser cover was used (Mendall and Aldous 1943). This preference was attributed to the need for more protection for the young.

Interspersion of cover is indicative of good woodcock habitat. Sheldon (1967:124) stated:

> The most productive covert I ever hunted grew on a hill in Maine and was formed by ideal juxtaposition of young alder, aspen, gray birch, and white birch, sprinkled with young white pines and broken by small openings.

Age of cover is an important factor in woodcock habitat. In Massachusetts, Sheldon (1967) found that young stands of alder, aspen, and other trees were ideal.

In Pennsylvania the density of cover influenced the use of cover by woodcock (Liscinsky 1965). Dunford (1971) also found that the density of cover was important in Maine: in hardwood conifer cover, canopy coverage averaged 53 percent and in alder cover 64 percent while vegetation covered 44 percent of the ground. In Massachusetts, woodcock were found in coverts with a wide variety of overstory density, but it seems that they needed some spots of low plant density that allowed freedom of movement during foraging (Sheldon 1967).

Vegetation, Litter, and Invertebrates

There are close relationships between dominant vegetation, ground

litter, and the invertebrate communities in the soil. Vegetation influences soil communities because it contributes most of the litter and other organic matter which is the food of decomposer organisms (Macfadyen 1969). Certain types of litter influence the soil type and the invertebrate community.

For example, many species of earthworms are very selective in the kind of plant material they accept, the palatability of the plant material being directly related to its nitrogen and sugar content. Leaves rich in these nutrients are those of nettle, wood-sorrel, hawthorne, ash, elm, alder, birch, hornbeam and sycamore (Walwork 1970).

These relationships have important implications to woodcock. In a study of summer habitat of woodcock in Maine, the overstory stratum of second-growth hardwoods was predominantly gray birch, red maple, American elm, white ash, and quaking aspen (Dunford 1971). These species are associated with good earthworm production.

Sheldon (1967) believed there is some correlation between tree species and earthworm distribution, and that this correlation may be a function of the amount of nutrients (notably N_2) in the litter produced by the dominant vegetation. Mendall and Aldous (1943) found the highest concentration of earthworms in alder coverts, or mixed coverts containing alders, where one expects to find more woodcock and worms. Handley (1954, see Sheldon 1967) noted that litter under alders had by far the highest percentage of nitrogen (2.5 percent) of any of the 24 genera of trees he studied in England. Alder is one of the few tree species hosting nitrogen-fixing soil bacteria.

Breeding Behavior

The first indications of woodcock migration in the spring are the courtship performances of male woodcock on singing sites at dusk and dawn during evenings and mornings. "Singing sites" are territories established by male woodcock in fields or forest openings, in the spring breeding season, on which they perform courtship activities (a series of aerial displays and calls or "peents") to attract female woodcock. The courtship performances increase in intensity as spring progresses, and a peak of activity ensues after which the performances decrease in intensity and numbers, until, by late spring, only partially completed flights occur.

Male woodcock begin to sing as soon as they arrive in Massachusetts at the end of March and continue until 20 May, when singing gradually diminishes (Sheldon 1967). Courtship ceases by 1 June in most years. Further north, the breeding season begins about a week later, and in southern states, such as North Carolina and Kentucky, breeding starts a month earlier and ends by 1 May (Sheldon 1967).

There is usually a greater number of displaying male woodcock early in the breeding season. These may represent migrating birds which temporarily stop and select a singing site in an area. Pitelka (1943) noticed this phenomenon in Illinois where male woodcock which had selected a site early in the breeding season left and did not remain to breed that season. Norris et al. (1940) reported migrating movements of woodcock and variations in numbers of singing males during the first week of April in central Pennsylvania; after the first week, numbers were more or less stabilized and territories were definitely established.

In Michigan, Goudy (1960) noticed that courtship periods each year extended from the last week in March to the first week in June. Gradually increasing numbers of migrants and cessation of breeding, respectively, seemed to be largely responsible for the variation in numbers of woodcock heard at the beginning and end of each breeding season.

Singing Site Characteristics

Characteristics of woodcock singing sites differ from one region to another and many factors interact to determine the use of a site by a male woodcock.

Succession is one of the most crucial factors affecting the use of singing sites by woodcock. Unless openings are sufficiently large with moderately sparse ground cover, they receive little or no use. Mowing of plots is often used to set back succession, thus creating artificial singing sites for use by male woodcock in the spring. In 1940, 37 artificial singing sites were created at Moosehorn National Wildlife Refuge in Maine ranging in size from 0.06 to 0.78 ha. All were subsequently used by courting male birds (Mendall and Aldous 1943).

The size of singing sites varies from state to state and from one habitat type to another within a state. In Pennsylvania, singing sites are in very small clearings, 6.4 m by 11.3 m (0.007 ha), whereas in Maine the majority of the singing sites are in clearings with over 0.1 ha (Mendall and Aldous 1943). Singing sites in Illinois are generally circular and 15.2 to 22.9 m in diameter (0.02 to 0.04 ha) (Pitelka 1943). Pettingill (1936) stated that singing sites are seldom larger than 15 m square (0.02 ha) and that a single field at Connecticut Hill, New York, had an average diameter no greater than 9.1 m (0.007 ha). In Minnesota,

Dangler and Marshall (1950) found singing sites of 21 to 40 m in diameter (0.03 to 0.13 ha). Ritcher (1948) found the average diameter of singing sites to be 22 to 34 m (0.04 to 0.09 ha). Although Mendall and Aldous (1943) stated that the size of the opening is of little importance, they cited a minimum of 2.3 m^2 (0.0002 ha) and no maximum (very often, birds used portions of larger fields).

Singing sites are never very close together because woodcock are highly territorial in their spring displays. Mendall and Aldous (1943) and Norris et al. (1940) remarked that most singing sites are at least 137.2 m apart. In Minnesota, seemingly equitable sites were located 32 to 91 m apart but were not used simultaneously (Marshall 1958).

The physical characteristics of and surrounding the singing site may be very important in determining its use by woodcock. Mendall and Aldous (1943) studied the size, shape, slope, exposure, degree of cover, and many other physical characteristics of singing sites in many possible combinations. No preferences by woodcock were apparent. Yet, Barclay (personal communication, 1973) observed preferences on the Oklahoma State University Ecology Preserve where certain sections of a field were used more than others. Mendall and Aldous (1943:74) noticed the same phenomenon in Maine: ". . . on certain of these, when males were collected, the grounds would invariably be reoccupied the following year."

On the other hand, there are many apparently suitable sites which are never or seldom occupied (Marshall 1958).

Pitelka (1943) felt that the requirement for a good singing site is the presence of some shrubby areas within the display territory. Sheldon (1967) stated that one universal requirement is a "getaway"

route for the bird's aerial flight, and that high surrounding trees may limit the usefulness of an otherwise good site.

Mendall and Aldous (1943) found that most singing sites in Maine were near diurnal nesting cover and that there was a preference for relatively open rather than brushy clearings.

There seem to be differences of opinion about the relationships between soil characteristics and selectivity of an area by woodcock as a singing site. In Maine, Mendall and Aldous (1943) found no relationships between soils and the presence of singing sites. In Minnesota, nearly all singing sites were located on loamy and alluvial soils (Marshall, 1958). Blankenship (1957, see Sheldon 1967) analyzed the soil on 80 singing sites in Michigan; 29 sites were on sand, 10 on loamy soil, 17 on loam, 2 on muck, and 6 on peat. In Massachusetts, singing sites were usually established on sandy loam soils (Sheldon 1967).

Utilization of singing sites by woodcock may be closely correlated with the associated flora. In Massachusetts, certain plant species kept appearing in Sheldon's (1967) tabulations of flora at singing sites; bluestem grasses and meadowsweet were common in most of the fields.

Among the 29 best singing sites Mendall and Aldous (1943) studied in Maine, 10 were occupied primarily by small bushes, and 6 were occupied by high bushes. In Minnesota, intensive studies of 17 singing sites demonstrated that the plants occurring in them and the activities of the males using them compared closely with the findings reported by Mendall and Aldous (Dangler 1950, cited by Sheldon 1967).

Nest and Brood Cover Characteristics

Mendall and Aldous (1943) classified the habitat of 228 woodcock

nests: 44 percent were in mixed growths of birch, aspen, other hardwoods and conifers; 26 percent were in hardwoods; and the remaining 9 percent were in brushland, blueberry land, or old fields. Sheldon (1967) found nests in abandoned fields, conifer plantations, brushy areas, mixed forests of different ages, and in blueberry fields.

Brood cover in Maine and Massachusetts was basically the same as nesting cover (Mendall and Aldous 1943; Sheldon 1967), but the same may or may not be true of Oklahoma, where the habitat and climate differ considerably.

CHAPTER III

STUDY AREA

The Ecology Preserve

The 62.3 ha Oklahoma State University Ecology Preserve (Figure 1) is located 14.5 km west of Stillwater near Highway 51 in a region of gently rolling tall grass prairie interspersed with broken tracts of brush and scrub oak forest (savannah). Along with other land surrounding Lake Carl Blackwell, the Bureau of Reclamation acquired it by eminent domain in 1936. By the late 1930's, Oklahoma State University became responsible for its management and until recently, it was leased to private landowners for livestock grazing. Beginning in 1968 it was protected from grazing and designated as The Oklahoma State University (OSU) Ecology Preserve.

Four major habitat types occur on the Preserve: bottomland hardwood, upland hardwood, brushland, and grassland.

Bottomland hardwoods occur along the drainage of Harrington Creek and the small stream entering it from the northwest. The dominant tree species in the overstory are chinquapin oak and American elm. Occasionally, these trees reach heights of 15 m but more commonly they are 10 to 15 m high. The understory species are chinquapin oak, American elm, red mulberry, and localized thickets of eastern redbud. The ground cover consists of broad-leaf uniola, leafy elephant foot, beggar's lice,

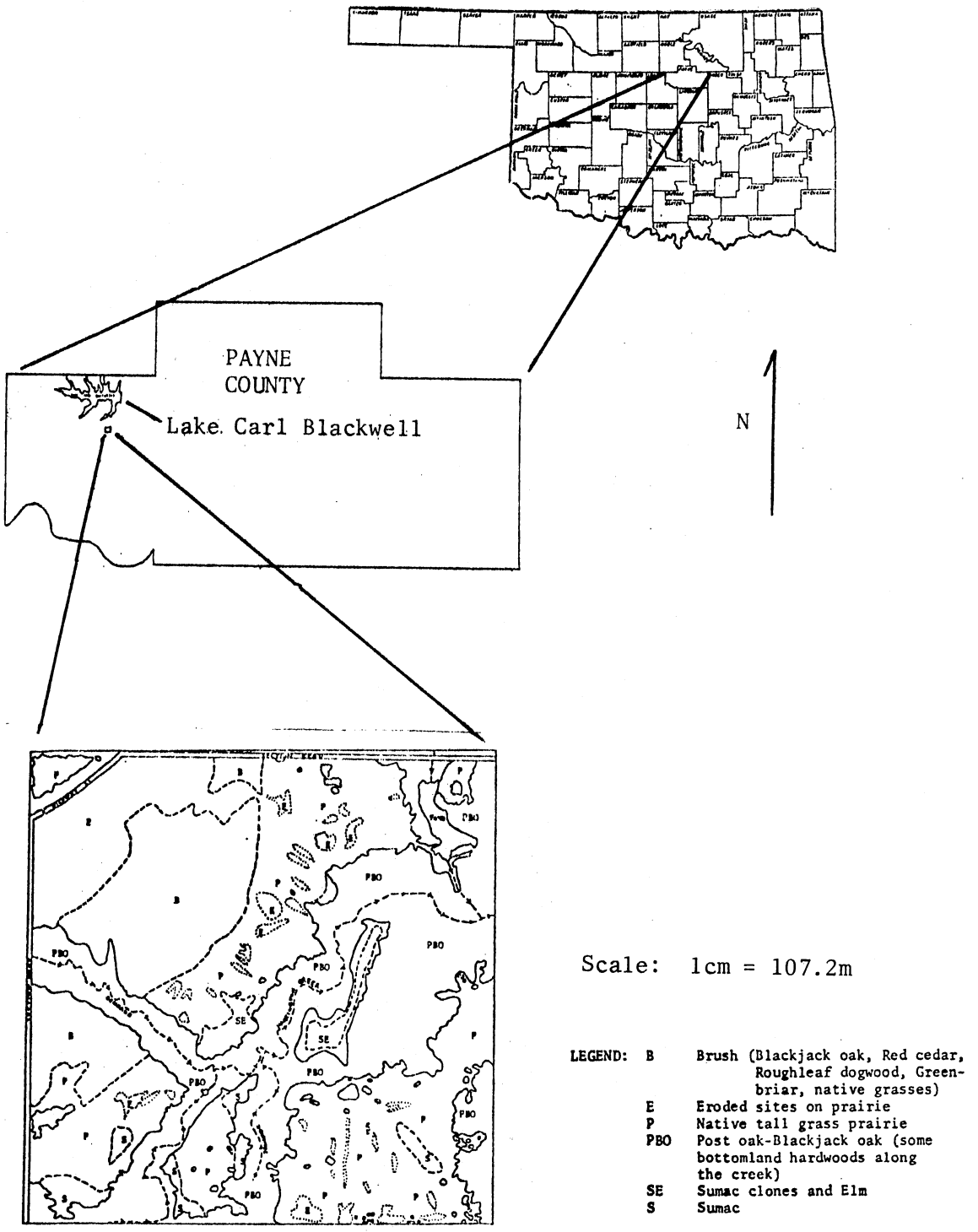


Figure 1. Location and habitat type map of the Oklahoma State University Ecology Preserve study area (NW 1/4, T28-19N-51E).

aster, crown-beard, clover, ryegrass, giant ragweed, and poison ivy. In many areas along the creek drainages the ground cover is dominated by a thick, nearly impenetrable growth of greenbriar.

The upland hardwoods generally border the bottomlands and grasslands. The dominant tree species in the overstory is post oak, and its associates are blackjack oak, chinquapin oak, and hackberry. These tree species rarely exceed heights of 10 m. Common understory species are post oak, red cedar, blackjack oak, chinquapin oak, American elm, chittamwood, roughleaf dogwood, and smooth and winged sumacs. Ground cover consists of buckbrush, crown-beard, leafy elephant foot, rye grass, Scribner panicum and occasionally dense thickets of greenbriar.

The brushland areas are interspersed throughout the upland hardwoods and the grasslands. They consist of a low (3 m) dense growth of scrub oak, red cedar, American elm, buckbrush, clones of sumac, dogwood, and an often rank growth of greenbriar. These areas were sprayed with herbicides in the 1940's to create pasture but are now reverting to the original post oak-blackjack oak communities.

The grasslands on the Preserve have been protected from grazing since 1967. The more common grasses are Indian grass, switchgrass, little bluestem, silver bluestem, and split-beard bluestem. Common forbs occurring in the grasslands are Canada goldenrod, Missouri goldenrod, stiff goldenrod, western ragweed, giant ragweed, large patches of slender lespedeza, Scribner panicum, heath aster, silver-leaf nightshade, Torrey nightshade, prickly pear cactus and other prairie plant species.

At various locations, both sheet and gully erosion are evidence of former improper land use practices and disrupt the natural beauty of the native grasses. The erosion in some areas has produced deep gullies and

depressions marked by weedy vegetation such as annual broomweed, western ragweed, and silver bluestem. Where the topsoil has been washed away, the residual materials lack the friability characteristic of the soil on the rest of the area.

The soils on the Preserve are mostly redbud sandstone silt deposits, often sandy or loamy depending on the distance from the drainages. They are very subject to erosion and in many places the creeks have eroded gullies over five meters high.

Harrington Creek drains through the Preserve in a northeasterly direction. Although water is present in the creek throughout the year, the flow is heaviest in early spring and fall and nearly dry in late summer. A small drainage joins Harrington Creek at the southern end of the Preserve and is nearly dry most of the summer.

In the northeast corner of the Preserve is a small pond, impounded by a dam at the south end.

Payne County

Payne County is located in northcentral Oklahoma (Figure 1). Much of it is treeless prairie, but there are usually forested belts along the major rivers and drainages. It lies in a region known as the central prairies or "cross timbers" which run north and south through the east-central part of Oklahoma (Park 1938).

The dominant upland tree species are post oak and blackjack oak which often intersperse with the native prairie in what is often called savannah. The dominant bottomland species are American elm, chinquapin oak and hickory. Many non-native tree species such as black locust,

osage-orange, and red cedar are now well established throughout the region (Park 1938).

Little and big bluestem grasses are the climax native prairie vegetation but, due to excessive grazing, have been commonly replaced with ragweed, broomweed, snow-on-the-mountain, and other pioneer species.

The topography is gently rolling and the county as a whole is well drained by the Cimarron River. The principal tributary of the Cimarron River within Payne County is Stillwater Creek, which drains the northwestern and northcentral parts of the county and joins the Cimarron River near Ripley.

Several large impoundments have been constructed in Payne County since the 1920's for flood control, water supply, and recreation--notably Lakes Carl Blackwell, McMurtry, Boomer, and Ham (2,070 ha). These have flooded considerable land and added much shoreline habitat along their banks and tributaries.

The climate of Payne County is generally mild and agreeable, but during the summer months the days are extremely hot for periods of a week or more. Occasionally, during the winter, sudden changes of temperature caused by "northers" make the climate temporarily very severe. The mean annual temperature is about 15°C. Temperatures of 40°C to 42°C frequently occur during the months of July and August, and temperatures of 38°C have been recorded in all the months from April to September inclusive. The mean temperature of the winter months is 3°C. The highest winter temperature on record is 32°C and the lowest is -28°C, both of which occurred in the month of February (Park 1938; Myers, unpublished weather summary for Stillwater, Oklahoma, 1971). Occasional

light snows fall in the winter, but they do not remain for any length of time.

The average annual rainfall is about 81 cm with most of it falling during late spring and early fall. Precipitation is ample when it is favorably distributed, but often periods of heavy rainfall alternate with long periods of drought during which crops suffer.

The soils of Payne County are dark-colored redbed soils with heavy claypan subsoils. The surface soils have a dark brown friable texture, a rather well-developed granular structure, and a low content of carbonates. The subsoils are much heavier in texture, hard and intractable when dry, and plastic when wet. The high iron content of the soils accounts for their reddish color (Park 1938).

Due to their sandy nature, these soils are highly susceptible to erosion. Overgrazing by cattle combined with the frequent hard rains of the region have severely impoverished many formerly productive pasture and crop lands.

CHAPTER IV

METHODS AND ANALYSES

Null Hypotheses

The following null hypotheses were used to test theories associated with the objectives mentioned in the Introduction.

Breeding Behavior

1. Seasonal and yearly variations in courtship display behavior of breeding woodcock do not occur in northcentral Oklahoma.

2. Meteorological phenomena at the time of courtship displays of male woodcock (cloud cover, temperature, moon phase and day, barometric pressure, and other weather factors) do not affect woodcock courtship displays in northcentral Oklahoma.

3. Vegetation characteristics of signing sites (density, height, and composition of flora) do not affect woodcock selection of singing sites in northcentral Oklahoma.

4. Physical characteristics of singing sites (perimeter, area, slope, aspect, elevation, and shape) do not affect woodcock selection of singing sites in northcentral Oklahoma.

5. Spatial characteristics (distance between singing sites, and distances from singing sites to ecotone or diurnal cover and water) do not affect woodcock selection of singing sites in northcentral Oklahoma.

6. Soil characteristics of singing sites (pH, moisture, texture, and availability and presence of invertebrates) do not affect woodcock selection of singing sites in northcentral Oklahoma.

Habitat Manipulation

Singing sites are not a limiting factor to woodcock breeding in northcentral Oklahoma, hence, mowing of plots will not increase the number of performing males nor the breeding population of woodcock on the Oklahoma State University Ecology Preserve.

Summer Habitat Conditions

Absence or unavailability of earthworms and other invertebrate woodcock foods are not reasons for the conspicuous scarcity of woodcock in northcentral Oklahoma in the mid and late summer months.

Breeding Behavior

Courtship Display

The behavior of woodcock on the Ecology Preserve was monitored in the spring months of 1970 to 1975. Each evening during the display seasons, 1 to 5 observers were stationed at singing sites on the Preserve (in 1974 and 1975, morning displays were also observed). Observers arrived at singing sites about 15 min before display activity started. They were supplied with a watch with a second-hand, a thermometer, a pen light, and data sheets. I stressed the importance of silence and concealment from the birds at the singing site so that displaying woodcock would not be disturbed.

The number and duration of calls and flights made by displaying male woodcock, time of initiation and termination of flights and calls, and other behavioral data were recorded to the nearest 5 seconds.

The following meteorological data were also recorded at the beginning and at the end of woodcock courtship display performances: temperature, wind speed (nearest 8 Km per hour), wind direction, relative humidity (read off charts from the weather station on the study area), barometric pressure (a barograph was kept in good working condition on campus), visibility, percent sky cover, precipitation, day of the moon (obtained from the Farmers' Amanacs), and ground moisture conditions.

Observers left the area approximately 5 to 10 min after courtship display performances by male woodcock ended.

Woodcock were mist-netted on singing sites in all years in an effort to monitor territorial fidelity by male woodcock in one season, territorial homing by male woodcock from one season to the next, replacement of one male woodcock by another on singing sites, and weight loss of displaying males during dry periods. Standard measurements (Pettingill 1970) were made on woodcock captured and their sex and age determined by the method described by Martin (1964).

Data for 1970 to 1975 were transferred to computer cards, and correlation analyses, analyses of variance, and factor analyses of principal components (Morrison 1967) were used to determine the effects of meterological factors on courtship display behavior of male woodcock.

In the correlation analyses, the effects of 24 meteorological, time, and other independent variables on 6 courtship or behavioral dependent variables were analyzed. A courtship performance was defined as the entire series of flights and calls during any one evening or

morning by one male woodcock from one or more singing sites.

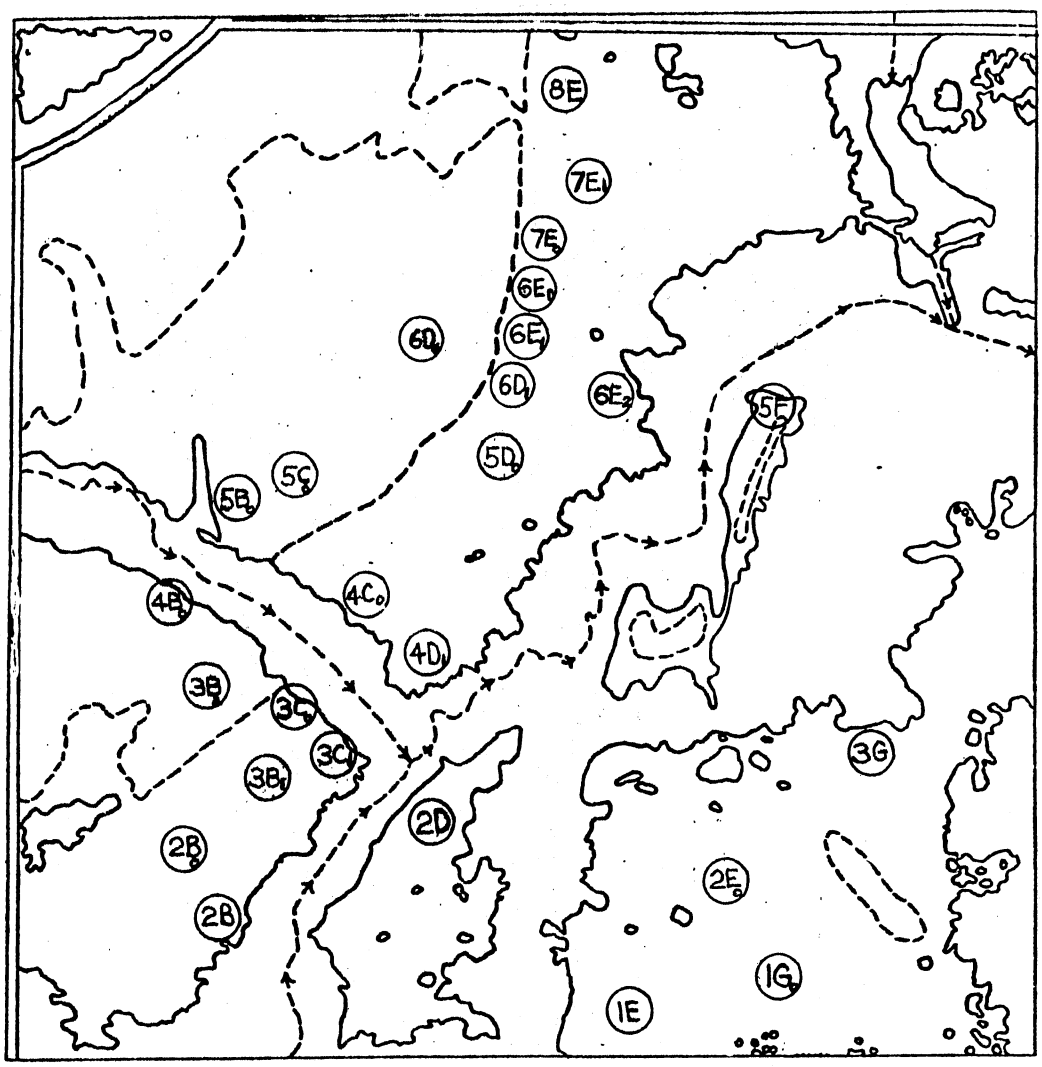
Although correlation analyses assume linear relationships between variables, and are not favorably viewed by many statisticians, they often give insight and reinforcement to many intuitive ideas about important relationships. They provided such insight in this study.

In the analyses of variance, basically the same relationships between independent and dependent variables were analyzed. When a dependent variable was tested against merely two classes of an independent variable (for example, number of calls in one evening when cloud cover was greater than 95 percent as opposed to when cloud cover was less than 95 percent), a straightforward analysis of variance was used. However, when a dependent variable was tested against more than two classes of an independent variable (for example, the number of calls at four different wind speeds), multiple comparison tests were used. A modification of the least significant difference test was used because the parameter means analyzed in this manner involved different sample sizes. The modification made the test more exact for experiments with unequal sample sizes.

The principal components analysis conducted was similar to that performed by LaPerriere and Haugen (1972) in their study of factors influencing calling activity of wild mourning doves.

Singing Site Analysis

Natural and artificial (mowed) singing sites used by woodcock on the study area were analyzed and compared to arbitrarily selected unused sites in identical habitat adjacent to used sites (Figure 2). Habitat parameters analyzed were vegatation (general composition, aerial



Scale: 1 cm = 61.5 m

N

(2B) Location and number of singing site

Figure 2. The Ecology Preserve showing singing sites where vegetation, physical, spatial, and soil characteristics were measured.

vegetation density at three different height intervals, and ground vegetation density), spatial (distances between singing sites, distances from singing sites to water, to ecotone or diurnal cover), physical (size, perimeter, area, slope, aspect, and elevation) and soil (pH, moisture, texture, and availability and presence of earthworms or other woodcock foods). Aerial vegetation density was a measure of the obscuring effect of vegetation on the presumed visibility by male woodcock at a singing site. Ground vegetation density was a measure of the percent surface area of a singing site covered by the stems of plants, by soil, or by soil litter.

The five different terms selected to describe the existing categories of potential singing sites on the upland prairie habitat of the Preserve included: used eroded, unused eroded, used mowed, unused mowed and unused native prairie. Eroded sites were once either highly overgrazed or used as salting areas for cattle and, consequently, were characterized by weedy plants and bare soil. Mowed sites were located on upland grass or brush areas. Unused native prairie sites were healthy grassland areas which had either never been eroded or had recovered from such erosion. A straightforward analysis of variance was used to test for habitat parameters between site classifications.

The vegetative composition of singing sites was determined with a 10-point sampling frame. The frame was placed at 15 randomly selected points at each singing site, the first vegetative part of a plant touched by each point on the frame being recorded as an individual of that species. This method gave a total of 150 sample points at each site. The sites were analyzed in early August, 1974. By then, sufficient time had elapsed for the vegetation on the mowed sites to recover

from mowing, and most of the native grasses and forbs were readily identifiable.

A density board (Figure 3) was used to measure aerial vegetative density on each site at six 10 cm height intervals (only the first three height intervals provided sufficient data for analysis). The density board had 40 squares (each 1 cm by 1 cm) at each of the six height intervals, and it was placed randomly at 30 different locations on each site. The number of squares obscured by vegetation at each interval as observed from approximately 1 m away were recorded.

A point sample frame was used to measure the ground vegetative density and the percent exposed soil and litter at each site.

Distances between singing sites; distances from singing sites to water, to ecotone or diurnal cover; and area and perimeter of singing sites were determined by pacing or by measuring aerial photos or maps. Slope and aspect were measured with a protractor and compass. Elevation was estimated from a topographic map. Soil pH at each site was measured with a Beckman pH meter. Other soil characteristics (texture, moisture, friability) were subjectively evaluated.

Diurnal Habitat Analysis

Periodically, I conducted intensive searches in habitat along the drainages of the Ecology Preserve and extensive searches in surrounding areas. When woodcock or sign of woodcock were found, major habitat features were recorded.

I searched for broods and nests of woodcock using trained dogs whenever possible. I scheduled the searches on dates when woodcock chicks would have been 1 1/2 to 2 wks old. This was done because of the female

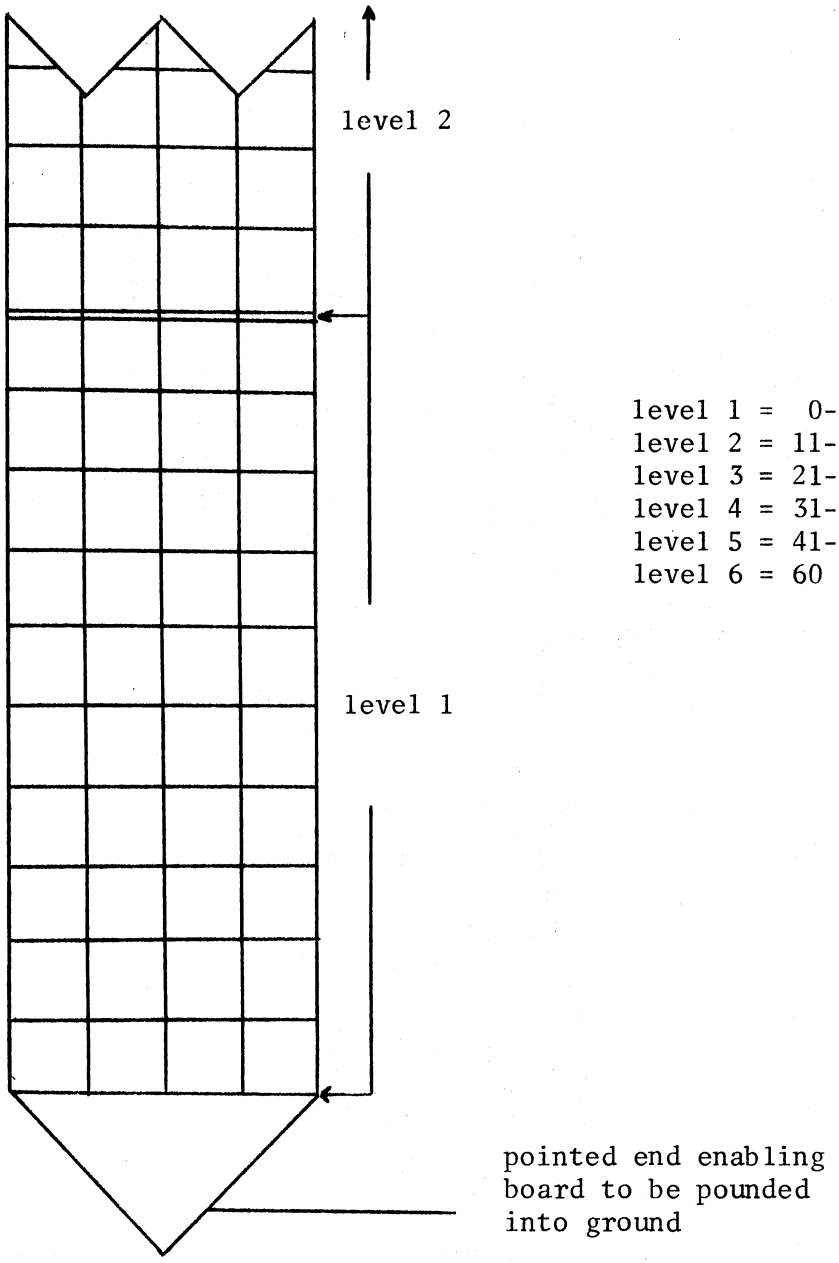


Figure 3. Diagram of density board used to measure aerial vegetation density at singing sites.

woodcock's tendency to abandon her nest after disturbance by dogs or humans, especially during the early stages of incubation (Mendall and Aldous 1943, Amman 1963, Simon et al. 1971). The dates when we searched for chicks and the search effort are: 25 March (4 persons, 2 dogs), 5 April (2 persons, 2 dogs), and 23 April (3 persons, 2 dogs).

Habitat Manipulation

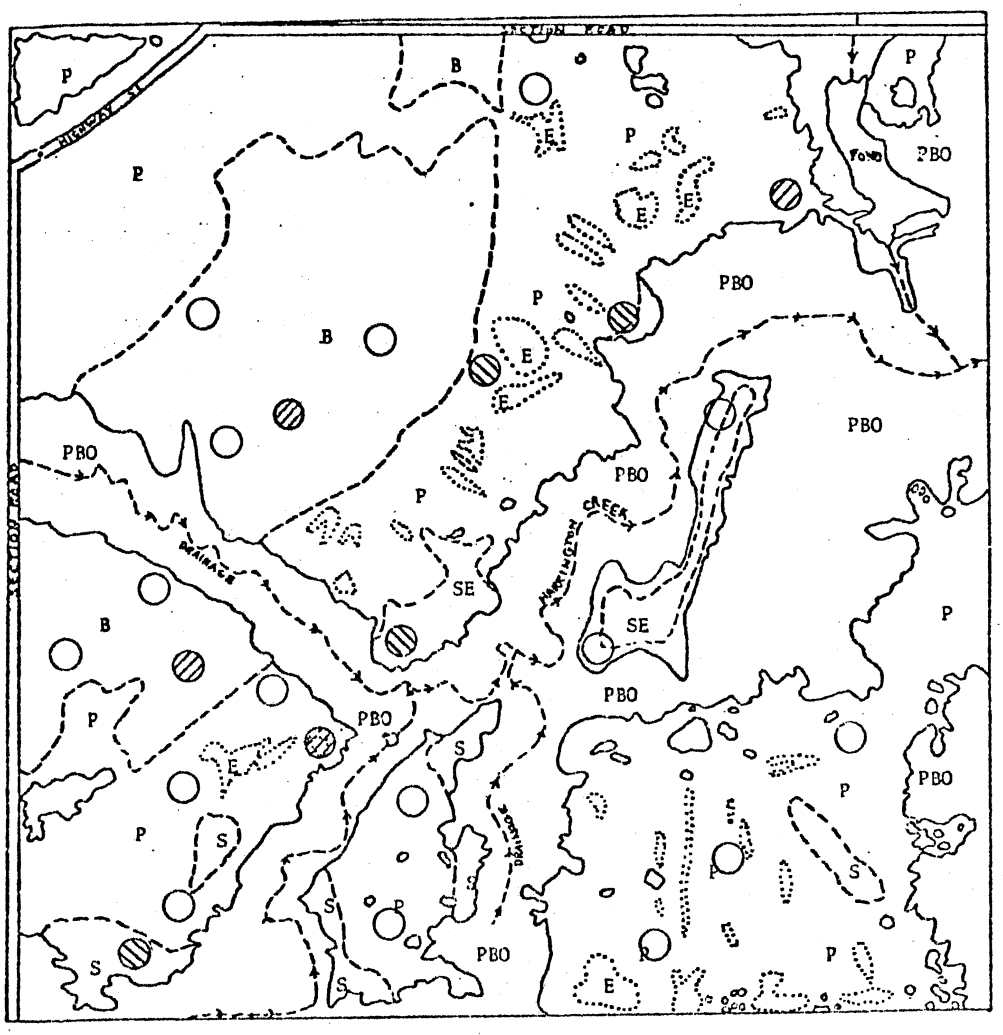
To observe the response of a breeding woodcock population to habitat manipulation, circular to oval plots 18 m in diameter (0.03 ha) were mowed with a brushog in the brushland and grassland areas of the Preserve (Figure 4). In 1974, 19 plots were mowed--16 were new sites and three were singing sites which had decreased in use or were no longer being used by woodcock, presumably due to vegetative succession. In 1975, 20 plots were mowed, including two which had not been mowed in 1974. Three that were mowed in 1974 were not mowed in 1975 (Figure 5).

The plots were observed regularly throughout each breeding season and, if used by woodcock, subjected to the analyses described above.

Seasonal Numbers and Distribution

I made regular searches of potential woodcock habitat in the vicinity of Stillwater throughout the study in an effort to determine presence of woodcock and dates of woodcock migration in northcentral Oklahoma. The shorelines of the following lakes and their tributaries were searched: Ham's Lake, Lake Carl Blackwell, Boomer Lake, Yost Lake, and Lake McMurtry. When woodcock or sign of woodcock were observed, major habitat features were recorded on data sheets.

Figure 4. Aerial view of plots mowed to serve as artificial singing sites on the Ecology Preserve, 1974.



LEGEND:

	B	Brush (Blackjack oak, Red cedar, Roughleaf dogwood, Greenbriar, native grasses)
	E	Eroded sites on prairie
	P	Native tall grass prairie
N	PBO	Post oak-Blackjack oak (some bottomland hardwoods along the creek)
	SE	Sumac clones and Elm
	S	Sumac

Scale 1cm = 61.5m

○ plot mowed both years

⊘ plot mowed only in 1975

⊘ plot mowed only in 1974

Figure 5. Map of the Ecology Preserve showing the plots mowed to serve as artificial singing sites (1974-75).

I solicited information on woodcock sightings from faculty, students, hunters, and conservation groups in the Stillwater area. Self-addressed postcard questionnaires were distributed to the major retail sporting goods stores in Stillwater. The stores agreed to give one postcard out with every hunting license sold.

Summer Habitat Conditions

To determine if drought and lack of invertebrates were influencing the scarcity of woodcock in summer months, I sampled earthworm populations and soil moisture at 15 arbitrarily selected sites along two transects which crossed the better woodcock habitat of the Preserve. The sites were checked biweekly from 22 April to 26 June 1974. Moisture content of the soils was determined by the gravimetric method. To sample earthworms, I saturated 450 cm^2 of soil area with a liter of 0.075 percent formalin solution (Phillipson 1971). After 10 min I collected the worms that emerged and determined their dry weights in the laboratory.

CHAPTER V

RESULTS AND DISCUSSION

Breeding Behavior

Courtship Display

Seasonal and Yearly Variations. The beginning and ending dates of the breeding season of woodcock in northcentral Oklahoma varied 2 to 3 wks since 1970 (Table 1) and appeared to correspond with the spring migration of woodcock through northcentral Oklahoma. With warm January and February temperatures, woodcock migrated northward through Oklahoma earlier and the breeding season occurred earlier (1971 and 1975) than with cold January and February temperatures (1972, 1973, and 1974).

It is possible that male woodcock did not begin courtship displays immediately upon their arrival at singing sites in northcentral Oklahoma. In 1975, I first observed a woodcock at the Ecology Preserve on the evening of 19 January. Every evening from that date to 27 January, I observed what I believed to be the same woodcock fly about 4 to 5 m over the southeast corner of the Preserve. This bird did not perform courtship displays but rather weaved in and out of brush and small open areas as if searching for a suitable singing site. I believe this bird was either an early migrant through northcentral Oklahoma due to the warm weather in early January, or a winter resident in northcentral Oklahoma.

Table 1. Earliest and latest dates and total days of courtship display activity by male woodcock on the Ecology Preserve (1970-75).

Displays Observed	Year					
	1970	1971	1972	1973	1974	1975
Earliest Date	27 Feb.[1]	26 Jan.	12 Feb.[2]	5 Feb.	5 Feb.	27 Jan.
Latest Date	8 Apr.	16 Mar.	29 Mar.	4 Apr.	11 Mar.	23 Mar.
Total Days in Period	41	50	47	59	38	56

[1]Birds first discovered on this date. Earlier displays probable.

[2]Though displays were observed on 26 December 1971, under unseasonably warm temperatures, they were not considered as part of the normal breeding season.

The woodcock breeding season in northcentral Oklahoma was considerably earlier than in other states. Sheldon (1967) reported initial activity in Massachusetts in mid-to-late March and termination of most activity by 1 June. Both times are 6 wks later than the same events in northcentral Oklahoma.

The average length of evening courtship displays by male woodcock in northcentral Oklahoma, from 1971-75, was 19.3 min (Table 2). This time interval is considerably shorter than in more northern latitudes (45 min average in New Brunswick) and approximately the same as in similar latitudes (20 min average in Maryland) (Sheldon 1967).

The average length of courtship displays, average number of peent calls per display, and average number of flights per display from 1971-75 are summarized in Table 2. The variations in display activity from year

Table 2. Average evening courtship display in parameters, (sample size), and total number of male woodcock known to be present on the Ecology Preserve (1970-75).

Average Number	1971	1972	1973	1974	1975	Weighted Average
Length of Display (min)	21.2 (18)	21.3 (17)	18.0 (26)	16.8 (43)	21.1 (52)	19.3 (153)
Calls per Display	206 (16)	166 (17)	198 (27)	174 (45)	234 (44)	198 (148)
Flights per Display	6.8 (19)	4.0 (17)	5.6 (18)	3.6 (47)	4.8 (49)	4.6 (148)
Number of Males Present	5	7	5	4	7	6

to year may have been due to physiological differences among male woodcock, the influence of territorial behavior among male woodcock, or the influence of environmental factors on courtship display behavior of male woodcock.

The number of displaying male woodcock present on the Preserve from 1971-75 varied from 4 to 7 (assuming we banded every bird present each year). Though Table 2 does not show any clear relationship between the number of males present and the intensity of courtship display each year, I observed that on any given night a high number of male displaying woodcock was usually associated with a high intensity of courtship display behavior by male woodcock.

The intensity of evening display activity of male woodcock in all years did not remain constant throughout the breeding season. There were two peaks of courtship display activity (Figures 6, 7, 8, 9). For the courtship parameters, weekly average minutes of dispaly activity, weekly average number of calls, weekly average number of flights, and weekly average percent time spent in flight, a peak usually occurred around the 2nd, 3rd, or 4th week of display (depending on environmental and behavioral factors present each year), and a second peak usually occurred around the 7th or 8th week of display.

Sheldon (1967) also noted a second peak of courtship display activity in the latter part of the breeding season in Massachusetts. However, he alluded more specifically to an increase in the number of singing males and not so much to an increase in the intensity of display activity among the same birds. I believe that on the Ecology Preserve an increase in courtship display intensity at the end of the breeding season is

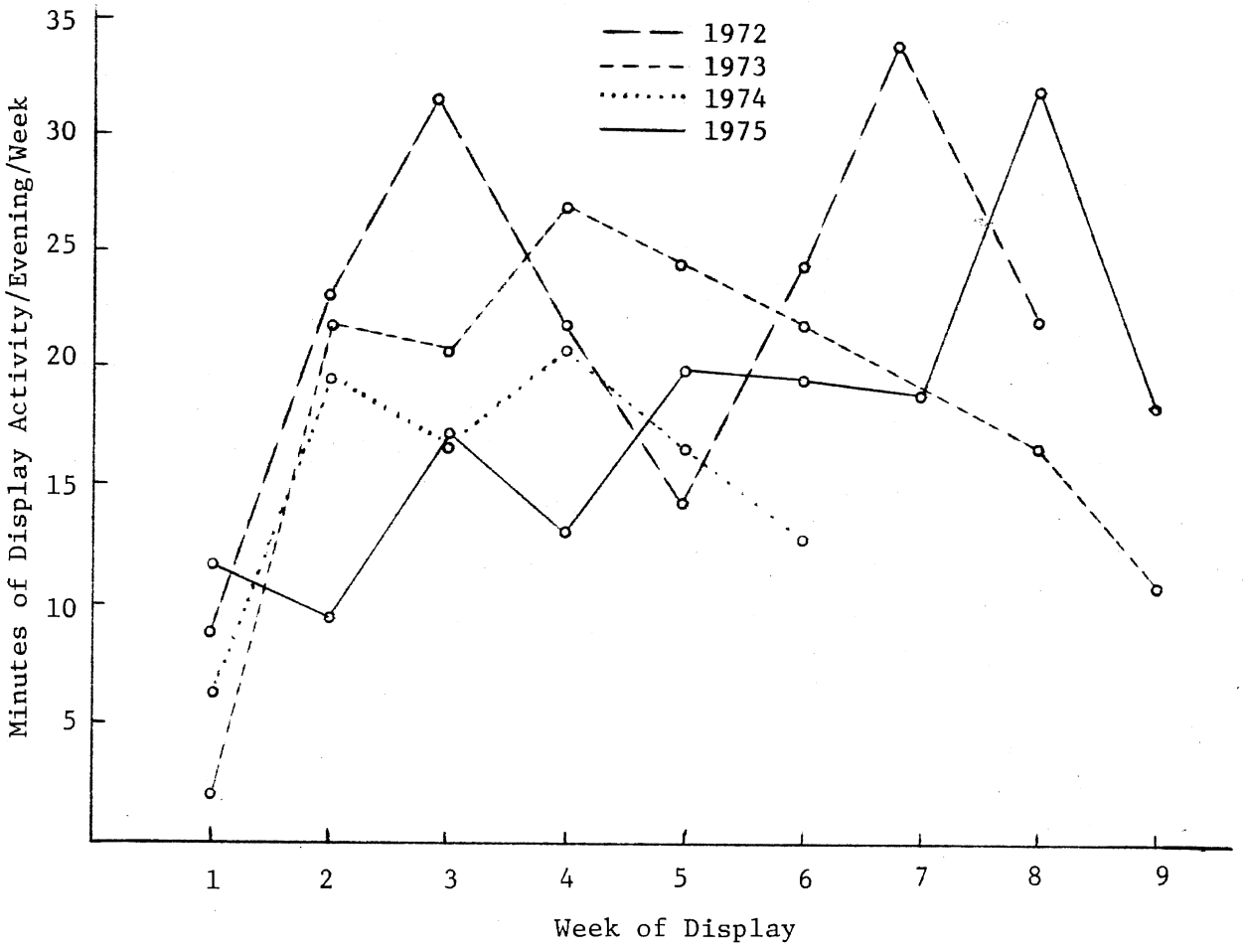


Figure 6. Weekly average duration per evening of courtship display activity by male woodcock on the Ecology Preserve (1972-75).

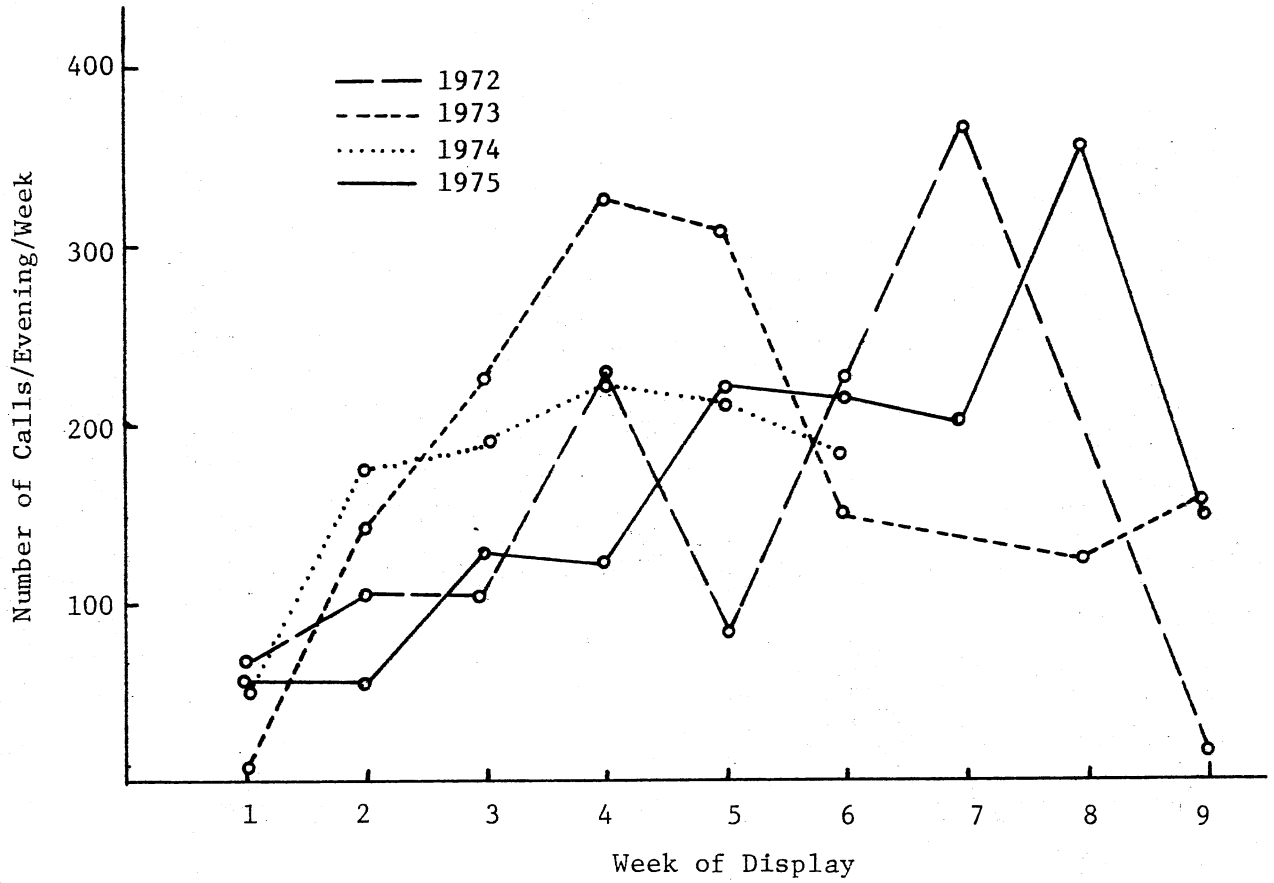


Figure 7. Weekly average number of peent calls per evening of courtship display activity by male woodcock on the Ecology Preserve (1972-75).

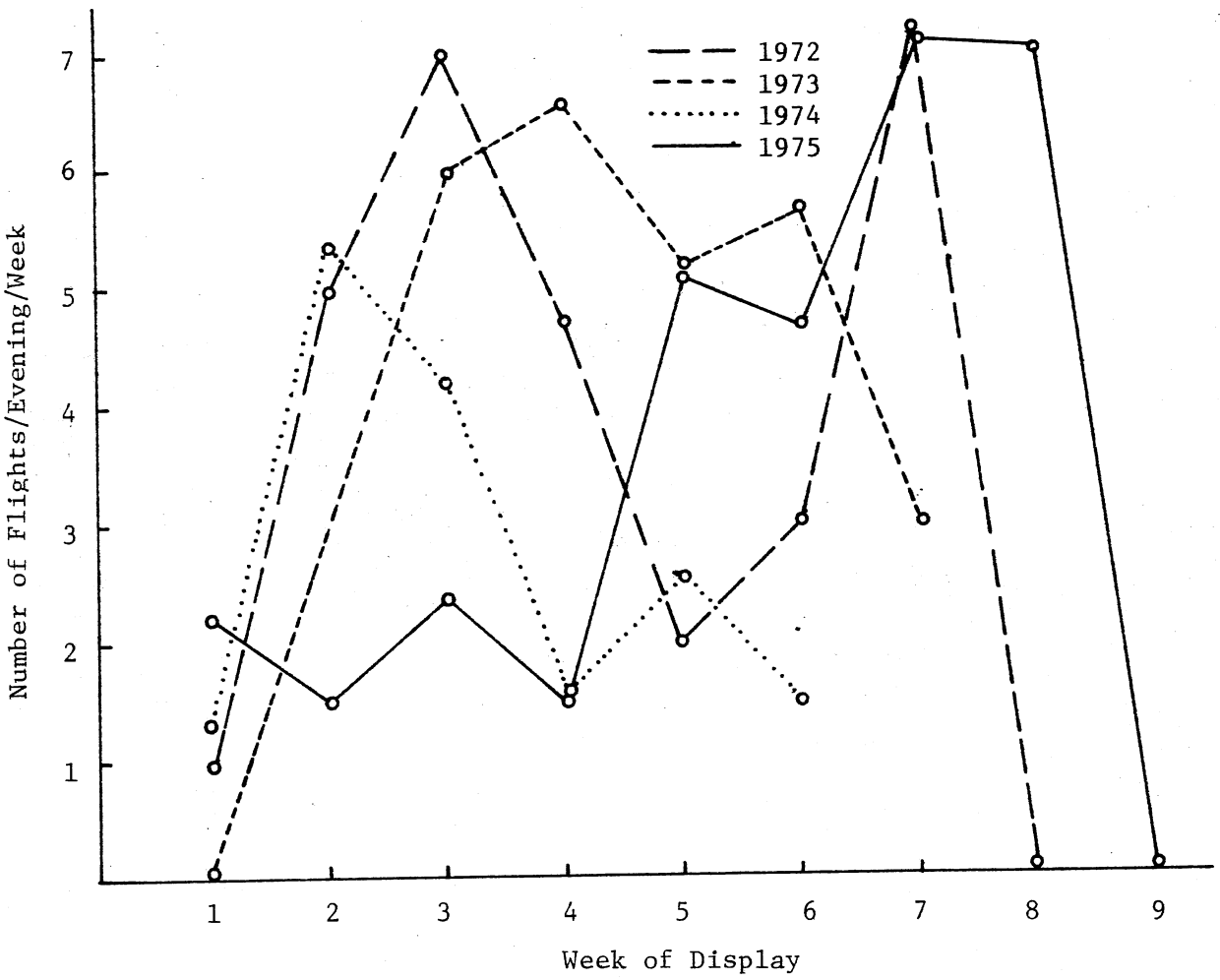


Figure 8. Weekly average number of display flights per evening of courtship display activity by male woodcock on the Ecology Preserve (1972-75).

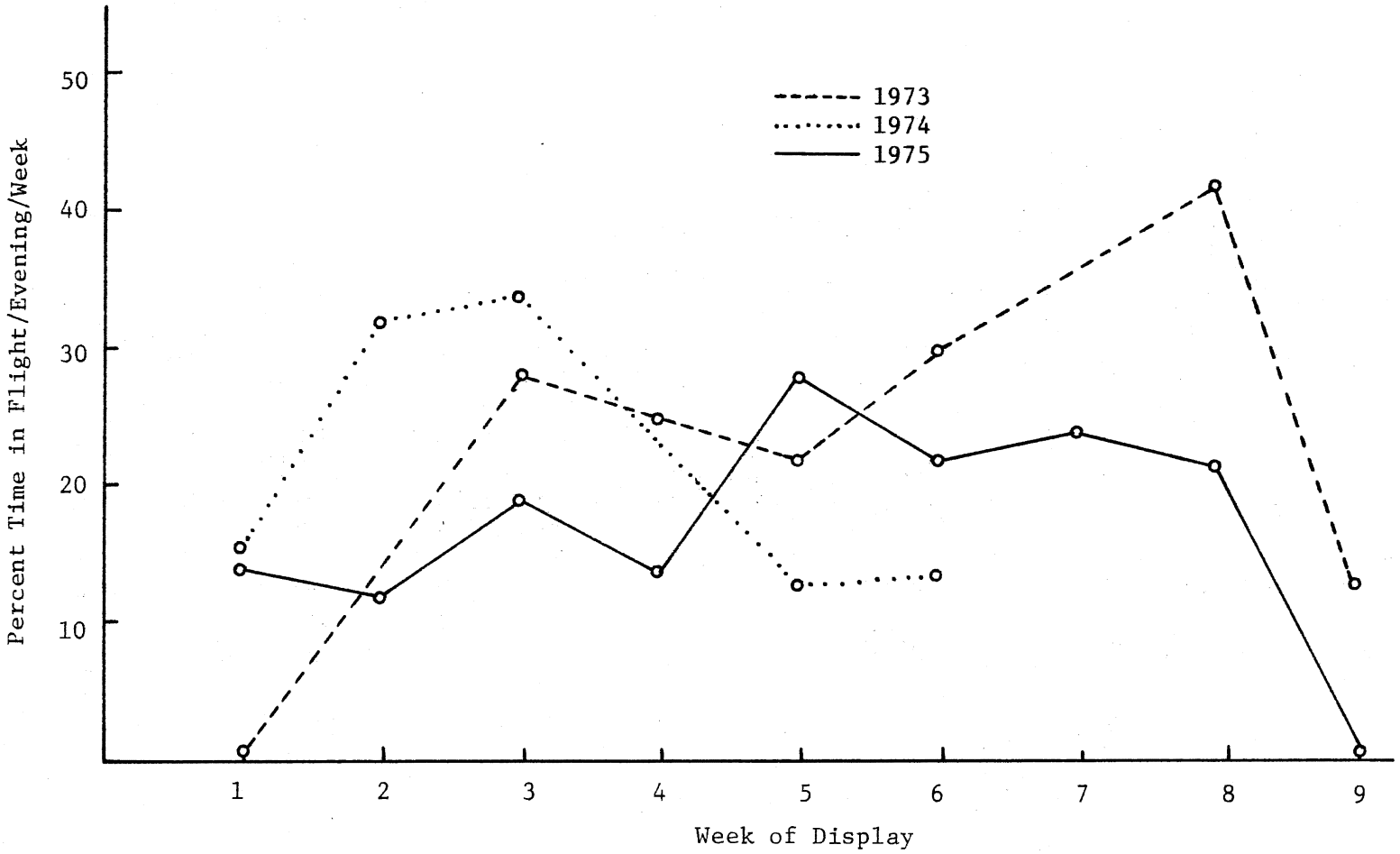


Figure 9. Weekly average % time in flight per evening of courtship display activity by male woodcock on the Ecology Preserve (1973-75).

probably correlated either with renesting attempts or the peak of the hatching season, or both.

Whitcomb (1974) hypothesized that there may be dominant-subdominant male relationships at work throughout the display season with older, dominant birds displaying intensively at the beginning of the season but becoming inactive and being replaced, at singing sites, by younger, subdominant males in the latter part of the season. A change in age ratios of males captured in the latter part of the display season led Whitcomb (1974) to this theory. Although we did not observe such a change in age ratios on the Preserve, our population was very small, and it is possible that Whitcomb's theory has merit. This behavioral change would supply the younger male woodcock with experience in courtship behavior and insure ample opportunity of renesting at the height of the hatch if the first nests failed.

Figures 6 to 9 also illustrate the effects of temperature and other weather factors on display activity of male woodcock. The breeding season in 1974 was only 6 wks long, probably due to the unseasonably warm temperatures in the 5th and 6th weeks of display. The warm weather seems to have "compressed" the entire breeding season, and the two peaks of display appeared during the 2nd and between the 4th and 5th weeks.

In 1975, the early weeks of display were very cold, wet, and snowy. The cool weather had a marked effect on courtship activity, suppressing the intensity of all display parameters. The two peaks of display also appeared quite later: the first occurred the 5th week and the second occurred the 8th week.

In 1974 and 1975, observations were made of morning and evening courtship display behavior. Comparisons between morning and evening courtship displays by male woodcock suggest a greater number of display flights in the mornings ($\bar{X}$ = 6.5, n = 33) than in the evenings ($\bar{X}$ = 4.2, n = 96) (Table 3).

Subtle changes in morning and evening courtship display behavior of male woodcock occurred as the breeding season progressed (Figures 10, 11, 12, 13). In 1974, all display parameters were more intensive in the mornings than in the evenings in the first weeks of courtship display, but the same parameters were more intensive in the evenings than in the mornings in the last weeks of courtship display. In 1975, the opposite situation occurred; all display parameters were more intensive in the evenings than in the mornings in the first weeks of courtship display, but the same parameters were more intensive in the mornings than in the evenings in the last weeks of courtship display.

An explanation for the above phenomenon is difficult at this time because only two years of data were available for comparison, and fewer data were collected on morning courtship displays in 1974 than in 1975. It seems, however, that a shift in intensity of courtship display behavior from mornings to evenings as the breeding season progresses indicates a complex interaction of behavioral, physiological, and environmental factors at work. Such factors as temperature during the day, temperature during the evening, moisture conditions, and availability of food may interact to produce physiological and behavioral stress on male woodcock, thus affecting the intensity of their courtship displays on a seasonal basis.

Table 3. Average courtship display parameters and (sample size) in evenings and mornings on the Ecology Preserve (1974-75).

Average Number	1974	1975	Weighted Average	1974	1975	Weighted Average
Length of Display (min)	16.8 (43)	21.1 (52)	19.2 (95)	21.2 (12)	21.8 (29)	21.6 (41)
Calls per Display	174 (45)	234 (44)	189 (96)	205 (11)	234 (24)	225 (35)
Flights per Display	3.6 (47)	4.8 (49)	4.2 (96)	6.6 (22)	6.6 (22)	6.5 (33)

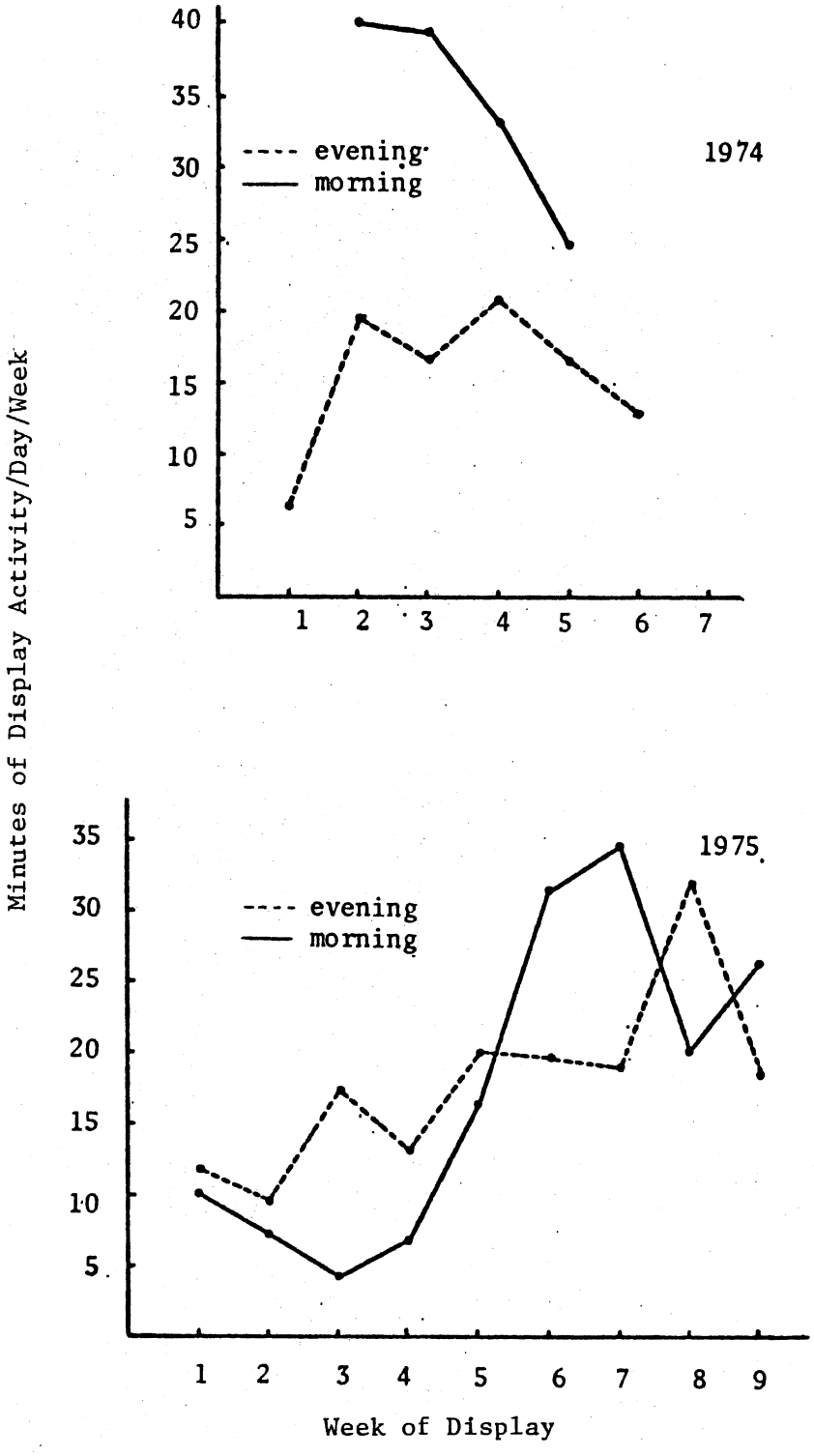


Figure 10. Comparison between weekly average duration per evening and weekly average duration per morning of courtship display activity by male woodcock on the Ecology Preserve (1974-75).

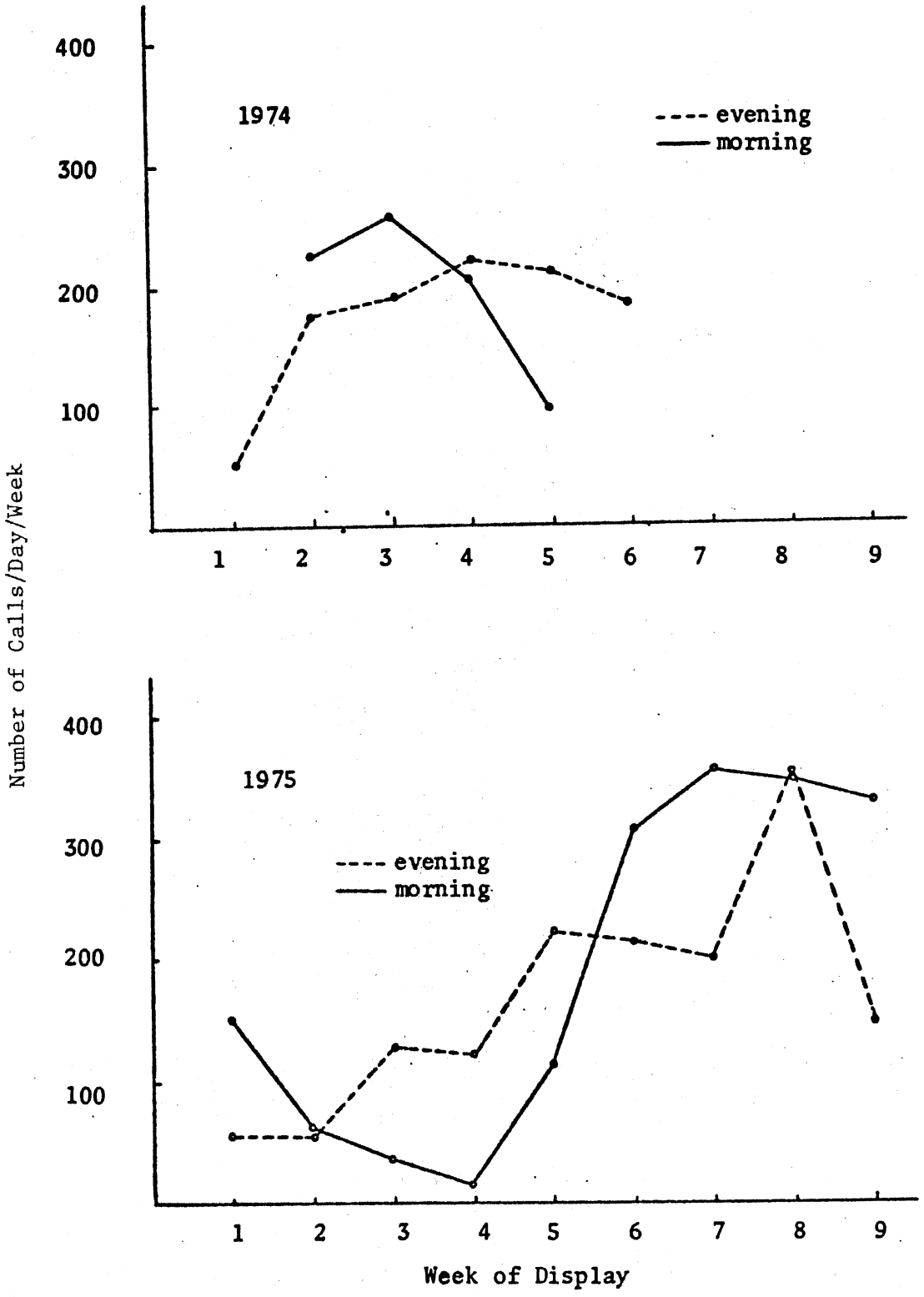


Figure 11. Comparison between weekly average number of peent calls per evening and weekly average number of peent calls per morning of courtship display activity by male woodcock on the Ecology Preserve (1974-75).

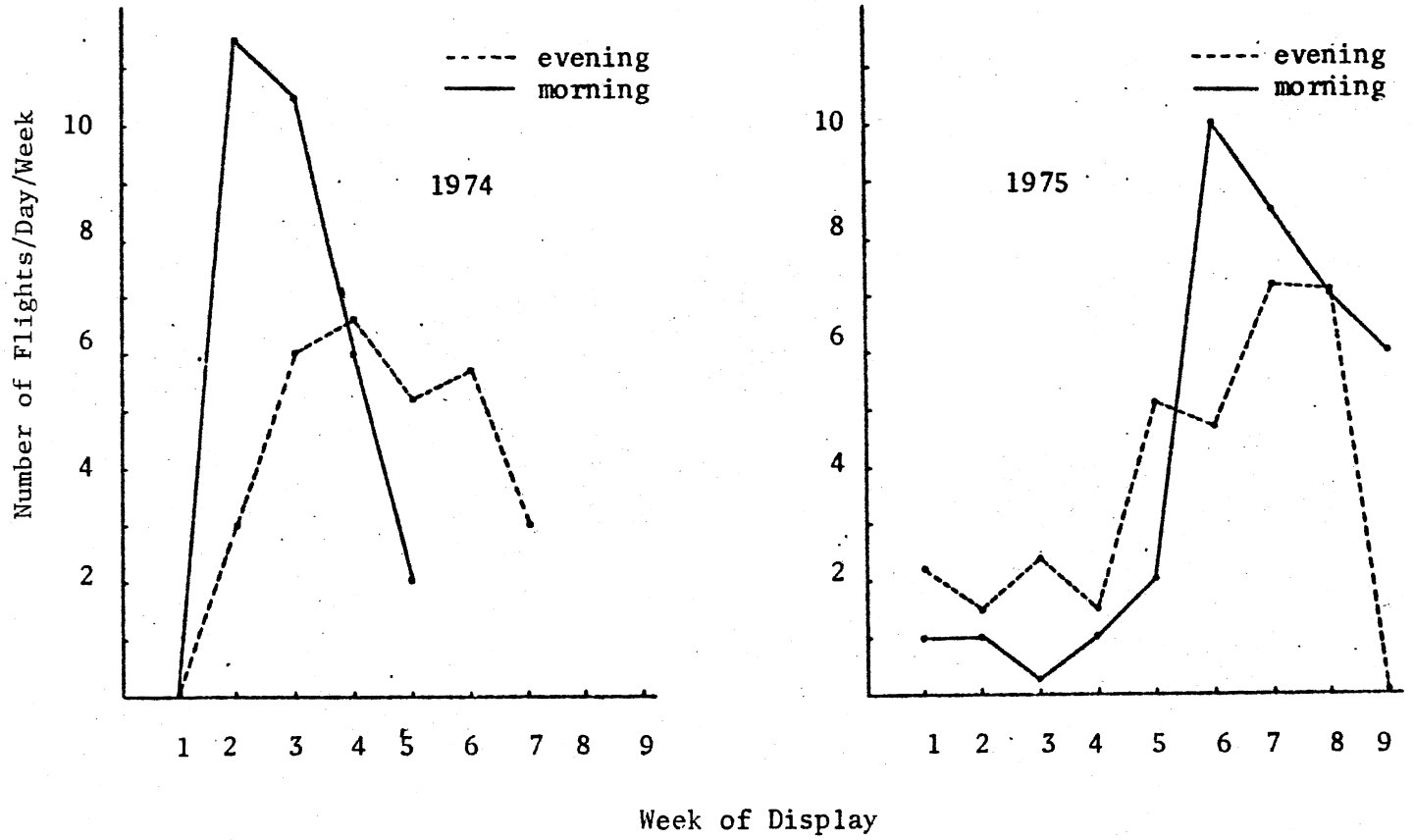


Figure 12. Comparison between weekly average number of flights per evening and weekly average number of flights per morning of courtship display activity by male woodcock on the Ecology Preserve (1974-75).

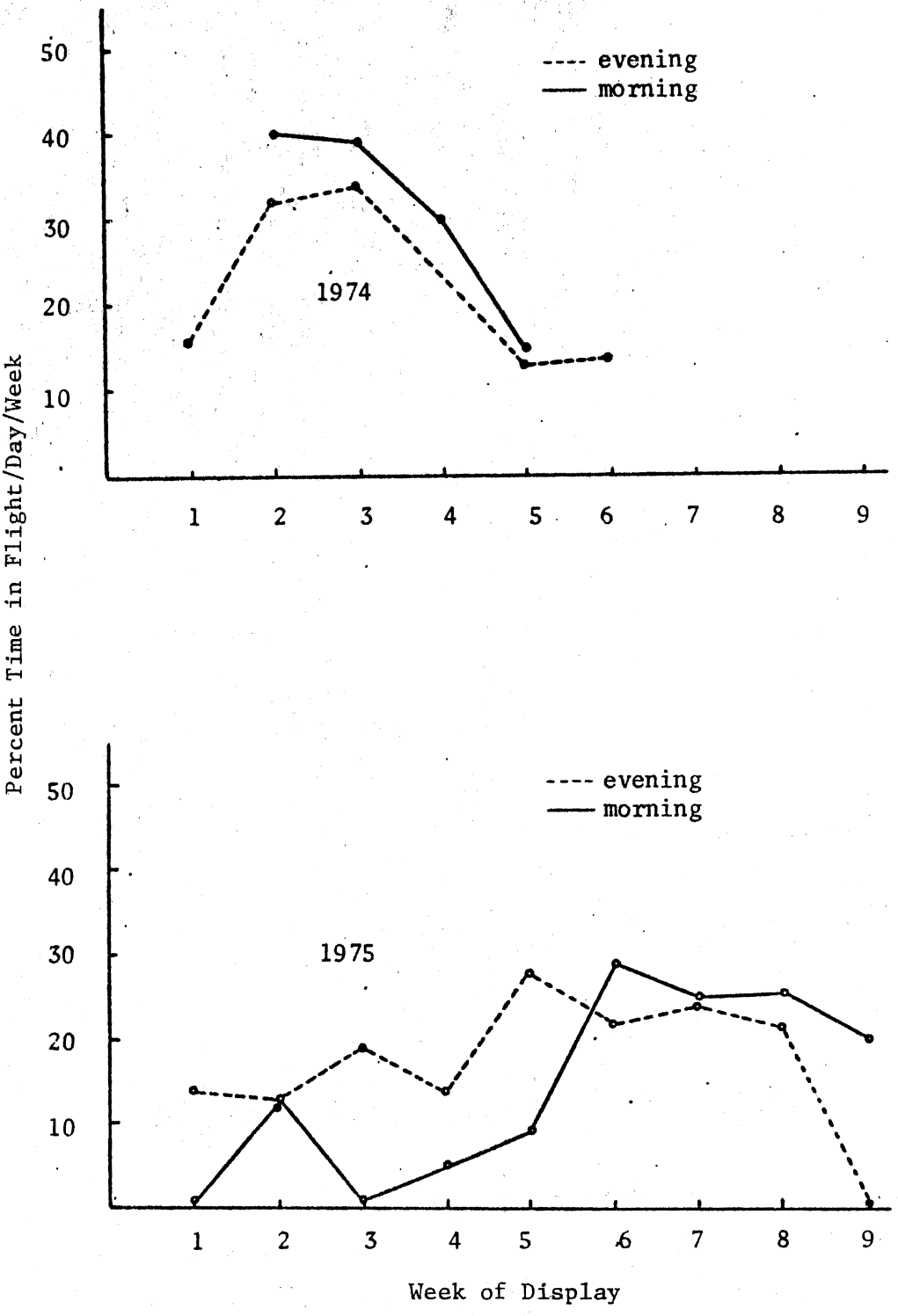


Figure 13. Comparison between weekly average % time in flight per evening and weekly average % time in flight per morning of courtship display activity by male woodcock on the Ecology Preserve (1974-75).

Meteorological and Courtship Parameters. The results of the effects of meteorological factors on courtship display behavior of male woodcock (Tables 4, 5, and 6), in most cases, supported the observations of previous researchers.

Of all the meteorological factors examined, temperature seemed to have the most pronounced effects on display activity. Early in the breeding season, low temperatures, especially below freezing, curtailed nearly all display activity. However, later in the breeding season, male woodcock performed "normal" courtship displays at temperatures as low as -10°C.

Correlation analyses indicated that low temperatures were significantly ($P \leq 0.005$) correlated with decreased intensity of nearly all courtship display parameters in evening and morning courtship display performances by male woodcock (Table 4). Analyses of variance indicated that temperatures below 0°C resulted in significantly less time spent in flight, time spent on the ground at the singing site, percent time spent in flight, number of flights, and number of peent calls by male woodcock ($P \leq 0.025$, 0.025, 0.005, 0.005, and 0.010 respectively for morning courtship displays and all at $P \leq 0.005$ for evening courtship displays) (Table 5). These findings were in general agreement with studies in Michigan by Goudy (1960) and by Blankenship (1957, see Sheldon 1967) where 5°C and 2°C respectively were reported to be the critical temperatures below which male woodcock would not perform courtship displays.

Wind speed did not seem to influence the courtship display behavior of male woodcock during evening and morning displays. Correlation analyses of variance, factor analyses of principal components, and graphs

Table 4. Correlation analyses between meteorological and male woodcock courtship display parameters on the Ecology Preserve, mornings (1974-75) and evenings (1972-75).

	Mornings						Evenings					
Parameters	Time in Flight	Time on Ground	Total Time	% Time in Flight	Number of Calls	Number of Flights	Time in Flight	Time on Ground	Total Time	% Time in Flight	Number of Calls	Number of Flights
Temperature at Beginning	47[1] + ***	47 + *	57 + ***	48 + ***	48 + *	49 + ***	127 + *	128 + *	139 + *	118 +	126 + ***	138 + ***
Temperature at End	47 + ***	47 + *	57 + ***	48 + ***	48 + *	49 + ***	125 +	124 + ***	136 + ***	117	126 + ***	136 + *
Maximum Temperature	44 + ***	44 + ***	54 + ***	44 +	46 +	47 +	127	126 + ***	138 + **	122 +	123 + ***	132
Minimum Temperature	44 + ***	44 + *	54 + ***	44 + **	46 +	47 + *	127	126 + ***	138 + ***	122	123 + ***	132 +
Wind Speed	35 + *	35	45 +	36 + *	36	37 + *	124	125	136	123	123	131
Wind Direction	46 + ***	46 + ***	55 + ***	47 + ***	47 + ***	48 + ***	128	129	140	123	125	135 + *
Humidity at Beginning	46	46	56	47	47	48	101 -	102 - ***	113 - ***	96	101 - ***	112 - *

Table 4 (Continued).

Parameters	Mornings						Evenings					
	Time in Flight	Time on Ground	Total Time	% Time in Flight	Number of Calls	Number of Flights	Time in Flight	Time on Ground	Total Time	% Time in Flight	Number of Calls	Number of Flights
Humidity at End	46	46	56	47	47	48	100	100 - ***	112 - **	95	103 - ***	112
% Cloud Cover	46	46	56	46	46	47	134	134	146 -	127	134 - *	144
Visibility	45	45	55	45	45	46	134 +	135	146 + *	130 + *	133 + **	142
Barometric Pressure	46	46	56	47 -	47	48 -	131 - ***	130 - ***	142 - ***	128 - ***	128 - ***	136 - ***
Barometer Rising	46 + *	46	56 + *	47	47	48 +	134	134	145	131	132	141
Day of Moon	47	47	57	48 +	48	49 + *	105	105 -	117	102	106	115 -
Quarter of Moon	47	47	57	48	48	49	105	105	117	102	106	115 - *

Table 4 (Continued).

Parameters	Mornings						Evenings					
	Time in Flight	Time on Ground	Total Time	% Time in Flight	Number of Calls	Number of Flights	Time in Flight	Time on Ground	Total Time	% Time in Flight	Number of Calls	Number of Flights
Precipitation	40	40	49	41	40	40	118	119	131	119	117	124
							+	+	+	+	+	+
									*	***	***	
Ground Moisture	47	47	57	47	47	47	138	138	150	135	136	145
	+	+	+	+	+	+	+	+		+	+	
		*	***	*	***		*			*		
Week of Display	47	47	57	48	48	49	133	132	144	128	129	138
		+	+		+	+	+	+	+		+	+
		***	***		***	***	*	***	***		***	***

[1]Number of observations.

+ = positive correlation, - = negative correlation, * = significant to 0.05, ** = significant to 0.01, *** = significant to 0.005, no asterisk = significant only to 0.1.

Table 5. Analyses of variance between meteorological and male woodcock courtship display parameters on the Ecology Preserve, mornings (1974-75) and evenings (1972-75).

Time Period and Condition	Parameter Averages	n	F	Level of Significance
MORNING:				
Temperature (°C)	Time in flight (sec)			
≤ 0	213	20	7.09	0.025
> 0	579	27		
	Time on ground (sec)			
≤ 0	416	20	6.77	0.025
> 0	850	27		
	% Time in flight			
≤ 0	7	20	22.67	0.005
> 0	25	28		
	Number of flights			
≤ 0	2	21	10.10	0.005
> 0	6	28		
	Number of calls			
≤ 0	96	21	8.40	0.010
> 0	206	27		
EVENING:				
Temperature (°C)	Time in flight (sec)			
≤ 0	53	14	14.03	0.005
> 0	251	106		
	Time on ground (sec)			
≤ 0	114	14	21.00	0.005
> 0	798	106		

Table 5 (Continued).

Time Period and Condition	Parameter Averages	n	F	Level of Significance
EVENING (Con't.)				
Temperature (°C)	% Time in flight			
≤ 0	6	12	14.90	0.005
> 0	22	100		
	Number of flights			
≤ 0	1	16	13.65	0.005
> 0	4	116		
	Number of calls			
≤ 0	29	15	25.82	0.005
> 0	193	106		
Cloud cover (%)	Time on ground (sec)			
< 95	811	95	5.90	0.025
≥ 95	551	39		
	Number of calls			
< 95	194	98	8.02	0.010
≥ 95	124	36		
Barometric Pressure	Time in flight (sec)			
Rising	302	31	6.47	0.025
Falling	680	15		
	Number of flights			
Rising	3.4	31	3.08	0.100
Falling	5.8	17		

Table 5 (Continued).

Time Period and Condition	Parameter Averages	n	F	Level of Significance
EVENING (Con't.)				
Humidity	Time in flight (sec)			
Rising	180	27	4.52	0.050
Falling	274			
	Time on ground (sec)			
Rising	457	27	5.99	0.025
Falling	777	66		
	% Time in flight			
Rising	16	26	5.44	0.025
Falling	24	62		
	Number of calls			
Rising	98	26	11.99	0.005
Falling	194	69		
MORNING:				
Cloud Cover (%)	Time before sunrise (min)			
< 95	32.4	42	1.87	
≥ 95	24.7	18		
EVENING:				
Cloud Cover (%)	Time after sunset (min)			
< 95	12.0	134	19.74	0.005
≥ 95	5.87	45		

Relationships which were not significant ($P \leq 0.05$) are not included.

Table 6. Factor analyses of principal components of meteorological and male woodcock courtship display parameters on the Ecology Preserve, mornings (1974-75) and evenings (1972-75).

Factor	Variable	Coefficient
1	High temperature at beginning	+0.795
	High temperature at end	+0.751
	West, southwest to south winds	+0.524
	Humidity at beginning	-0.605
	Humidity at end	-0.598
	Maximum temperature for day	+0.687
	Minimum temperature for day	+0.534
	Time on ground	+0.652
	% time in flight	+0.579
	Number of flights	+0.561
	Number of calls	+0.719
	Number of birds	+0.558
2	Humidity at beginning	+0.584
	Humidity at end	+0.614
	Visibility	-0.489
	Precipitation (- = wet, + = dry)	-0.500
	Time of day (- = morning, + = night)	-0.499
	Time after sunset or before sunrise)	+0.575
	Time in flight	+0.632
	Number of flights	+0.643
	Number of calls	+0.424
	Time on ground	+0.413
6	Week of display	-0.374
	Half moon	+0.558
	New moon	-0.520
	Time of day	+0.392
	Number of birds	+0.347
	Territorial conflict	+0.301
7	Week of display	+0.557
	Time in flight	-0.312
	Time on ground	+0.350
	% time in flight	-0.358
	Number of calls	+0.373
8	North, northeast to east winds	-0.436
	% cloud cover	+0.184
	Falling barometric pressure	+0.212
	Dry ground conditions	+0.550
	Full moon	+0.427
	Time in flight	+0.169
	% time in flight	+0.141
	Number of flights	+0.173
	Territorial conflict	-0.213

of the effect of wind speed on courtship display behavior of male woodcock supported this conclusion.

The influence of wind direction on courtship display behavior of male woodcock seemed to be important, particularly in the mornings, with south winds promoting more intensive display performances than north winds. Correlation analyses indicated that in the mornings south winds were very significantly ($P \leq 0.005$) correlated with a greater time spent in flight, time spent on the ground at the singing site, total display time, percent time spent in flight, number of peent calls, and number of flights by male woodcock than during other wind directions (Table 4). A similar correlation was not obtained for evening courtship display performance.

Table 7 further illustrates the relationship between wind direction and courtship display behavior of male woodcock. In the mornings, there seemed to be a trend towards less time spent in flight, less time spent on the ground at the singing site, a smaller percentage of time spent in flight, fewer flights, and fewer calls by displaying male woodcock during north, northwest and west wind directions (Category 1, Table 7) than during other wind directions. Least significant difference tests showed significant differences ($P \leq 0.05$) between wind direction categories 1 and 2 for all five courtship display parameters in morning display performances. No significant differences ($P \leq 0.05$) were present between wind direction categories 2 and 3, 3 and 4, and 2 and 4 for all courtship display parameters in morning display performances. Significant differences ($P \leq 0.05$) were present between wind direction categories 1 and 2, 1 and 3, and 1 and 4 for the display parameters time

Table 7. Averages of male woodcock courtship display parameters at different wind direction categories on the Ecology Preserve, mornings (1974-75) and evenings (1972-75).

Wind Direction[1]	Parameter Averages (Number of Observations)				
	Time in Flight (sec)	Time on Ground (sec)	% time in Flight	Number of Flights	Number of Calls
Mornings:					
1	158 (22)	299 (22)	7.9 (24)	2.0 (24)	77 (23)
2	606 (17)	867 (17)	25.5 (18)	5.8 (17)	200 (17)
3	657 (4)	1205 (4)	26.5 (4)	8.8 (4)	304 (4)
4	1028 (3)	1153 (3)	23.3 (3)	7.3 (3)	285 (3)
Evenings:					
1	178 (47)	577 (49)	17.6 (45)	2.9 (51)	128 (48)
2	273 (40)	852 (41)	25.9 (40)	3.8 (44)	209 (40)
3	210 (20)	811 (20)	21.4 (20)	4.2 (20)	224 (18)
4	249 (21)	572 (19)	18.3 (18)	4.2 (20)	148 (18)

[1]Wind directions were grouped in four categories: 1 = N, W, and NW (wind directions associated with recent frontal passages, low temperatures and rising barometric pressure); 2 = S and SW (wind directions associated with warm weather); 3 = NE, E, and SE (wind directions associated with stormy weather); 4 = calm.

spent on the ground at the singing sites and time spent in flight by displaying male woodcock.

In the evenings, the influence of wind direction on courtship display behavior by male woodcock seemed to be less than in the mornings. In the evenings, no significant differences ($P \leq 0.05$) were present between any wind direction categories for the courtship parameters time spent in flight, time spent on the ground at the singing site, percentage of time spent in flight, and number of flights by displaying male woodcock. Significant differences ($P \leq 0.05$) were present between wind direction categories 1 and 2, and 1 and 3 for the number of peent calls by male woodcock.

Though statistical analyses showed discrepancies between the influences of wind direction on the courtship display behavior of male woodcock in morning and evening courtship displays, it was my experience that the intensity of courtship display performance was low when north, northwest, and west winds (associated with recent cold weather frontal passages) were present.

Warm weather frontal passages, on the other hand, seemed to intensify courtship display activity by male woodcock. Factor 8 (Table 6) indicated that oncoming warm fronts (winds from the north, northeast or east, and a falling barometric pressure) were associated with a high number of flights, more time spent in flight and little territorial conflict among displaying male woodcock.

The relationship between humidity and courtship displays by male woodcock appeared to be different during evenings than during mornings. Correlation analyses indicated that in the evenings, high humidity was correlated with significantly less time spent on the ground at the

singing site, total display time, and number of peent calls by male woodcock ($P \leq 0.05$) (Table 4). Analyses of variance also showed that in the evenings, time spent in flight, time spent on the ground at the singing site, percentage of time spent in flight, and number of calls by displaying male woodcock were significantly less ($P \leq 0.050$, 0.025, 0.025, and 0.005 respectively) when the humidity was rising than when it was falling (Table 5).

Though correlation analyses and analyses of variance indicated no significant ($P \leq 0.05$) relationships between humidity and courtship behavior in the mornings (Tables 4 and 5), the principal components analysis indicated that humidity may have an opposite affect on courtship displays by male woodcock in the mornings than in the evenings. Factor 2 (Table 6) indicated that mornings with high humidity, low visibility, and either misty, drizzly, or foggy conditions were associated with an overall increase in courtship display intensity by displaying male woodcock. This relationship is more in agreement with my personal observations. On misty, foggy, drizzly mornings I observed that woodcock displayed markedly longer and more intensively than on clear, dry mornings. Perhaps the increased intensity of courtship display behavior by male woodcock on foggy or drizzly mornings was due to the fact that under these weather conditions, the light intensity triggering and conducive to male woodcock display behavior lingered longer.

The influences of 10 sky conditions or visibility classes (snow, hail, sleet, rain, mist, fog, dust, smoke, haze, and clear--numbered 1-10 consecutively in the correlation analysis) on the courtship display behavior of male woodcock differed during the evenings than during

the mornings. In the evenings, clear or slightly hazy skies (high visibility) were significantly correlated ($P \leq 0.05$) with long display times, high percentage of time spent in flight, and a high number of peent calls made by displaying male woodcock (Table 4).

Table 8 further illustrates the relationships between sky conditions and courtship display behavior of male woodcock. In the evenings, analyses of variance (least significant difference tests) indicated that the number of peent calls, the percentage of time spent in flight and the time spent on the ground at the singing site by displaying male woodcock were significantly less ($P \leq 0.05$) in snow, sleet, or hail conditions than in hazy or clear conditions.

Correlation analyses and analyses of variance did not show any significant ($P \leq 0.05$) relationships between different sky conditions and the intensity of courtship display behavior by male woodcock in the mornings (perhaps due to the small number of observations made of morning courtship displays). However, my personal observations were that male woodcock performed normal courtship displays unless there were heavy snows, sleet, hail, or rain which virtually curtailed all courtship activity in both evenings and mornings.

The relationship between ground moisture at the singing site and courtship display behavior of male woodcock was similar in both mornings and evenings. Correlation analyses indicated that moist or dry sites were significantly ($P \leq 0.05$) correlated with a high intensity of nearly all courtship parameters in morning and evening courtship displays by male woodcock (Table 4). (Four ground moisture classes were analyzed on each singing site: snow, wet, moist, and dry--numbered 1-4 consecutively.) Table 9 also suggests that greater intensity of courtship

Table 8. Averages of male woodcock courtship display parameters at different sky conditions on the Ecology Preserve, mornings (1974-75) and evenings (1972-75).

Sky Condition	Parameter Averages (Number of Observations)				
	Time in Flight (sec)	Time on Ground (sec)	% time in Flight	Number of Flights	Number of Calls
Mornings:					
Snow, Sleet, or Hail	0 (2)	0 (2)	0.0 (2)	0.0 (2)	0 (2)
Fog	551 (12)	952 (12)	6.3 (13)	6.3 (13)	205 (13)
Haze	1022 (2)	992 (2)	12.0 (2)	12.0 (2)	258 (2)
Clear	370 (24)	666 (24)	3.9 (23)	3.9 (23)	169 (23)
Evenings:					
Snow, Sleet, or Hail	0 (4)	0 (4)	0.0 (4)	0.0 (4)	0 (4)
Rain	200 (6)	943 (6)	14.0 (6)	3.1 (7)	140 (6)
Fog	299 (5)	598 (5)	21.0 (5)	5.8 (5)	142 (5)
Haze	216 (8)	1164 (8)	16.0 (8)	4.0 (9)	277 (9)
Clear	250 (95)	795 (96)	23.0 (96)	4.0 (99)	195 (93)

Table 9. Averages of male woodcock courtship display parameters at different singing site moisture conditions on the Ecology Preserve, mornings (1974-75) and evenings (1972-75).

Ground Moisture	Parameter Averages (Number of Observations)				
	Time in Flight (sec)	Time on Ground (sec)	% time in Flight	Number of Flights	Number of Calls
Mornings:					
Snow	0 (4)	0 (4)	10.0 (4)	0.0 (4)	0 (4)
Wet	440 (29)	636 (29)	19.0 (29)	4.2 (31)	151 (30)
Moist	439 (13)	919 (13)	19.0 (13)	5.7 (12)	236 (12)
Dry	1425 (1)	860 (1)	40.0 (1)	12.0 (1)	207 (1)
Evenings:					
Snow	8 (5)	183 (5)	5.6 (5)	1.6 (5)	51 (5)
Wet	222 (76)	729 (77)	21.0 (75)	3.6 (81)	17 (75)
Moist	235 (35)	777 (35)	22.0 (32)	3.9 (34)	188 (34)
Dry	304 (22)	849 (21)	25.0 (25)	4.3 (25)	202 (22)

display behavior by male woodcock occurred on moist to dry sites than on wet to snow covered sites. Perhaps the greater intensity of courtship behavior on moist to dry sites can be attributed to the greater comfort to and facility in feeding by male woodcock on these sites as opposed to snow or water covered sites.

The influence of percentage of cloud cover on courtship behavior of male woodcock seemed to be minimal and more evident for evening displays than for morning displays (Tables 4 and 5). In the evenings, male woodcock spent significantly ($P \leq 0.025$) less time on the ground and made fewer ($P \leq 0.01$) peent calls under cloud cover greater than or equal to 95 percent as opposed to cloud cover less than 95 percent (Table 5).

Male woodcock began their courtship displays significantly earlier ($P \leq 0.005$) in evenings with more than 95 percent cloud cover than in evenings with less than 95 percent cloud cover (Table 5). This relationship between cloud cover and initiation of courtship displays by male woodcock supports the conclusions of Leopold and Eynon (1961) that light intensity is the controlling factor in initiating courtship displays by woodcock.

Further illustration of the influence of light intensity on the initiation of courtship displays by male woodcock is shown in Figure 14. Woodcock began their evening courtship displays approximately 20 to 30 min after sunset and their morning courtship displays approximately 20 to 30 min before sunrise.

The relationship between barometric pressure and the courtship display behavior of male woodcock was unclear. Correlation analyses indicated that in the evenings high barometric pressures were significantly correlated ($P \leq 0.005$) with decreased intensity of all courtship

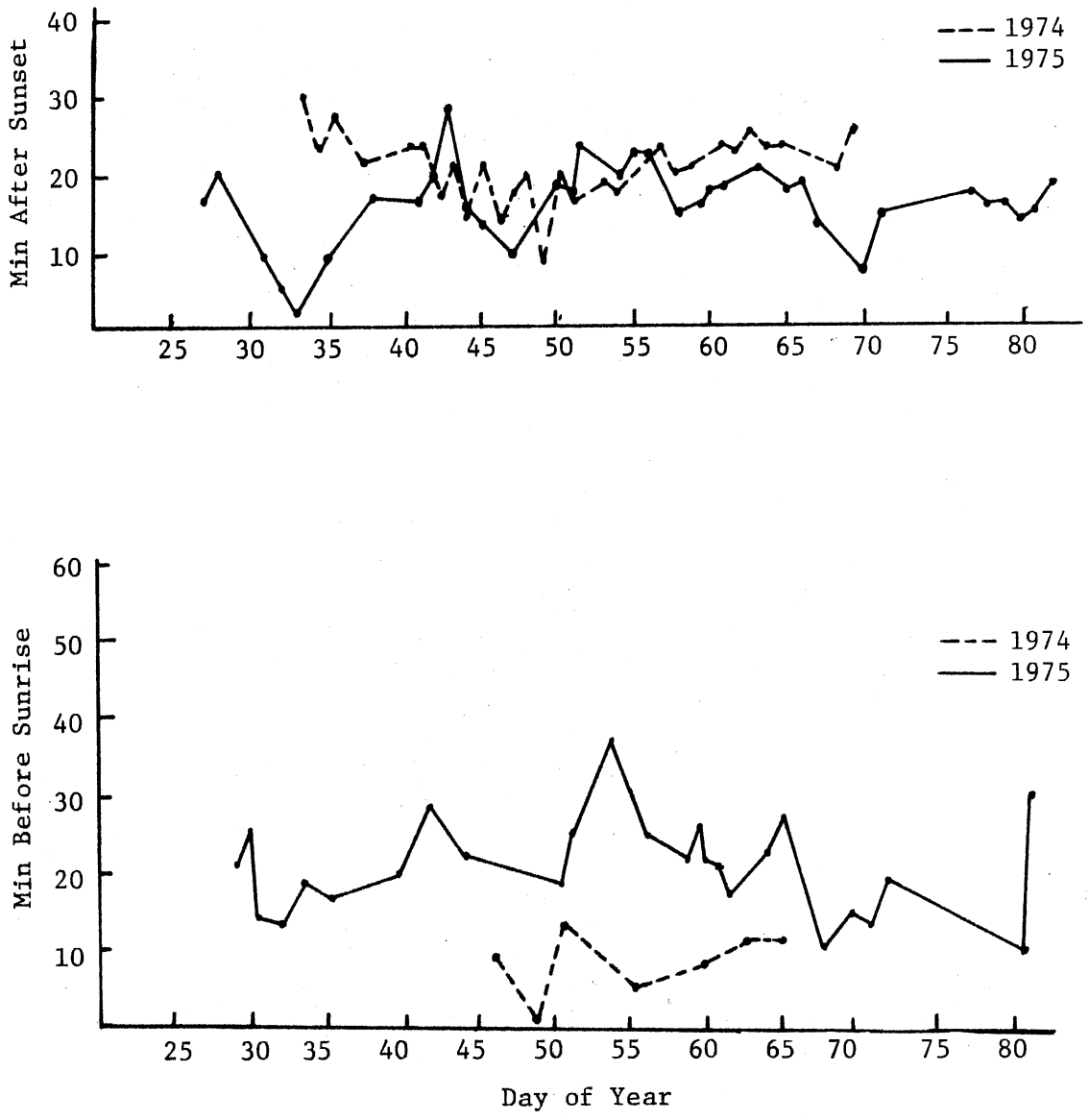


Figure 14. Time at which courtship display activity by male woodcock on the Ecology Preserve began after sunset and ended before sunrise (1974-75).

parameters (Table 4). This relationship was not evident in morning displays (perhaps due to the small number of observations of courtship display behavior in the mornings). Analyses of variance yielded no significant relationships ($P \leq 0.05$) between barometric pressure and the intensity of courtship display behavior by male woodcock.

Both correlation analyses and analyses of variance indicated no significant relationships ($P \leq 0.05$) between rising or falling (as opposed to high and low) barometric pressure and courtship behavior of male woodcock.

I believe barometric pressure was probably important only as a function of the passage of weather fronts.

The influence of moon phase and day of the moon on the courtship display behavior of male woodcock appeared to be minor. Three categories of moon phase were arbitrarily designated as follows: full moon = day 10 to day 16; quarter moon = day 3 to day 9, and day 17 to day 25; and new moon = day 0 to day 2, and day 26 to day 28. Correlation analyses and analyses of variance did not indicate that moon phase or day of the moon significantly ($P \leq 0.05$) affected any courtship parameter. This was in contrast to observations made by Sheldon (1967) in Massachusetts where male woodcock often displayed erratically throughout moonlit nights. On my study area, in 1974, the peak of display activity by male woodcock coincided with the period of a full moon, but I believe this was a coincidence. In 1975, the peak of woodcock courtship display activity coincided with a new or quarter moon.

To determine the influences of <u>combinations</u> of meteorological factors on courtship display behavior by male woodcock, the factor analysis of principal components proved useful. The interpretation of the results

of an analysis of this type is somewhat subjective, yet the analysis is a useful tool when used in the light of personal experience and corroborating results from other different statistical analyses.

Factor 1 (Table 6) indicated that moderate temperatures (5°C-11°C), light winds (2-4) on the Beaufort Scale, and low humidity were associated with a high display intensity, long duration of total display performance, high number of flights, high number of peent calls by male woodcock, and a high number of male woodcock displaying. This association conformed with the analyses of variance, the correlation analyses, and my personal observations that woodcock displayed more intensively in fair weather than in unfavorable weather.

Factor 2 has been previously discussed. Factors 3, 4, and 5 depicted relationships which were either unclear or which did not make sense in the light of personal observations and other analyses and are, therefore, not discussed here.

Factor 6, useful when interpreted in the light of personal observation and experience, indicated that evenings in the first weeks of display were associated with a high number of male woodcock displaying and high territorial conflict among male woodcock. The reason for a high number of displaying male woodcock early in the breeding season may be that these weeks coincide with spring migration of woodcock through northcentral Oklahoma.

Factor 7 indicated that the last week of the breeding season was associated with a sharp decrease in courtship display behavior by male woodcock. This agreed with my observations, for on several occasions during the last 2 or 3 days of the breeding season I observed woodcock merely call for 15 to 20 min and not make a display flight.

In summary, various statistical analyses and personal observations indicated that fair weather conditions favored greater courtship display intensity by male woodcock than unfavorable weather conditions. Temperatures below freezing, especially in the early part of the breeding season, curtailed nearly all courtship display activity by male woodcock. Later in the breeding season, as woodcock reached a peak in their reproductive cycle, the effect of cold temperatures (even as low as -10°C) on courtship displays of male woodcock was reduced.

Wind speeds, unless exceptionally high, did not appear to influence courtship display behavior of male woodcock. South winds and associated warm weather usually resulted in high courtship display intensity by male woodcock.

Oncoming warm weather frontal passages seemed to increase courtship display intensity, and recent cold weather frontal passages seemed to suppress courtship display intensity of male woodcock. The influence of barometric pressure on courtship display activity of male woodcock was related to cold and warm weather frontal passages.

Misty, foggy, and drizzly weather conditions seemed to increase display intensity, whereas heavy rains, sleet, hail, and snow stopped all courtship display activity by male woodcock.

The phase of the moon did not appear to influence the courtship display behavior of male woodcock.

Male woodcock seemed to display more intensively on singing sites which were moist to dry than on singing sites covered with water or snow.

Light intensity was the major stimulus initiating courtship display activity by male woodcock on a daily basis.

Differences in influences of some meteorological factors between evening and morning courtship display behavior of male woodcock were either clarified when examined in the light of personal observations or were attributed to an insufficient amount of data collected.

Territorial Behavior. In this study, I made many observations on the territorial behavior of male woodcock on their singing sites. I quite frequently had the opportunity to observe the "dual" flight described by Davis (1970) where two woodcock flew together over a singing site in tandem fashion. Davis (1970) reported that the two woodcock he saw made physical contact at approximately 20 to 25 m, ascended another 10 to 45 m, fluttered breast to breast, then locked together and fell 15 to 25 m before breaking apart. One woodcock then flew off in a north-northwesterly direction and was closely pursued by the other until they were both lost sight of in the dusk.

There has been much confusion about the nature of this dual flight and the sex of the participating woodcock. Pitelka (1943) suggested that the dual flight is due to the accidental simultaneous initiation of display flights by two male woodcock. Some ornithologists have maintained that the dual flight is a mating flight, but no evidence has ever been produced to justify this claim.

I and other students observed this dual or tandem flight by two woodcock on the Ecology Preserve approximately 15 to 20 times. The typical pattern of a dual flight was as follows: One male woodcock would be calling or peenting from his singing site, when another male woodcock would fly directly over him, constantly cackling and circling in ever smaller concentric circles, until both males would go up in a

dual flight. They would rise 75 to 100 m breast to breast, flutter but never touch, and hover for a few seconds. Then both birds would fly away, one in pursuit of the other, in a straight and level direction. Usually the initial calling male would return to his site a minute or two later while the antagonist would find another site or retreat into the woods for the rest of the evening.

Among all of these observations, not once were the woodcock seen to touch. The flights did not appear to be accidental simultaneous courtship display flights by two males, nor were they believed to be mating flights. Instead, the dual flights appeared to be deliberate confrontations between two male woodcock that were competing for the same singing site. On the evening of 21 February 1975, we caught, in a mist net, two woodcock that were involved in the late stages of a dual flight. Both birds were males.

Often, particularly in the first two weeks of the display season, territorial conflict between males was so intensive and confusing that we could not keep track of which birds were which.

Territorial conflict among male woodcock on singing sites was not always manifested in the form of dual flights. Most of the time the only evidence of territorial conflict was cackling by one male above a singing site occupied by a second male. A few times, I observed an antagonist or cackling male woodcock circle five or six times over another male calling from a singing site without a dual flight resulting. The cackling male would then return to his singing site and resume calling.

There appeared to be a trend towards an increased intensity of courtship display behavior of male woodcock during evenings when

intensive territorial conflicts among displaying males occurred (Table 10).

In the mornings, least significant difference tests indicated significantly ($P \leq 0.05$) more time spent on the ground and a greater number of calls under territorial category B than under category A. In the evenings, least significant difference tests indicated significantly ($P \leq 0.05$) greater percentage of time spent in flight under category C than under category A.

Certain locations on the Ecology Preserve were preferred year after year by male woodcock as singing sites (Figure 15). A typical male used several singing sites covering a fairly well defined geographical area of the Preserve over the course of the breeding season and sometimes in one single evening of courtship display. I combined these groups of sites used by single woodcock into territories which outlined an area where a male woodcock was dominant (Figure 16). The boundaries of these territories remained fairly constant throughout the study (1970-75). Territories A, B, and C encompassed the greater number of individual singing sites and were the most preferred by displaying male woodcock.

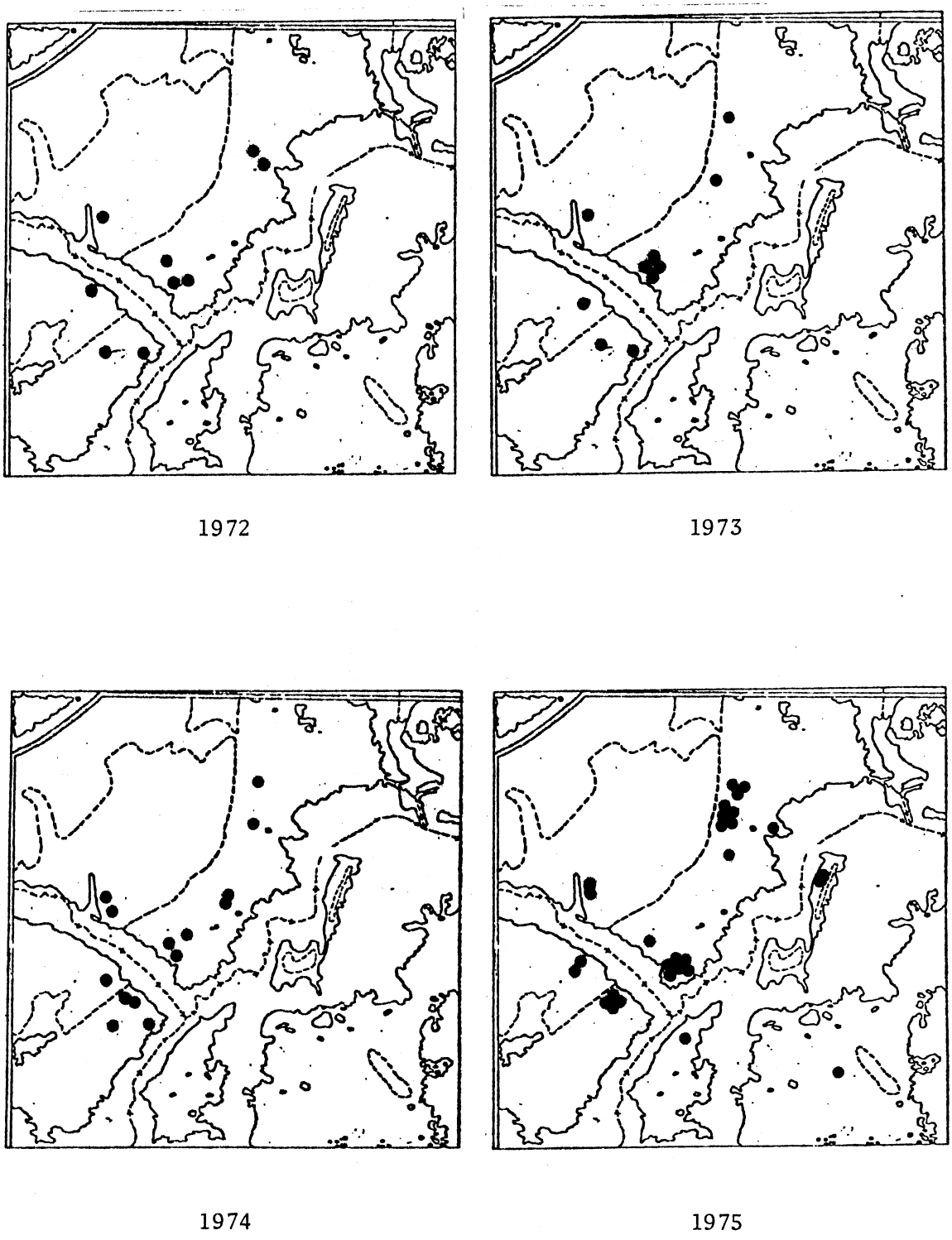
Territory A consisted of six sites: $4C_o$, $4D_o$, $4D_1$, $5B_o$, $5C_o$, and $5D_o$. Before 1975, Site $4C_o$ was the center of activity (the site where a male woodcock performed most of his courtship display activity) and the other sites received occasional use only. In 1975, however, mowed Site $4D_1$ was the center of activity and the other sites (including Site $4C_o$) received occasional use only.

Territory B consisted of three singing sites: $6E_o$, $6E_1$, and $7E_o$. Occasionally, a male woodcock in Territory B would use Site $5D_o$ of

Table 10. Averages of male woodcock courtship display parameters within different territorial conflict categories on the Ecology Preserve, mornings (1974-75) and evenings (1972-75).

Territorial Conflict Category[1]	Parameter Averages (Number of Observations)				
	Time in Flight (sec)	Time on Ground (sec)	% Time in Flight	Number of Flights	Number of Calls
Mornings:					
A	407 (36)	545 (36)	15 (37)	3.8 (36)	129 (36)
B	622 (8)	1206 (8)	27 (8)	7.4 (9)	282 (8)
C	205 (1)	1125 (1)	15 (1)	3.0 (1)	218 (1)
Evenings:					
A	205 (70)	647 (68)	16 (67)	3.4 (72)	162 (69)
B	278 (20)	677 (20)	26 (21)	3.9 (24)	187 (20)
C	352 (10)	734 (12)	34 (10)	3.9 (17)	173 (13)

[1] A = no territorial conflict, B = only cackling observed, C = intensive cackling accompanied by a dual flight.



● = minimum of five-use-nights

Figure 15. Yearly location and use intensity of singing sites used by male woodcock during evening courtship displays on the Ecology Preserve (1972-75).

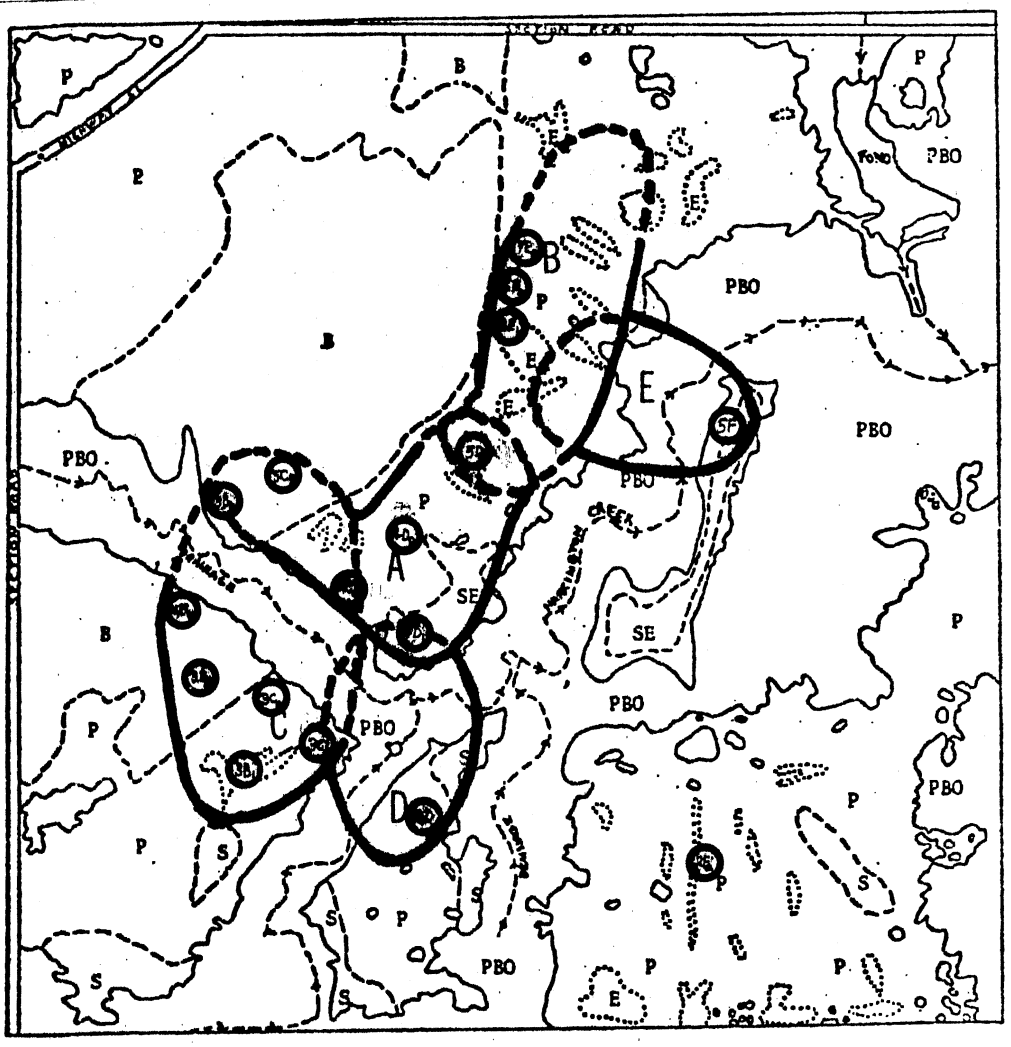


Figure 16. Approximate boundaries of territories established by displaying male woodcock on the Ecology Preserve (1972-75).

Territory A. Though each year Territory B would start receiving use 2 to 3 wks later than Territories A or C, it assumed prime importance and several woodcock would often compete for the sites on it. It was the territory where the most woodcock feeding sign was observed, and its importance was probably due to the fact that its sites were sparsely vegetated with midgrasses and interrupted with many patches of bare soil which were ideal for feeding by woodcock.

The reason Territory B would start receiving use later in the season than other territories is unclear but may be due to differential display starting times by individual woodcock or a change of preference for singing sites by male woodcock as the breeding season progressed. Whitcomb (1974) reported that in Michigan, seasonal activity was not the same on all singing istes and that some sites were abandoned by mid May, whereas other sites were occupied until 2 June.

Territory C consisted of five singing sites: $3B_1$, $3B_2$, $3C_o$, $3C_1$, and $4B_o$. Prior to 1974, Site $3B_1$ was the center of activity with Sites $3C_1$, $3B_o$, and $4B_o$ occasionally receiving moderate use. In 1974 and 1975, however, Site $3C_o$ was mowed and it became the center of courtship display activity with Sites $3B_1$, $4B_o$, and $3B_2$ assuming secondary importance. Occasionally, a male woodcock in Territory C would use Site $4C_o$ of Territory A.

Territories D (mowed Site 2D) and E (mowed site 5F) were not used before 1975, although the mowed sites were present in 1974. However, even in 1975 these two territories were not used very intensively, but rather male woodcock using these territories appeared to be suppressed by the activity of woodcock displaying in Territories A, B, and C. Often a woodcock in Territory D spent much time calling or peenting and

made only one or two flights in any one night. A woodcock in Territory E would often start displaying on Site 5F and would then go to Territory A, B, or C and seemingly attempt to dominate the bird there by cackling overhead.

The approximate areas of the five territories used by male woodcock during courtship display flights on the Ecology Preserve were: Territory A, 28,972 m^2; Territory B, 26,966 m^2; Territory C, 37,079 m^2; Territory D, 17,799 m^2; Territory E, 16,687 m^2. Territories A, B, and C covered a considerably larger area than did Territories D or E. I believe that the size of the territory was probably indicative of the dominance of a male woodcock occupying the territory, with the more dominant woodcock occupying the territory having the largest area.

Age and Sex Ratios. Woodcock were mist-netted on singing sites from 1970-75. Of the 21 males and 3 females banded, 13 were adults, 3 were immature, and 8 were of unknown age. Assuming that half the woodcock of unknown age were immature, this is an adult to juvenile ratio of about 3 to 1. The high ratio of adult to juvenile woodcock caught on singing sites each year indicates that there may be a surplus population of breeding males--younger subdominant male woodcock who are unable to successfully compete for singing sites as yearlings.

From 1970-75, two banded woodcock (returns from the previous year) were captured on singing sites: one adult male in 1974 which had originally been captured in 1973, one adult male in 1973 which had originally been captured in 1972. That male woodcock return to the Ecology Preserve to establish singing sites a second year testifies to their homing instinct and to at least moderately attractive breeding habitat in localized areas of northcentral Oklahoma.

Weight Loss and Soil Moisture. There was some indication that male woodcock lost or gained weight during the display season depending on moisture conditions. Woodcock recaptured after heavy rains weighed more than the first time they were captured a few days to a week earlier. Woodcock recaptured after drought periods weighed less than the first time they were captured a few days to a week earlier. Wet weather probably assures ample feeding opportunity where worms become readily available and woodcock gain weight. During dry weather, worms become progressively less available and displaying woodcock lose weight.

Singing Site Analysis

Aerial Vegetation Density. Aerial vegetation density was a measure of the obscuring effect of vegetation on the presumed likelihood of visibility of woodcock (either to see or be seen, or both) while at the singing site. The aerial vegetation density on used eroded and/or mowed singing sites was significantly less ($P \leq 0.05$) than on unused native grass sites (Tables 11 and 12). These results indicate that the obscuring effect of tall grasses was unattractive to male displaying woodcock. There were no significant differences ($P \leq 0.05$) in aerial vegetation density between used mowed and used eroded sites nor between used mowed sites and unused mowed sites.

There were no significant aerial density differences ($P \leq 0.05$) between used mowed sites and unused mowed sites because of the similar mowing procedure on each type of site. We deliberately mowed more sites than were likely to be used. The spacing influence of territorial behavior by male woodcock, along with other physical site characteristics

Table 11. Average aerial vegetation density results (percent) for different categories of singing sites on the Ecology Preserve.

Type and (Number of Singing Sites)	% of Squares Obscured by Vegetation		
	First Level (0-10 cm) Interval	Second Level (10-20 cm) Interval	Third Level (20-30 cm) Interval
Eroded Sites			
Used (6)			
Range	30-57	1-15	0.5-7
Average	44.3	2.5	0.6
Unused (6)			
Range	19-52	1-14	0-2.6
Average	32.7	8.0	1.3
Mowed Plots			
Used (5)			
Range	35-51	0-12	0-7
Average	44.0	4.6	1.6
Unused (5)			
Range	23-53	1.9-4.7	0-1.3
Average	43.4	3.7	0.6
Control Plots			
Unused Native Prairie (4)			
Range	60-82	6-39	2-14
Average	73.0	26.5	9.8

Table 12. Analyses of variance for aerial and ground vegetation densities between different categories of singing sites on the Ecology Preserve.

Sampling Level	F Value and (Significance Level)				
	Used Eroded vs. Unused Native	Used Eroded vs. Unused Eroded	Used Mowed vs. Unused Native	Used Mowed vs. Unused Mowed	Used Mowed vs. Used Eroded
Aerial Density					
First (0-10 cm)	21.16 (0.005)	3.78 (0.100)	25.08 (0.005)	0.009 *	0.004 *
Second (10-20 cm)	8.90 (0.025)	0.08 *	9.64 (0.025)	0.15 *	0.84 *
Third (20-30 cm)	8.31 (0.025)	1.00 *	8.29 (0.025)	0.48 *	0.29 *
Ground Density	13.24 (0.025)	0.03 *	831.52 (0.005)	4.63 (0.10)	5.29 (0.10)

*F value not significant.

discussed below, appeared to be responsible for the preferred use by displaying male woodcock for certain mowed sites over others.

Eroded sites used by woodcock were slightly more ($P \leq 0.10$) densely vegetated at the first level (0-10 cm) than were eroded unused sites, suggesting a preference by woodcock for subtle, specific aerial vegetation density conditions near ground level. One eroded site, $4C_o$, was sampled in both 1974 and 1975. In 1975, it received very little use, whereas in 1974 it received heavy use as a singing site by male woodcock. The results of sampling showed that it decreased in aerial vegetation density from 1974 to 1975, probably due to the drought that occurred in summer 1974. Because of the drought, I suspect that many of the sites analyzed in 1974 decreased in aerial vegetation density in 1975. It seems that the attractiveness of eroded sites to woodcock could easily change from year to year because of high site susceptibility to further erosion after drought conditions followed by heavy rains.

Ground Vegetation Density. Ground vegetation density was a measure of the percentage of a singing site surface covered by the parts of plants, by soil, or by soil litter. The vegetation density at ground level on used singing sites was much less than on unused sites (Table 13). Unused native grass sites had significantly less ($P \leq 0.05$) vegetation litter and bare soil (Table 12) than did eroded or mowed sites used by woodcock. Virtually no differences in litter and bare soil existed between eroded used and eroded unused sites. Mowed used sites had more ($P \leq 0.10$) bare soil and litter than mowed unused sites. Unused mowed sites also had more litter and exposed soil ($P \leq 0.10$) than did the used eroded sites. Although significant to only 0.10, the above two

Table 13. Average ground vegetation density for different categories of singing sites on the Ecology Preserve.

Site and Year	Possible Hits	Hits on Vegetation	% Vegetation	Hits on Soil and Litter	% Soil and Litter
Used Mowed (n=3)					
Total	457	212	139	245	162
Average	152	71	46	82	54
Used Eroded (n=4)					
Total	597	400	268	197	132
Average	149	100	67	49	33
Unused Native (n=4)					
Total	596	564	379	32	21
Average	149	133	95	8	5
Unused Mowed (n=3)					
Total	450	260	173	190	127
Average	150	87	58	63	42
Unused Eroded (n=4)					
Total	599	399	259	210	141
Average	150	44	65	52	35

relationships suggest that more exposed soil and litter was necessary to attract woodcock on used mowed plots than on used eroded and unused mowed sites.

Composition of Vegetation. The composition of vegetation on singing sites (Table 14) did not suggest any statistically significant preferences by woodcock for any particular plant species. This was in accord with the findings on singing sites in Maine (Mendall and Aldous 1943). However, three species which were not generally associated with used eroded sites were Scribner panicum, indian grass, and big bluestem. The latter two are very tall grasses that would obscure a woodcock's vision while on a site and hinder flight to and from the site. Areas containing these tall grasses were used readily when mowed. Thus, it was probably not the species of vegetation which made the singing site attractive to woodcock but the aerial and ground level vegetation density at the site.

Physical Characteristics. Elevation and slope appeared to be the only physical characteristics of singing sites which were influential in a woodcock's selection of a site (Table 15). Elevation ranged from 297 to 305 m (average 301 to 302 m) on all used sites, while all unused sites ranged from 299 to 312 m (average 306 to 308 m). Unused mowed sites, however, were at very significantly ($P \leq 0.005$) higher elevations than were used eroded sites. This use difference may have been due to the latter sites' proximity to water or to higher soil moistures at the lower level elevations where these sites were found (see spatial characteristics below). Used eroded sites were on significantly ($P \leq 0.025$) greater slopes than were eroded sites unused by woodcock (Table 16),

Table 14. Composition of vegetation of used eroded, unused eroded and native grass singing sites on the Ecology Preserve.

Plant Species	% Sites Occupied by the Species		
	Used Eroded	Unused Native Grass (Controls)	Unused Eroded (Controls)
Little and Split-beard bluestems	32.5	35.9	35.2
Tall dropseed	8.9	0.1	
Goldenrod	3.2	0.1	5.0
Silver bluestem	2.2		
Heath aster	1.7	0.3	
Johnson grass	1.4		
Yellow broomweed	0.5		
Fescue	0.4		
Western ragweed	0.4	1.2	
Prairie acacia	0.4	0.1	1.0
Sedge	0.3		
Flax	0.3		0.4
Scribner panicum	0.5	4.6	0.4
Prairie three-awn	1.7		
Indian grass	0.2	19.3	1.6
Japanese brome grass	0.2	0.5	
Croton	0.2		
Hawkweed	0.2	0.1	
Slender lespedeza	0.2		
Big bluestem		6.1	3.0
Purple top		1.2	
Dallis grass		0.1	
Torrey nightshade		0.4	
Thistle		0.1	
Smooth sumac		0.5	
Roughleaf dogwood		0.7	
Greenbriar		0.1	
Buckbrush		1.3	
Switchgrass		0.1	
Dogbane		0.1	
Purple prairie clover		0.1	0.8
Mint		0.1	
Hairy grama			
Wild bean			1.0
Acalypha			0.4
Dotted gayfeather			1.1
Unknown		0.4	1.0
Bare soil	12.0	0.1	9.0
Ground litter	7.4	4.6	4.6
Standing litter	24.7	20.8	29.4

Table 15. Physical characteristics of different categories of singing sites on the Ecology Preserve.

Category and Site	Perimeter (m)	Area (m^2)	Slope (%)	Aspect	Elevation (m)	Shape
Used Eroded						
$5D_o$	-	-	5.0	SE	302	Irregular
$4C_o$	-	-	3.0	SSE	302	Irregular
$6E_o$	-	-	5.0	SSE	302	Irregular
$7E_o$	-	-	6.0	SSE	302	Irregular
$6E_1$	-	-	6.0	E	302	Irregular
Average			5.0		302	
Unused Eroded						
1E	-	-	0.0	N	312	Irregular
$3B_1$	-	-	5.0	ENE	305	Irregular
$4C_o$	-	-	3.0	SSE	302	Irregular
$3C_1$	-	-	2.0	E	302	Irregular
$2F_o$	-	-	1.0	NW	312	Irregular
Average			2.2		307	
Unused Native Prairie						
$2B_o$	-	-	9.0	ESE	308	Irregular
$1G_o$	-	-	3.0	NE	311	Irregular
$7E_1$	-	-	4.0	SSE	305	Irregular
$6E_2$	-	-	6.0	E	299	Irregular
Average			5.5		306	

Table 15 (Continued).

Category and Site	Perimeter (m)	Area (m^2)	Slope (%)	Aspect	Elevation (m)	Shape
Used Mowed Plots						
$3C_o$	141	1422	9.0	E	302	Oval
$5C_o$	137	1372	8.0	SSE	305	Circular
$4D_o$	150	1661	9.0	E	300	Circular
$5F_1$	128	1134	0.0	E	297	Circular
Average	139	1397	6.5		301	
Unused Mowed Plots						
$6D_o$	123	1280	8.0	E	308	Oval
$3G_o$	141	1515	0.0	NE	308	Oval
2B	149	1488	9.0	E	308	Circular
$6D_1$	138	1461	5.0	SE	308	Circular
8E	139	1515	3.0	SE	308	Circular
Average	138	1452	5.0		308	

Table 16. Analyses of variance for physical and spatial characteristics between different categories of singing sites on the Ecology Preserve.

Categories	F Value and (Significance Level)				
	Used Eroded vs. Unused Mowed	Used Eroded vs. Unused Eroded	Used Mowed vs. Unused Eroded	Used Mowed vs. Unused Mowed	Used Mowed vs. Used Eroded
Physical Aspects					
Slope	0.00 *	7.61 (0.025)	3.86 (0.10)	0.29 *	0.48 *
Elevation	16.67 (0.005)	3.09 *	2.65 *	2.53 *	0.30 *
Spatial Characteristics					
Distance to Water	1.41 *	0.38 *	1.62 *	29.85 (0.005)	7.89 (0.025)
Distance to Nearest Site	6.52 (0.05)	2.01 *	0.19 *	0.49 *	0.54 *
Distance to Ecotone	* *	0.57 *	2.37 *	1.33 *	5.01 (0.01)

* = F value not significant.

probably because the latter sites often accumulated standing water which was avoided by woodcock.

The sizes of the singing sites on our study area ranged from 20 to 25 m in diameter (0.03-0.05 ha) and did not differ from the sizes of those in other states. As Sheldon (1967) suggested, there did seem to be a requirement of a "getaway" route for the bird's aerial flight. Several sites mowed in the midst of tall trees and thick brush on our study area were not used very intensively, and this may have been due to unsuitable getaway routes.

Spatial Characteristics. Spatial characteristics of singing sites (Table 17) suggested that distances from singing sites to either diurnal cover or water may have been critical to a woodcock's selection of a singing site. Mowed used sites were very significantly ($P \leq 0.005$, Table 16) closer to the nearest surface drainage or diurnal cover than were mowed unused sites, suggesting that woodcock singing sites in northcentral Oklahoma need to be close to water or moist soils. This is further explained by the fact that used eroded sites, though further away from the creeks on the Preserve (average = 125 m) than used mowed sites (average = 56 m), were almost always at the source of a seasonally wet draw which drained from the eroded site to a creek.

Distances between used singing sites varied, depending on existing conditions. Used singing sites not separated by a creek or draw averaged 280 to 300 m apart. However, two used singing sites separated by a small drainage and associated woody vegetation were only 150 m apart. Apparently, the wooded draw reduced visual contact and muffled the acoustical activities of the two adjacent male woodcock. The

Table 17. Spatial characteristics of different categories of singing sites on the Ecology Preserve.

Category and Site	Distance to Nearest Used Singing Site (m)	Distance to Water (m)	Distance to Ecotone (m)
Used Eroded			
$5D_o$	300 (to $3C_o$)	110	45
$4C_o$	105 (to $3C_o$)	45	20
$6E_o$	250 (to $5C_o$)	150	45
$7E_o$	280 (to $5C_o$)	165	20
$6E_1$	270 (to $5C_o$)	155	30
Average	241	125	32
Unused Eroded			
1E	225 (to 2D)	110	45
$4C_o$	105 (to $3C_o$)	45	20
$3C_1$	55 (to $3C_o$)	45	15
$2F_o$	225 (to 2D)	190	135
Average	152	98	54
Unused Native Prairie			
$2B_o$	135 (to $3C_o$)	120	60
$1G_o$	450 (to $4C_o$)	200	135
$7E_1$	50 (to $6E_o$)	200	45
$6E_2$	45 (to $6D_1$)	100	25
Average	170	155	66
Used Mowed			
$2B_o$	65 (to $3C_o$)	65	0
$3C_o$	105 (to $4C_o$)	55	15
$5C_o$	250 (to $6E_o$)	90	30
$4D_1$	270 (to $6E_1$)	45	22
5F	200 (to $6E_1$)	25	10
Average	178	56	15
Unused Mowed			
$6D_o$	90 (to $6D_1$)	225	0
3G	270 (to 5F)	225	25
2B	155 (to $3C_1$)	50	20
$6D_1$	45 (to $6E_1$)	160	15
8E	135 (to $7E_1$)	225	80
Average	139	177	28

territorial conflict which did exist may not have been intensive enough to rule out use of the sites by separate birds.

Soil Characteristics. No differences in soil characteristics were apparent between used and unused display sites (Table 18). Soil pH levels between any two categories of singing sites were not significantly different ($P \leq 0.05$), and soil textures on all sites were generally the same.

Summary. In summary, displaying male woodcock on the Ecology Preserve preferred singing sites that were sparsely vegetated, relatively close to either moisture or diurnal cover, well drained, and adequately spaced. Other physical, spatial, soil, and vegetation characteristics of singing sites appeared to influence woodcock selection of sites only insofar as the above conditions were met.

Sparsely vegetated sites maximized courtship display flight take-off and landing requirements, freedom of movement during mating or other feeding activities on the singing site, and general visibility by the calling male woodcock of predators, female woodcock, and other displaying male woodcock. Composition of vegetation affected the choice of a singing site by male woodcock only when the plant species present were very tall and thus eliminated the advantages of sparsely vegetated sites. Unused native prairie sites were readily used after mowing when other site requirements were met.

Heavily used singing sites were in close proximity to water. Mowed sites and eroded sites which were not close to water were not used, even though they were adequately spaced apart from each other. The only

Table 18. Soil characteristics of different categories of singing sites on the Ecology Preserve.

Category and Site	pH	Texture
Used Eroded		
$5D_o$	7.7	Red silty clay
$4C_o$	6.3	Red clay
$6E_o$	6.2	Red clay
$7E_o$	6.3	Red sandy clay
$6E_1$	6.1	Red sandy clay
Average	6.5	
Unused Eroded		
1E	7.4	Red sandy clay
$3B_1$	6.4	Red sandy silt
$4C_o$	6.3	Red clay
$3C_1$	6.0	Red sandy clay
$3B_1$	6.4	Red sandy silt
$2F_o$	6.2	Red sandy loam
Average	6.5	
Used Mowed		
$3C_o$	6.5	Dark sandy loam
$5C_o$	6.8	Dark sandy loam
$4D_1$	6.3	Dark sandy loam
5F	6.3	Dark sandy loam
Average	6.5	
Unused Mowed		
3G	6.7	Red sandy loam
2B	6.4	Dark sandy loam
$6D_1$	6.8	Red sandy loam
8E	6.2	Dark sandy loam
Average	6.5	
Unused Native Prairie		
$2B_o$	6.4	Dark sandy loam
$1G_o$	6.4	Dark sandy loam
$7E_1$	6.0	Dark sandy loam
$6E_2$	6.3	Dark sandy loam
Average	6.3	

exceptions to this were the temporary use of drier sites during the peak of migration by presumed migrant or surplus male woodcock.

The success of artificially created singing sites seemed to be limited by their distance from water and by adequate spacing of the sites from each other.

Feeding Activity on Singing Sites

In 1974 and 1975, I made intensive efforts to locate woodcock feeding sign (probe holes) on singing sites used by displaying male woodcock on the Ecology Preserve. The number of probe holes found per site on any one day ranged from 100 to 300, and all were found on eroded sites.

To determine why only eroded sites and not mowed sites were used as feeding sites by woodcock, soil and earthworm samples were taken on one used mowed and one used eroded site in 1975. The soil on the eroded site was red sandy clay while the soil on the mowed site was dark loam. There were no differences in earthworm content between the two sites. I believe that woodcock fed only on eroded sites because to feed they needed areas of either bare soil or soft mud, features which were not present on mowed sites.

Feeding by woodcock on singing sites began several weeks after the sites received initial use as display sites. In 1974, courtship display activity on sites $6E_o$, $6E_1$, and $7E_o$ occurred from 28 February to 7 March whereas feeding activity on these sites began on 8 March. In 1975, courtship display activity on the same sites occurred from 19 February to 12 March whereas feeding activity on these sites began on 13 March. I suspect that the reason for the delayed feeding activity on singing sites is that earthworms did not come to the surface of singing sites

until soil temperatures were warm enough. Results of sampling singing sites for earthworms and other invertebrates in 1974 (Table 19) indicated that earthworms were present in the topsoil of singing sites by early March, roughly the same time that singing sites began to receive use as feeding sites.

Table 19. Number of earthworms found on singing sites on the Ecology Preserve (1974).

Date	Sites and (Number of Samples)					
	$4C_o(4)$	$5D_o(8)$	$4C_1(4)$	$6E_o(4)$	$3B_1(8)$	$7E_o(4)$
20 Feb.	0	0	0	0	0	0
26 Feb.	0	0	0	0	0	2
5 Mar.	0	7	1	4	5	7

Diurnal Habitat Characteristics

Woodcock or their sign (probe holes and droppings) in diurnal cover along creek drainages of the Preserve were observed inconsistently in 1971-75 from December through July. In 1974, in spite of intensive searching efforts, no woodcock or their sign were observed in diurnal cover on the Ecology Preserve. In 1975, efforts were more productive and 12 observations of either woodcock or their sign were made (Table 20, Figure 17), during the period of 7 February to 14 April.

The diurnal cover used by woodcock on the Preserve was similar in many respects to the diurnal cover used by woodcock in other states (best summarized by Sheldon 1967). Important characteristics of diurnal

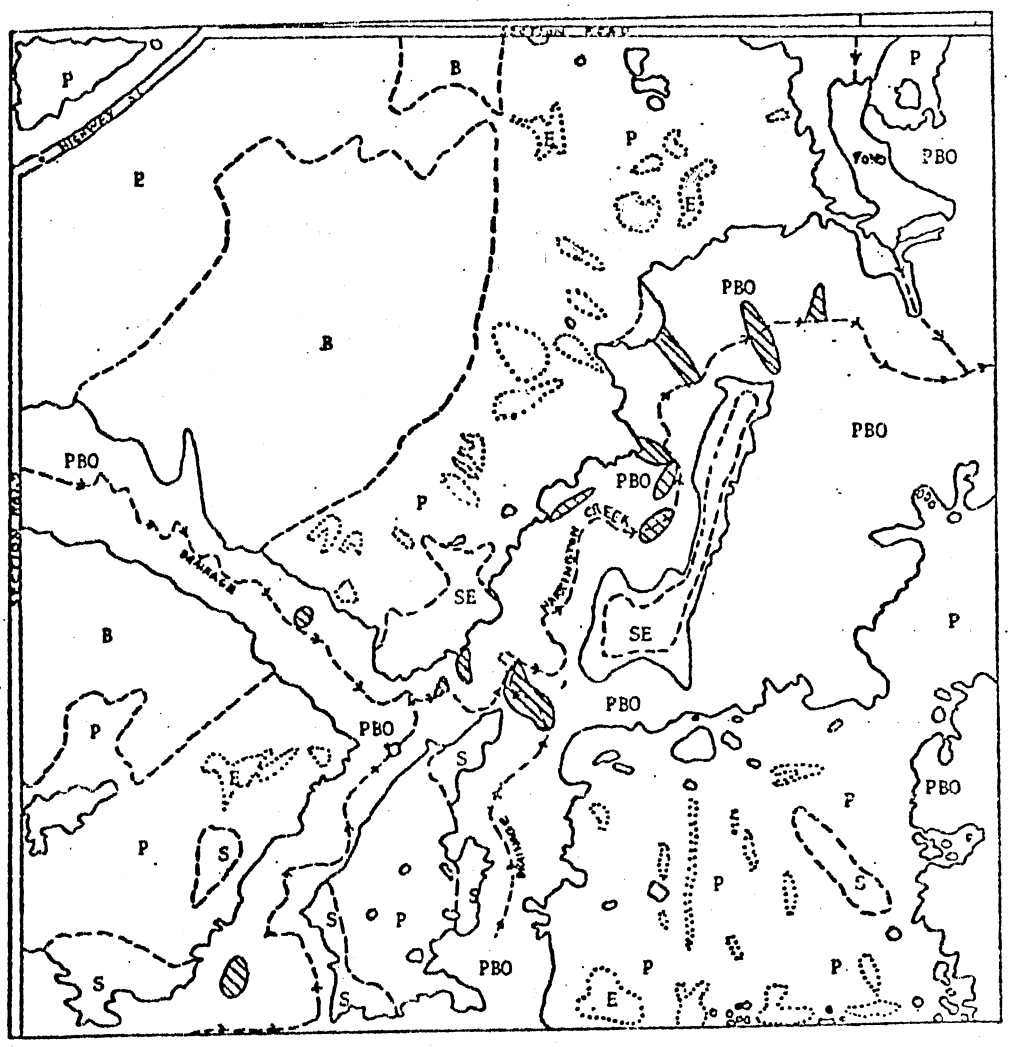
Table 20. Characteristics of habitat where woodcock and feeding sign were observed on the Ecology Preserve (1975).

Date	Dominant Overstory	Dominant Understory	Ground Cover	% Ground Covered by Vegetation	Soil	Moisture	Proximity to Creek (m)
07-02	100% Po[1] 10-12m	None	U, Gr, Gra	25-50	Dark, alluvial loam	Wet	10-25
07-02	20% Rb 6m, 80% Hn 10m	100% Rb 3m	U, L, Gra	50-75	Dark, alluvial loam	Wet	1-10
17-02	50% Em 13-15m and Hk 13-15m, 50% Rb 5m	75% Rb 3m, 25% Dg 3m	Gr	0-25	Red, alluvial silt deposits	Wet	10-25
18-02	100% Po and Bo 10-12m	None	Leaves and dead limbs	0-25	Dark loam	Wet	10-25
21-02	100% Em 6-10m	100% Rb 2-3m	U, L, Gr	0-25	Dark loam	Moist to Wet	10-25
27-02	100% Po and Bo 13-15m	None	L, Gr, Wr	0-25	Red silty loam	Moist	10-25
27-02	80% Em and 20% Co 13-15m	100% Rb 3-4m	U, Bb, Gr	25-50	Dark red silt loam	Moist	1-10
08-03	100% Po 13-15m	100% Rb 3-5m	Gra, Dg, Gr	0-25	Red alluvial loam	Moist	1-10
24-03	100% Po 13-15m	100% Rb 3-4m	U, L, Gr	0-25	Dark alluvial loam	Wet	1-10

Table 20 (Continued).

Date	Dominant Overstory	Dominant Understory	Ground Cover	% Ground Covered by Vegetation	Soil	Moisture	Proximity to Creek (m)
23-03	50% Co 12-15m, 50% Hk and Em 10m	50% Rb 5m, 30% Dg 4m, 20% Gra	U, L, Gr	25-50	Red sandy loam	Wet	1-10
14-04	100% Co 20-25m	100% Dg 3-5m	Gr, Bb	25-50	Dark alluvial loam	Wet	1-10
14-04	25% Co 30m, 50% Em 15m, 20% Hk 5m, 5% Ah 15m	80% Rb 2-3m, 10% Hk 5m, 10% Rc 2m	Gr, Gra, U, Bb	25-50	Reddish sandy loam	Wet	1-10

[1]A = Green ash, Bb = Buckbrush, Co = Chinquapin oak, Dg = Roughleaf dogwood, Em = American elm, Gr = greenbriar, Gra = Wild grape, Hk = Hackberry, Hn = Honeylocust, L = Leafy elephant foot, Po = Post oak, Rb = Eastern redbud, U = Broad-leaf uniola.



LEGEND:

B	Brush (Blackjack oak, Red cedar, Roughleaf dogwood, Greenbriar, native grasses)
E	Eroded sites on prairie
P	Native tall grass prairie
PBO	Post oak-Blackjack oak (some bottomland hardwoods along the creek)
SE	Sumac clones and Elm
S	Sumac

Figure 17. Locations of observations of woodcock feeding sign in diurnal woodcock habitat on the Ecology Preserve (1975).

cover in northcentral Oklahoma were: close proximity to water (average of about 10 m), moist to wet soil conditions, approximately 25 percent of the ground covered by vegetation, understory and overstory cover dense enough to offer protection from predators and other disturbances such as grazing livestock, and shade conditions that offer relief from hot summer temperatures.

All 12 of the observations of diurnal woodcock cover were in or very close to the bottom of a draw draining from a nearby field into a creek on the Preserve (Figure 17). In nearly all cases there was either a trickle or small pool of water in this draw and woodcock or sign of woodcock were within 1 to 2 m of the water. Evidence indicated that woodcock fed on subsurface invertebrates in patches of bare soil interspersed with litter and dead branches on the ground. These sites were usually well shaded, but during cold weather they were on a south slope or bank of a creek. Two woodcock which I observed after a snow storm when there was still 1 to 4 cm of snow on the ground were on south slopes and were feeding in the soft mud where the snow had melted during the course of the morning.

As in previous studies in other states, diurnal woodcock cover on the Preserve was closely associated with certain plant species. Eastern redbud was present in the understory cover at 8 of 12 observations; greenbriar was present in the ground cover at 10 of 12 observations; broad-leaf uniola was present in the ground cover at 7 of the 12 observations; and leafy elephant foot was present in ground cover at 5 of the 12 observations. Eastern redbud seemed to be important in that it offered the necessary shrubby understory cover and shade protection offered by shrubby species such as alder in more northeastern states.

Greenbriar offered excellent escape cover while presenting a formidable barrier to livestock, large predators, and human intruders. Leafy elephant foot and broad-leaf uniola, two forbs not found where heavy grazing by livestock occurred in northcentral Oklahoma, may have afforded necessary ground cover.

It appeared that heavy grazing by livestock was incompatible with the habitat requirements of woodcock in northcentral Oklahoma. In all my searches for woodcock in diurnal cover, I rarely found them where heavy grazing occurred. This was because the constant trampling and grazing of bottomland cover by cattle eliminated almost all ground cover. The Ecology Preserve, having been protected from grazing since 1968, had a luxurious growth of ground vegetation along creek banks and associated bottomland hardwoods.

Nest and Brood Cover Characteristics

In 1973, a woodcock hen and chick were found on the Ecology Preserve on 7 April in mixed upland brushy cover (Barclay 1973, personal communication) (Figure 18). Tree species present were redbud and dogwood and were approximately 1 to 3 m high. Ground cover was patchy, consisting of buckbrush, greenbriar, and grasses. Probe holes in the area and vicinity indicated intensive feeding by the hen and chick. In 1974, intensive searches on the Ecology Preserve for woodcock nests, broods, or both, in late spring and summer with the use of dogs proved fruitless. A late snowstorm on 20 March and a severe frost on 21 March may have upset any nesting attempts. Frequent searches on the Preserve during 1975, although dogs were not used, yielded no results but individual woodcock were flushed and feeding sign were found on many occasions.

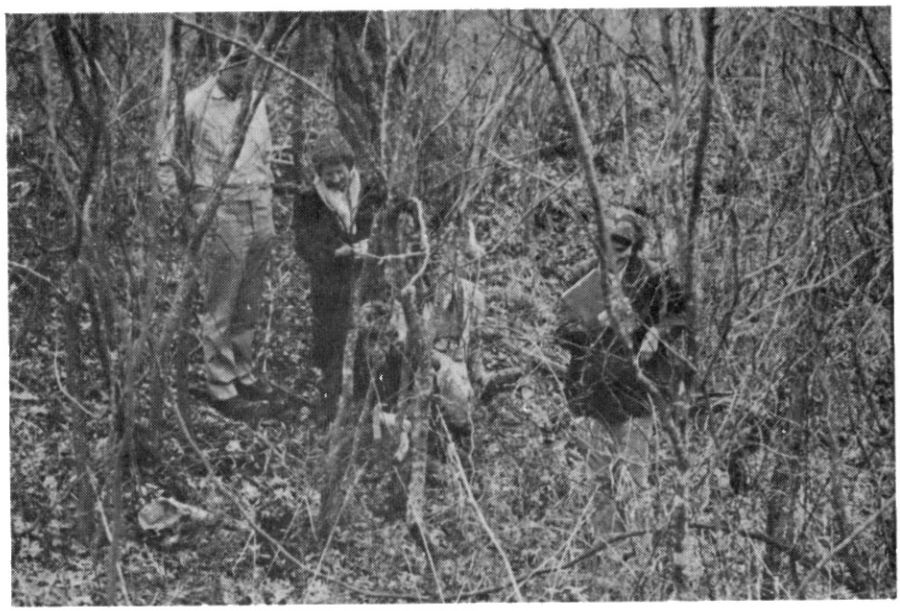


Figure 18. Upland brush cover where a woodcock hen and chick were found on the Ecology Preserve.

On 10 March 1975, a woodcock hen was found on a nest by Brooks Pybus, a Stillwater youth, at a wildlife sanctuary located at the north end of Boomer Lake at the northeast edge of Stillwater, Oklahoma. The next which contained four eggs was observed for four days by the youth, but was abandoned by the hen on 14 March after disturbance by young boys playing in the area. Two of the eggs then disappeared, and the other two were incubated by Pybus under a light bulb. One hatched on 29 March and lived for two days. The other egg did not hatch.

I made a subsequent investigation of the site and found a typical woodcock nest: a structure modestly constructed of willow and cottonwood leaves. It was raised about 3 to 4 cm above the ground at the base of a willow tree about 10 cm in diameter and 13 to 15 m high. The understory vegetation, consisting of wild grape and mulberry, was very sparse. The overstory vegetation, consisting almost exclusively of willow and cottonwood, was moderately dense. The overstory trees were 13 to 15 m high, about 10 cm in diameter, and 2 to 5 m apart.

Except for the composition of the vegetation, the growth forms and general characteristics of the habitat where woodcock nests and broods were found in northcentral Oklahoma did not differ greatly from typical nest and brood sites described by Mendall and Aldous (1943) and Sheldon (1967) in Maine and Massachusetts respectively.

Habitat Manipulation

Many of the characteristics of mowed sites have been discussed above. The actual response by woodcock to habitat manipulation (mowed sites) was excellent. Of the 19 plots mowed in 1974 (Figure 5), five were subsequently used as singing sites; four of these were in formerly

brushy areas, and one was in native grassland with some scattered sumac. Nine of the 20 plots mowed in 1975 were used: three were in brushy areas and six were in native grass or slightly brushy areas. The territorial behavior of male woodcock and, possibly, the proximity of mowed sites to water or diurnal cover may have limited the use of these sites, since we deliberately mowed more sites than would normally be used by male woodcock in a specific geographic area. The mowing provided openings in otherwise too dense cover and could prove to be a valuable woodcock management tool in eastern Oklahoma where a considerable number of courtship displays by male woodcock have been discovered (Smith 1975, personal communication).

Seasonal Numbers and Distribution

In over 100 hrs of searching potential woodcock cover in the Stillwater area from 21 August 1973 to 15 December 1974, I found only seven woodcock. However, I received many reports of woodcock sightings from students, hunters, and conservation and nature clubs in the area. Including the above observations, since 1944 approximately 50 sightings of woodcock (excluding hens with broods and singing male woodcock on the study area) have been reported in Payne County (my personal records; Barclay, unpublished records; Sutton, unpublished records). From these observations, preliminary conclusions were possible about the seasonal numbers and distribution of woodcock in northcentral Oklahoma.

The number of reports of woodcock or their sign was greatest for the 2nd or 3rd week in November (Figure 19). However, these dates correspond with the traditional opening of the quail season in Oklahoma on 20 November. It is more probable that peak fall migration occurs

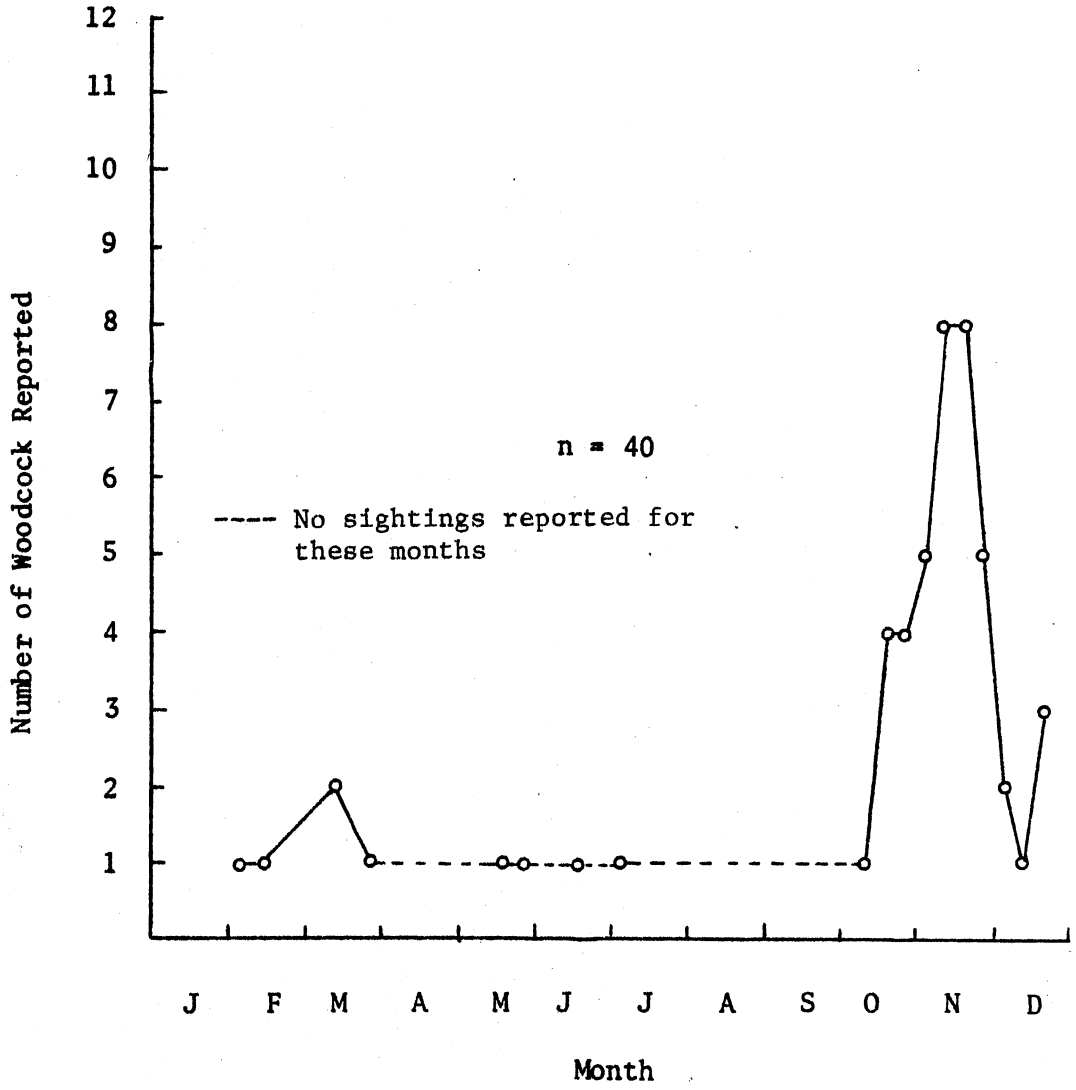


Figure 19. Number of woodcock sighted monthly from 1944-75 in northcentral Oklahoma, excluding observation of broods and sightings on the Ecology Preserve.

either the last week of October or the first week of November, depending on weather conditions (Barclay 1980, personal communication).

The most reliable criterion available to determine the dates of spring migration of woodcock through northcentral Oklahoma was that on the Ecology Preserve male woodcock began courtship displays by late January or early February (Table 1). These dates seemed to correspond with an influx of migrating woodcock through the area, though they differed with Sutton's (1967) estimates that the peak of spring woodcock migration through northcentral Oklahoma was from 10 March to 20 April.

Fall Cover Characteristics

Of the approximately 50 reports of woodcock sightings in Payne County mentioned above, 14 had a fair to good description of habitat characteristics at the observation site (Table 21). Most of these reports were sightings made by hunters in the fall. In the vegetation overstory, common species were American elm, hackberry, eastern cottonwood, and black willow. Elm is known for having leaves that are sweet and attractive to earthworms when they decay (Wallwork 1970). The understory plant species, including red mulberry, roughleaf dogwood, sumac, and sapling American elm, were rather shrubby and short. They probably fulfilled the function of shrubby alder and birch cover in good woodcock habitat of New England. The ground cover at the observation sites was composed of various grasses, forbs, and brush. The soils were nearly all moist to wet alluvial deposits. Most of the woodcock sightings were within 30 to 40 m of water, and in five situations where I observed feeding sign there was an abundance of earthworms in the soil. Severe

Table 21. Characteristics of habitat where woodcock were sighted during fall migration in northcentral Oklahoma.

Date	Dominant Overstory	Dominant Understory	Ground Cover	Soil	Moisture	Prox. to Water (m)	Apparent Food Utilized
14-10-73	Po,[1] Hk, Em, Hn, Cht, Rc	--	Gr, Sp, Bb, Rg, S, Sg	Dark silt loam	Moist	0-20	--
29-10-75	C, W, Em	—	Bb, Gr	Alluvial	Wet	3-5	--
07-11-73	C, W, A, Em	Rb, A	G, As, U	Red clay	Wet	0-3	Earthworms
07-11-73	C, W	Rb, Em	G, Rg, As, Jg	Dark alluvial	Wet	0-3	Earthworms
09-11-73	Em, W, C	Mb, Dg, Em	Grasses, brush	Dark alluvial	Moist	20-40	Earthworms
10-11-73	Em, C, W	Mb, Dg	Grasses, brush	Dark alluvial	Wet	5-10	Earthworms
13-11-73	C, W	Mb, Su	Bl, open	Dark alluvial	Moist	3-5	Earthworms
20-11-74	Em, Hk, W	Dg	E, Wv, Cr, grasses	Dark alluvial	Moist	5-10	--
20-11-74	Em, Hk	Dg	Brush	Dark alluvial	Moist	5-10	--
20-11-73	Po, Bo, Rc	--	Brush, grasses	--	--	100	--
24-11-73	Dense	—	Gr	Sandy	Wet	20	--

Table 21 (Continued).

Date	Dominant Overstory	Dominant Understory	Ground Cover	Soil	Moisture	Prox. to Water (m)	Apparent Food Utilized
04-12-73	Em, Hk	—	Bb, Gr, Jg	--	--	30-40	--
17-12-73	--	Su	--	--	Moist	40-50	--
22-12-73	Po, Bo	--	Ber, annuals	Sandy clay loam	Moist	50	--

[1]A = Green ash, As = Aster species, Bb = Buckbrush, Bermuda grass, Bl = Bluestem grasses, Bo = Blackjack oak, C = Eastern cottonwood, Cr = Crown-beard, Dg = Roughleaf dogwood, Em = American elm, Gr = Greenbriar, Hk = Hackberry, Hn = Honeylocust, Jg = Johnson grass, Mb = Red mulberry, Po = Post oak, Rb = Eastern redbud, Rc = Eastern red cedar, Rg = Ragweed species, S = Sumac species, Sp = Scribner panicum, W = Black willow, Wv = Wild violet, U = Broad-leaf uniola.

grazing occurred at only one site and limited grazing occurred at three of the 14 sites.

Summer Habitat Conditions

The results of sampling for earthworms and sampling of soil moisture content on the Ecology Preserve are illustrated in Figure 22. As percentage of moisture in the soil declined, so did earthworm populations. After 26 June 1974, Oklahoma experienced one of its driest summers on record. It would seem that woodcock remaining throughout the summer in northcentral Oklahoma under such dry conditions would have a difficult time surviving.

Woodcock feeding sign (probe holes) were found on the Ecology Preserve up to the first or second week of June in 1973, 1974, and 1975, which indicated that at least a few woodcock remained in the area until those dates. After mid-June, in all three years, no feeding sign were found along the drainages on the Preserve. However, in subsequent years, some feeding sign by woodcock were found along shaded drainages on the Ecology Preserve throughout the summer (Barclay 1980, personal communication).

The above observations seem to corroborate Sutton's (1968) hypothesis that woodcock in northcentral Oklahoma may move to wetter, cooler places during extremely dry summers or summer months.

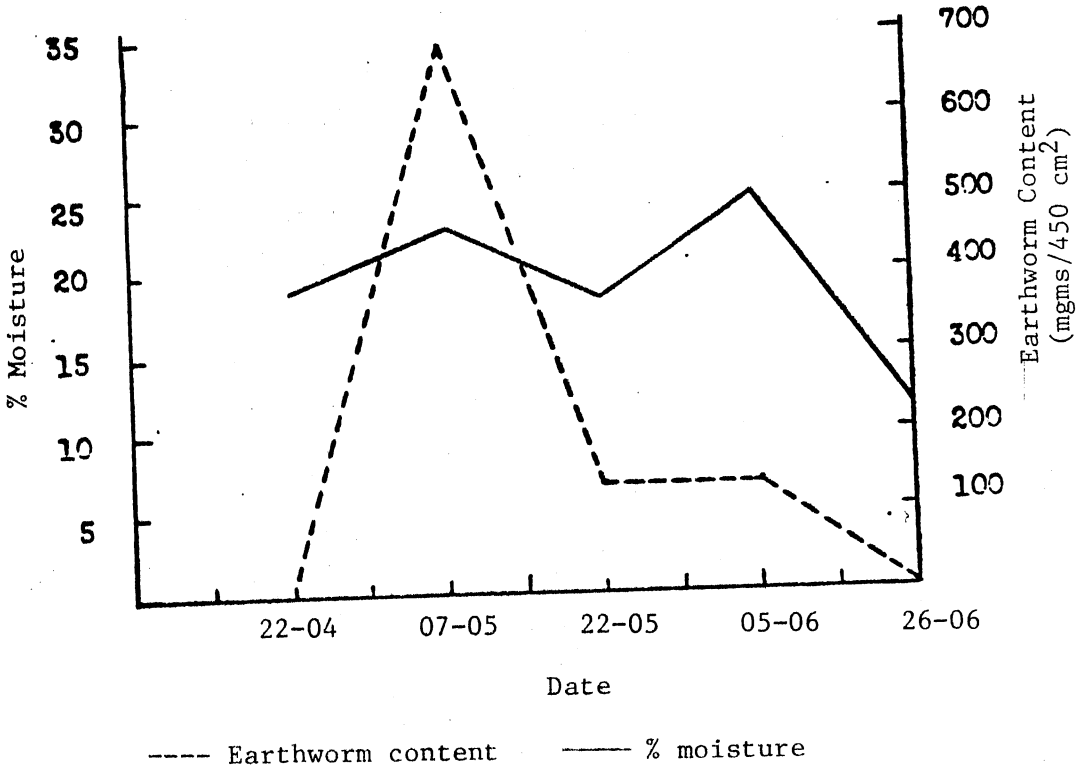


Figure 22. Average % moisture and total earthworm content at 15 sites sampled on the Ecology Preserve from 22 April to 26 June 1974.

CHAPTER VI

CONCLUSIONS AND RECOMMENDATIONS

The emphasis of this study was on the courtship display behavior and the habitat preferences of the American woodcock during its breeding season in northcentral Oklahoma. The initiation of courtship display behavior each season by male woodcock in northcentral Oklahoma was influenced by temperatures prevailing in January and early February, and appeared to correspond with the spring migration of woodcock through northcentral Oklahoma. Cold temperatures in January and early February resulted in late initiation of the breeding season, whereas warm temperatures at this time resulted in early initiation of the breeding season. Warm temperatures in early March curtailed all courtship display activity, resulting in a short breeding season.

The woodcock breeding season in northcentral Oklahoma was approximately 6 wks earlier than reported for other states. The average length of evening courtship displays by male woodcock in northcentral Oklahoma was shorter than in northern latitudes and approximately the same as in similar latitudes.

Two peaks of courtship display activity by male woodcock occurred. The first peak may have corresponded with the peak of migration of woodcock through the region. The second peak probably corresponded with renesting attempts or the peak of the hatching season. It is possible that young, subdominant male woodcock, who were relatively inactive in

the early part of the breeding season, became active in the latter part of the season and accounted for the second peak in courtship display activity.

Once the breeding season was under way, the meteorological factors most influential in depressing courtship display behavior of male woodcock were low temperatures, heavy rains, sleet, snow, and very high winds. As the breeding season progressed, the phase of the reproductive cycle of woodcock superseded the effects of harsh weather. Favorable weather and warm air preceding frontal passages stimulated courtship display activity, whereas unfavorable weather and recent cold weather frontal passages suppressed courtship display activity of male woodcock.

Light intensity was the major factor initiating courtship display behavior on a daily basis, with woodcock beginning their evening displays approximately 20 min after sunset and their morning displays approximately 20 min before sunrise.

A shift in the intensity of courtship display behavior from evenings to mornings as the breeding season progressed was attributed to the interaction of physiological, behavioral, and meteorological factors not fully understood.

Intensive territorial interaction among male woodcock was observed on the study area, including dual or tandem flights (Davis 1970). Physical contact between any two male woodcock participating in dual flights was never observed. Territorial behavior among male woodcock seemed to be a limitation to the usefulness of artificially created sites. The yearly presence of surplus subdominant male woodcock on the Preserve was suspected and their inactivity during part or all of the

breeding season was probably due to the territorial dominance of singing sites by older, more experienced woodcock.

Analyses of used and unused singing sites on the Preserve revealed that displaying male woodcock preferred sites that were sparsely vegetated, relatively close to either moisture or diurnal cover, well drained, and spaced adequately apart from each other (about 150 to 200 m). Feeding on singing sites was observed in the latter part of the breeding seasons throughout the study and was attributed to the gradual warming of the soil and subsequent surfacing of earthworms at this time. The creation of artificial singing sites by mowing was useful in setting back plant succession and the response by woodcock was excellent.

Important characteristics of spring diurnal woodcock cover in north-central Oklahoma were: close proximity to water, moist to set soil conditions, approximately 25 percent of the ground covered by vegetation, an understory cover dense enough to offer protection from predators and other disturbances such as grazing by livestock, and shade conditions that offer relief from hot summer temperatures and limit loss of soil moisture. Similar features characterized cover used by woodcock for nesting and during fall migration.

Fall reports of woodcock migrating through northcentral Oklahoma were most frequent during the 2nd or 3rd weeks of November. The absence of observations of woodcock throughout the study from late December through most of January indicate that there are few if any wintering woodcock in northcentral Oklahoma. Spring migration of woodcock through northcentral Oklahoma occurred in late January and early February. Observations of either woodcock or their sign in northcentral Oklahoma during the summer months were very few or nonexistent. The lack of

adequate moisture conditions and hot summer temperatures were probably responsible for this.

Heavy grazing by livestock appeared incompatible with good woodcock habitat at all seasons of the year.

The study of the habitat and behavior of the American woodcock in northcentral Oklahoma was unique for several reasons. The woodcock population studied was small and essentially restricted by land use practices to a limited area, but these same factors, plus the ease of access to the study area, enabled us to monitor the population closely. We were also able to analyze habitat components more intensively than is often the case in studies of this type. It was the first time that a small population of woodcock was studied so intensively through five successive breeding seasons (1971-75). The study area, the 62.3 ha Oklahoma State University Ecology Preserve, was on the fringe of the range of the woodcock in continental North America. The oak-prairie ecotone or savannah type of habitat on the study area was atypical in comparison to the better studied and more familiar habitat of the woodcock in northeastern states.

All available evidence, historical and contemporary, indicates that we have witnessed habitat colonization and/or range expansion by the American woodcock on the western periphery of its range. Opportunities to document such biological events are not common but were possible in this case by the woodcock's conspicuous breeding display and the localized presence of favorable habitat. Changes in land use practices in Oklahoma such as the building of detention reservoirs, the increase in pasture and decrease in cropland, and the control of prairie

fires seem to have created favorable habitat conditions for this very habitat-specific bird, the American woodcock.

Although the woodcock will probably never be a major game species in Oklahoma, there is evidence (Clark 1971, 1974) that the species is increasing in popularity over a wider portion of its range. The increasing number of sightings of woodcock in eastern Oklahoma (Smith 1975, personal communication) may mean an increased popularity of woodcock as a game species, at least in the eastern half of Oklahoma.

Management for woodcock in Oklahoma must take into account several factors. The amount of good quality habitat for woodcock decreases from eastern to central Oklahoma due to lack of adequate moisture conditions, hot summer temperatures, and unfavorable land use practices such as overgrazing. In addition, unpredictable temperatures and storm conditions in the spring of the year in northcentral Oklahoma seemed to make successful nesting and brood rearing difficult for woodcock.

This study has shown that though suitable, albeit perhaps marginal, woodcock habitat in northcentral Oklahoma is present in localized areas only, certain management practices are possible. In suitable habitat, light to moderate seasonal livestock grazing may be beneficial for retarding plant succession. The creation of artificial singing sites in favorable prairie habitats on an experimental management basis is strongly recommended. Woodcock habitat manipulation studies could be conducted on areas in the eastern half of Oklahoma where breeding displays have been observed.

Further research on the seasonal habitat preferences and food habits of woodcock in northcentral Oklahoma, using radio-telemetry and trained bird dogs to locate woodcock, could provide valuable information on

nesting, breeding, and seasonal cover preferences and thus enable realistic prairie woodcock management programs.

Ongoing census' of woodcock populations on their spring singing sites (especially in eastern Oklahoma), and continued monitoring of woodcock populations in Oklahoma through questionnaires sent to hunters by state and federal agencies are strongly encouraged.

The American woodcock is enjoyed by a wide variety of people. For the hunter, the woodcock is a challenging target and tasty table fare. For the bird watcher and nature enthusiast, observing the magnificent aerial dynamics of the male woodcock during the spring breeding season is reward enough in itself. Ultimately, woodcock management programs in Oklahoma will depend on the cooperation of landowners, the general public, and various state and federal agencies.

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APPENDIX

Table 22. List of common and scientific names of plants--after Fernald and Robinson (1908) and Waterfall (1966)

Common Name	Scientific Name
American beech	Fagus grandifolia
Alder	Alnus spp.
American hornbeam	Carpinus caroliniana
American elm	Ulmus americana
Ash	Fraxinus sp.
Aster	Aster sp.
Baldwin ironweed	Vernonia Baldwinii
Beggars ticks	Bidens sp.
Bermuda grass	Cynodon dactylon
Big bluestem	Andropogon Gerardii
Birch	Betula sp.
Black locust	Robinia pseudo-acacia
Black willow	Salix nigra
Blackjack oak	Quercus marilandica
Blueberry	Vaccinium spp.
Broad-leaf uniola	Uniola latifolia
Buckbrush	Symphoricarpus orbiculatus
Canada goldenrod	Solidago canadensis
Canada wild rye	Elymus canadensis
Chinquapin oak	Quercus Muehlenbergii
Chittamwood	Bumelia lanuginosa
Clover	Trifolium spp.
Croton	Croton capitatus

Table 22 (Continued).

Common Name	Scientific Name
Crown-beard	Verbesina helianthoides
Dallis grass	Paspalum dilatatum
Dogbane	Apocynum sp.
Dotted gayfeather	Liatris punctata
Eastern cottonwood	Populus deltoides
Eastern larch	Larix laricinia
Eastern redbud	Cercis canadensis
Eastern red cedar	Juniperus virginiana
Eupatorium	Eupatorium sp.
Fescue	Festuca sp.
Flax	Linum medium
Giant ragweed	Ambrosia trifida
Goldenrod	Solidago sp.
Gray birch	Betula populifolia
Green ash	Fraxinus pennsylvanica
Greenbriar	Smilax bona-nox
Hackberry	Celtis sp.
Hairy grama	Bouteloua hirsuta
Hawkweed	Hieracium aurantacium
Hawthorne	Crataegus sp.
Heath aster	Aster ericoides
Hickory	Carya sp.
Honeylocust	Gymnocladus dioica

Table 22 (Continued).

Common Name	Scientific Name
Hornbeam	Carpinus caroliniana
Indian grass	Sorghastrum nutans
Japanese brome grass	Bromus japonicus
Johnson grass	Sorghum halipense
Leafy elephant foot	Elephantopus carolinianus
Little bluestem	Andropogon scoparius
Meadowsweet	Spiraea alba
Mint	Caryophyllaceaea
Missouri goldenrod	Solidago missouriensis
Nettle	Urticaceae
Osage-orange	Maclura pomifera
Post oak	Quercus stellata
Poison ivy	Rhus radicans
Prairie acacia	Acacia angustissima
Prairie three awn	Aristida purpurea
Prickly pear	Opuntia sp.
Purple prairie clover	Dalea purpurea
Purple top	Tridens flavus
Quaking aspen	Populus tremuloides
Ragweed	Ambrosia sp.
Red maple	Acer rubrum
Red mulberry	Morus rubra
Roughleaf dogwood	Cornus Drummondii
Scribner panicum	Pancium oliganthes

Table 22 (Continued).

Common Name	Scientific Name
Sedge	*Cyperus* sp.
Silver bluestem	*Andropogon saccharoides*
Silver-leaf nightshade	*Solanum elaeagnifolium*
Slender lespedeza	*Lespedeza virginica*
Smooth sumac	*Rhus glabra*
Snow-on-the-mountain	*Euphorbia marginata*
Split-beard bluestem	*Andropogon ternarius*
Spruce	*Picea* spp.
Stiff goldenrod	*Solidago rigida*
Sumac	*Rhus* sp.
Switchgrass	*Panicum virgatum*
Sycamore	*Platanus occidentalis*
Tall dropseed	*Sporobulus asper*
Thistle	*Cirsium* sp.
Torrey nightshade	*Solanum Torreyi*
Western ragweed	*Ambrosia psylostachia*
White ash	*Fraxinus americana*
White pine	*Pinus strobus*
Wild bean	*Strophostyles* sp.
Wild grape	*Vitis* sp.
Wild violet	*Viola* sp.
Winged sumac	*Rhus copallina*
Wood sorrel	*Oxalis occidentalis*

Table 22 (Continued).

Common Name	Scientific Name
Yellow broomweed	*Gutierrezia dracunculoides*
Yucca	*Yucca glauca*

VITA[2]

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