Population Ecology of Woodcock In Wisconsin

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ABSTRACT

Information on woodcock distribution, breeding biology, habitat use, movements, and population dynamics gathered during a 13-year study in Wisconsin is summarized. From 1967 to 1980, censusing, nest searching, trapping and banding, radiotelemetry and observations of captive birds were employed to study various aspects of woodcock behavior and ecology. Field work took place primarily in the north central portion of the state and effort was confined to two large study areas during the final five years.

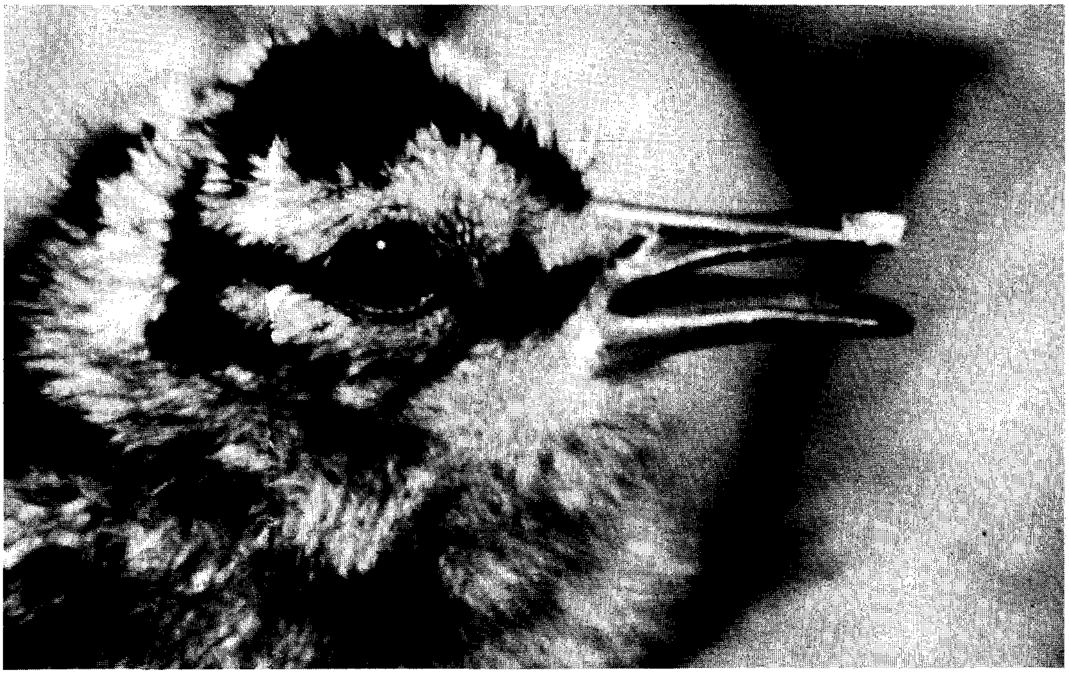
Counts of singing males conducted within our study areas and along routes distributed throughout the state provided indices to woodcock population fluctuations during the course of the study. In 1968, the federal singing ground survey was expanded and improved in Wisconsin through the inclusion of 119 randomly selected routes. In addition to the statewide survey, an intensive census of singing males was carried out each spring during 1976-80 throughout blocks of land totaling approximately 3,000 acres within our study areas.

Nest searches which resulted in locating 220 nests and more than 300 broods formed the basis for an investigation of woodcock breeding biology. Information gathered on nesting chronology, nest site selection, nest success, and chick growth is included in the present report.

Considerable data on woodcock movements and mortality were generated through trapping operations which yielded nearly 12,000 captures. More than 10,000 birds were banded during the course of the study, about 1,000 of which were subsequently recaptured on one or more occasions. Recovery data from approximately 400 Wisconsin-banded woodcock are reviewed and our present understanding of migration and homing is discussed.

Additional information on movements and habitat use was also obtained through analysis of approximately 900 locations accumulated during 1976-80 from 38 radio-tagged birds. Birds were tracked for periods up to 100 days despite problems with transmitter harnesses.

Published data from land-use and forest inventories were evaluated for their usefulness as measures of woodcock habitat in Wisconsin. Habitat types important to woodcock are discussed and recommendations for habitat management are provided.



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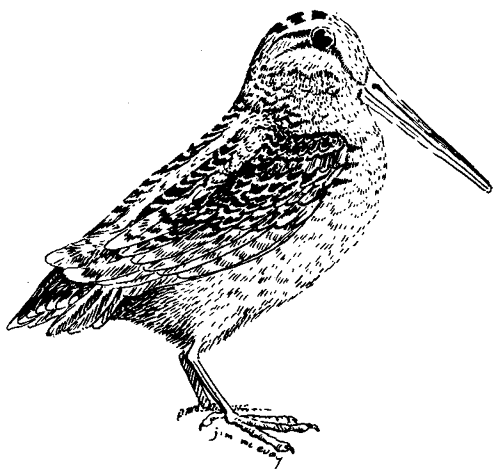


Introduction

The American Woodcock is a shorebird that lives in the woods. He is a recluse, maintaining such a low profile that most folks who live in woodcock country are unfamiliar with the species. Typical of the average person's cognizance of the bird was the old-timer who responded to our request to trap woodcock on his property with, "Woodcock? We always called 'em woodchucks!"

When Aldo Leopold described the sky dance of the woodcock in *A Sand County Almanac*, he indicated there were many mysteries surrounding the species. In an effort to learn more about the bird, Leopold initiated a study of sex and age ratios which was continued by others after his death in 1948 and eventually published (Greeley 1953). But because the woodcock was pursued by a relatively small number of hunters, the species received little attention in most research and management programs. Thus, most of the woodcock mysteries mentioned by Leopold persisted long after his death.

In the mid-1960's, however, efforts by a group of state and federal organizations and citizen groups were finally successful in obtaining special funds earmarked for new and accelerated studies of migratory upland game birds. The Accelerated Research Program began in 1967 and was administered by the U. S. Fish and Wildlife Service. The Wisconsin Department of Natural Resources (DNR) was the first agency to secure a contract to conduct research under the new program, with a woodcock and mourning dove project getting underway in September 1967. Two additional woodcock studies followed with field work on the final study being completed in 1980. Although some of the results of these studies have been published earlier (Hale and Gregg 1976, Gregg and Hale 1977, Gregg 1982), the following report is a compilation of our findings during the entire 13 years (1967-80) of woodcock research in Wisconsin.

The overall goal of the study was to obtain information on the present status and population dynamics of the woodcock in Wisconsin which required us to examine many aspects of the life history and ecology of the bird. Several objectives were established as an aid in meeting that goal, including: (1) determine woodcock distribution and density within the state during various seasons, (2) determine causes and rates of mortality for Wisconsin woodcock, and (3) identify valuable habitat types in Wisconsin and develop techniques to assure their continued availability.

In summarizing our results, I attempted to incorporate much of the literature in order to provide the reader with an overview of woodcock biology and management. This approach was deemed worthwhile since it aided in placing our efforts in perspective and because much current information is contained in woodcock symposium proceedings which are not always available to those persons responsible for managing the woodcock and its habitat.

STUDY AREAS

During the early years of the study, efforts involved in establishing random routes, nest/brood searching, and locating summer banding sites resulted in field work occurring over a large portion of the state. Either nest hunting or summer trapping was attempted at some point during the study in about one-third of the counties in the state. But the major share of our field work took place in the north central counties of Sawyer, Price, and Lincoln (Fig. 1).

Those counties are situated in what is known as the Northern Highland Geographical Province. The geological formation of the region is primarily glacial drift and the relatively flat topography and complex soils reflect the results of glaciation. Approximately 75% of the land area in the three counties is classed as commercial forest. Forestry and dairy farming are the prevailing types of land use in the area.

The climate of the region is classed as continental. Summers are relatively short and warm; winters are relatively long and cold. Annual precipitation averages 32 inches and peaks during June (Wisconsin Statistical Reporting Service 1967). Although droughts occur only occasionally, severe drought conditions prevailed throughout north central Wisconsin between the summer of 1976 and the spring of 1977. An emergency closure of the hunting season was imposed on 21 September 1976 and remained in effect until 20 October in 10 central Wisconsin counties because of the extreme fire hazard. Thunderstorms occur an average of 30 days/year in the region and are sometimes accompanied by damaging wind. On 4 July 1977 a very destructive thunderstorm moved across northern Wisconsin, causing extensive damage to trees and property in portions of Price and Sawyer counties.

Field work during the final 5 years of the study was concentrated in two study areas, both on publicly owned lands. The Kimberly-Clark Study Area (KCSA) consisted of the state-owned Kimberly-Clark Wildlife Area, while the Hay Creek Study Area (HCSA) consisted of the Hoffman Lake-Hay Creek Wildlife Area and an adjacent portion of the Chequamegon National Forest (Fig. 1).

The 8,300-acre KCSA is located 15 miles southwest of Park Falls and lies adjacent to an extensive area of swamps and bogs known locally as the "million-acre swamp". Lowland vegetation types are also abundant in the KCSA, accounting for 53% of the total land area. Management of the area is targeted at sharp-tailed grouse, and involves efforts to convert the forested uplands to mixtures of grass and brush by means of prescribed fire. Upland soils in the area are silt loams, predominantly of the Stambaugh-Fifield Association (U.S. Soil Conservation Service 1966). Poorly drained soils in the area belong to the Peat and Peat-Warman associations.

Aspen is the primary cover type on the uplands and occupies about 20% of the total land area. Nearly 40% of the upland acreage is of an open or brushy character due to repeated burns. Black spruce and alder are the two major lowland cover types and together comprise 47% of the land area. The forested portions of the study area were extensively damaged and a trailer which functioned as our field headquarters was blown down during the 1977 windstorm. Due to access problems resulting from the storm and to difficulties in achieving planned objectives while working in two relatively large study areas, our efforts were terminated in the KCSA at the end of the 1977 field season.

The HCSA is located 10 miles northeast of Park Falls and encompasses about 13,000 acres. Upland soils are sands and sandy loams belonging to the Iron River-Pence and Vilas-Pence associations (U.S. Soil Conservation Service 1971). Lowland soils are in the Organic Soil Association and include organic and alluvial soils in poorly drained basins and floodplains. Vegetative cover in the area is categorized as 57% upland and 43% lowland. Aspen is the most extensive forest type, accounting for 25% of total acreage. Other cover types of value to woodcock, including openings, upland brush, and alder, occupy 12% of the area. Management efforts on state-owned lands in the area are directed at improving habitats for ruffed grouse and deer.

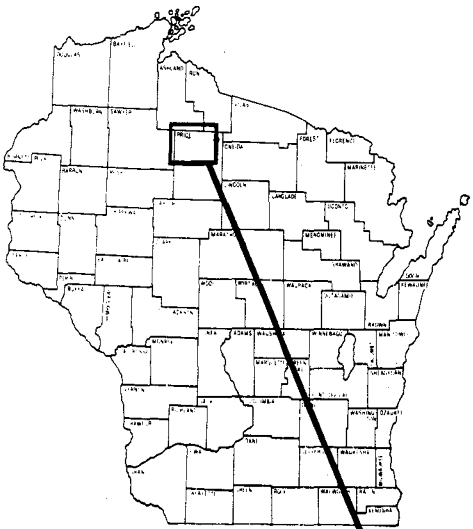
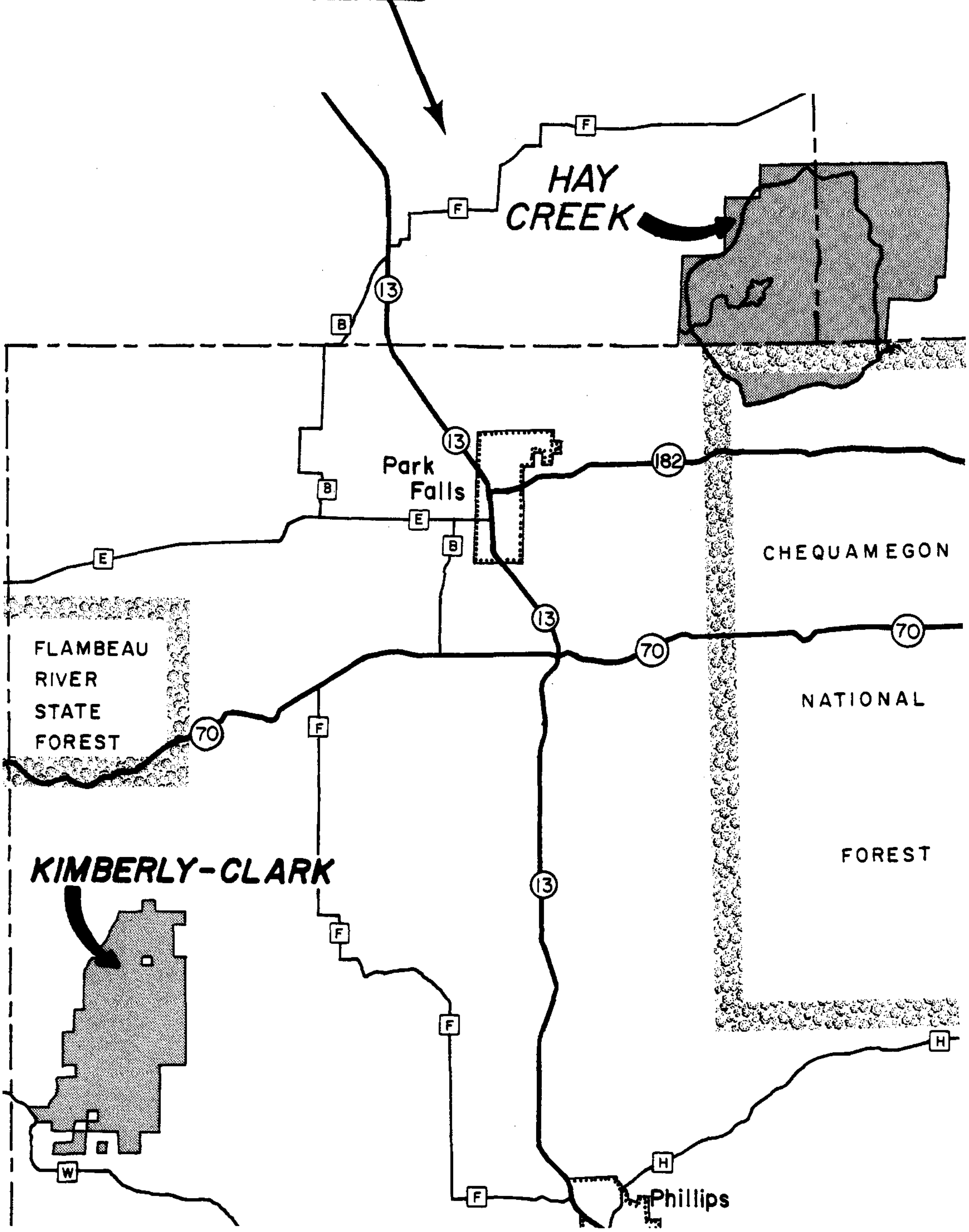


FIGURE 1. Location of primary woodcock study areas.



Methods

Censusing

In the spring, male woodcock carry out their courtship displays at dusk and dawn in forest openings called singing grounds. While engaged in these displays, the males emit characteristic vocalizations including the *peent* call given on the ground and aerial chirping which is done in conjunction with wing twittering to produce the flight song. These calls form the basis for censusing breeding woodcock. Counts of singing males conducted in the same areas each spring provide a measure of their relative abundance.

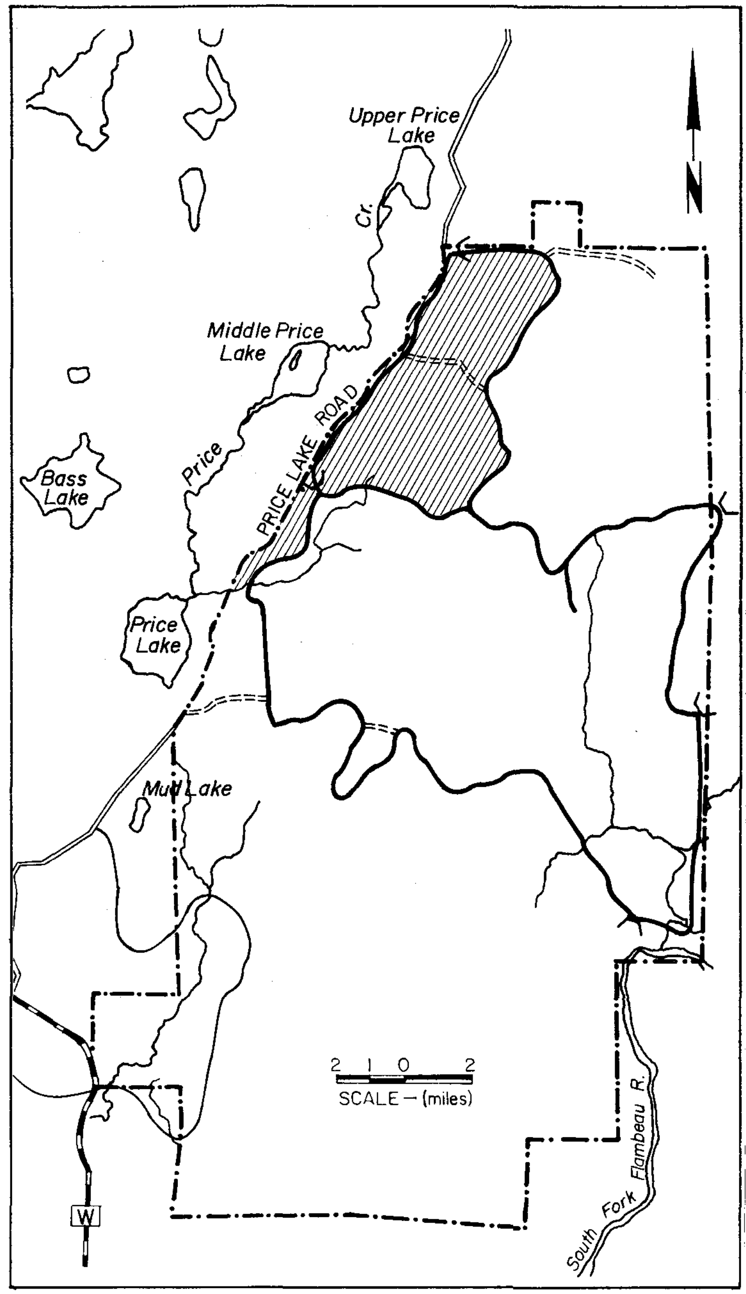
Mendall and Aldous (1943) evaluated several methods of censusing woodcock in Maine and recommended a yearly count of occupied singing grounds as the most reliable technique. Organization of such counts into a systematic survey soon followed throughout the woodcock range and the singing ground survey now serves as the sole method of monitoring trends in woodcock breeding populations. The survey is coordinated by the U.S. Fish and Wildlife Service and involves roadside counts of displaying males along selected routes. The singing ground survey has been periodically evaluated (Kozicky et al. 1954, Goudy 1960, Duke 1966, Tautin 1977), which has resulted in improvements in both the methods used in selecting route locations and in conducting the counts.

A singing ground survey has been conducted annually in Wisconsin since the early 1950's to provide an index of woodcock breeding population size. During the early years of the survey, routes were selected by cooperators in areas where woodcock were expected to be heard. Because the survey sampled only the better woodcock habitats, counts probably did not accurately reflect population changes. In addition, only 16 routes were involved so a relatively small portion of the breeding range within the state was represented. Cooperators were provided with few guidelines in establishing routes, so variations occurred in route length, number of stops, and distance between stops. Consequently, difficulties were encountered in comparing counts between routes or between years. Wisconsin's singing ground survey was reorganized in 1968 with the addition of 119 routes selected randomly throughout the state.

The transition to random routes was accomplished during 1968 and 1969, with an attempt made to survey both previously established and new routes during the conversion period. The improved distribution of random routes enabled the survey to provide information on regional differences in breeding woodcock densities. Comparability between routes was also improved with the adoption of random routes, since each random route was 3.6 miles long and consisted of 10 stops, 0.4 mile apart.

Counts of occupied singing grounds were taken in the KCSA during 1975-77 and in the HCSA during 1976-80. The KCSA included a block of land 1,100 to 1,500 acres in size (Fig. 2). In the HCSA, a 1,300-acre block was censused in 1976 and in 1977-80 a strip count was carried out along 18 miles of roadway circumscribing the study area (Fig. 3). The Hay Creek census transect was divided into 18 segments, each 1 mile in length. Transect width was determined to be 440 yd, based on an estimated 220-yd hearing distance for singing males.

Censusing was done during both morning and evening performance periods with up to 12 cooperators involved on some days. Counts were conducted on foot, with each cooperator working a designated block of land or stretch of roadway during any one session. Only singing grounds occupied on two or more occasions were included in annual totals.



Nest and Brood Searches

Nest searching began 1 to 2 weeks after the first woodcock was observed each spring and continued until all nests had hatched. Nest searches were carried out in a variety of habitats, but most effort was expended in young, second-growth woodlands and along the edges of upland openings that were reported to be preferred nesting habitats (Mendall and Aldous 1943, Ammann 1970). During the 1969-71 nesting seasons, searching occurred over a broad area including locations in southeastern,

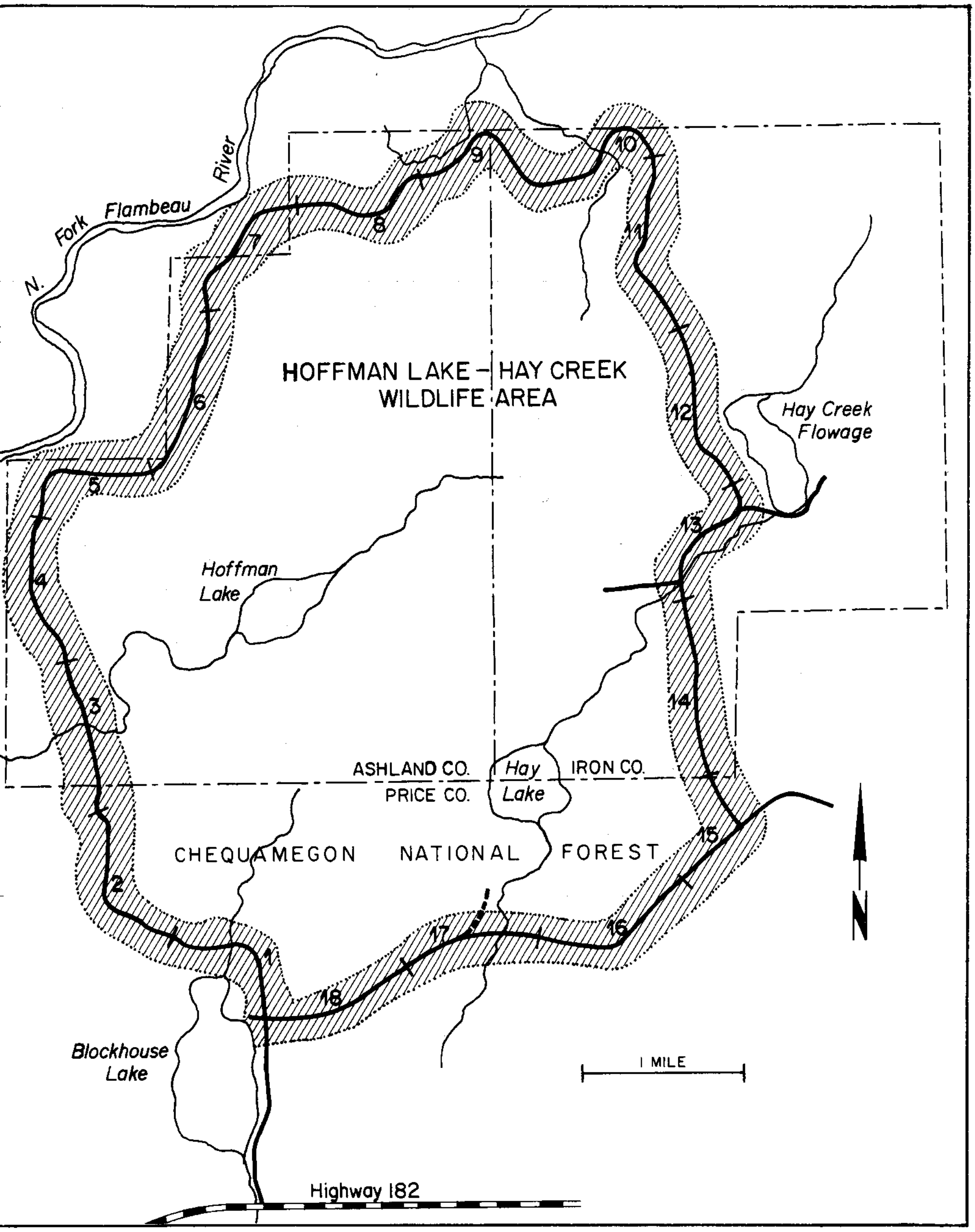


FIGURE 2. Woodcock census area on the Kimberly-Clark Wildlife Area. (Left)

FIGURE 3. Woodcock census area on the Hoffman Lake-Hay Creek Wildlife Area. (Right)

central, and northern Wisconsin. In subsequent years, nest hunting was confined to the north central portion of the state and during 1976-80 was restricted primarily to the KCSA and HCSA.

Nest hunting was done on foot with the searching crew typically consisting of 2 men and 1 or 2 bird dogs. A small number of cooperators assisted in searching efforts during 1 or more years, especially in 1975 when members of the state chapter of the Ruffed Grouse Society were invited to participate. Several high school classes also provided assistance in 1978. Records were maintained on man-hours of searching time, woodcock and ruffed grouse flushes, and all nests discovered.

When a nest was found, its location was marked with a small piece of flagging placed a short distance from the nest. At each nest the following data were recorded: age and type of surrounding forest stand; soil drainage; distance to nearest opening and to other known nest sites; and amount of concealment. In addition,

Counts of displaying males were conducted each spring to provide an index to woodcock population changes within our study areas.

vegetation surrounding all nest sites found during 1973 and 1974 was measured and analyzed (Gregg and Hale 1977).

Eggs from several clutches were weighed with a Pesola spring scale and egg dimensions were measured with vernier calipers. Eggs in those clutches were individually numbered to determine weight changes during incubation. Nest fates were classified as successful, destroyed by predators, deserted, or unknown. A nest was considered successful if at least 1 egg hatched. Successful nests contained chicks or egg shells having the membrane separated from the shell and exhibiting a characteristic lengthwise splitting and infolding (Mendall and Aldous 1943, Wetherbee and Bartlett 1962). Eggs from deserted nests and those remaining in successful nests were opened to determine fertility and stage of development. Egg shells from several nests were collected in 1971 in support of an investigation of changes in shell thickness (Kreitzer 1973).

The assistance of several high school groups in 1978 provided sufficient labor to intensively search several coverts in order to gain information on woodcock nesting densities. Ten of the 1-mile-long census segments were selected for intensive nest searching. A strip of cover 41 ft wide was searched on each side of the road resulting in coverage of a 10-acre strip within the census block. Generally, 10-15 students walked abreast down one side of the road and then back on the other side to cover each strip. Students were offered a reward incentive of $1/nest and were provided with an orientation session which included viewing a nesting woodcock. At least two checks were scheduled for each area during the nesting season, the first pass being made during the last week of April and another during the second week of May.

Searching Efficiency. Because estimates of nest density based on number of nests found in a particular area have little value without some knowledge of the proportion of existing nests that are discovered, simulated nests were used to provide a measure of searching efficiency. Ten artificial woodcock nests, small wooden blocks painted with camouflage colors, were placed in each of the areas scheduled for searching. To parallel woodcock nesting phenology, half of the simulated nests were put out prior to the first search and the remainder before the second search.

Predation Study. To obtain a index of predator activity and woodcock nesting predation, 100 dummy nests were set out on the KCSA and HCSA during the 1972 nesting season. Two pheasant eggs were used in each of the dummy nests. Nests were placed in habitats similar to those used by nesting woodcock and, in several cases, artificial nests were located on or near the exact spot where active nests had been found in previous years. Two 21-day exposure periods covered the interval of peak woodcock nesting activities in northern Wisconsin.

Twenty-five early nests were established in each study area in late April. These were checked after 10 days of exposure and picked up at the end of 21 days, at which time 25 late nests were set out in each area. When checked, a nest was considered destroyed if 1 or both eggs were broken or missing.

A time-lapse movie camera (Temple 1972) was also employed to record predation. The camera was set on a nearby

Pointing dogs were a necessity in locating broods because of the birds' effective camouflage.

Woodcock chicks have big feet and can be banded soon after hatching.

stump or on a small stool overlooking an active woodcock nest. The camera was housed in a waterproof box and included a timing-triggering device and an automatic night shutoff unit.

Trapping and Marking

The primary purpose in banding migratory game birds, including woodcock, is to obtain information on the characteristics of populations which can be used for management (Geis 1972). This information can be obtained only through a scientifically based banding program that ensures that adequate and representative samples of birds will be marked. The success of a banding program thus hinges upon the availability of tried and proven capture techniques.

Wilbur (1967) listed five methods for live-trapping woodcock and all were used to varying extents during the study: mist nets, spotlights, cloverleaf traps, decoy traps, and hand nets along with bird dogs. Despite the available array of woodcock capture methods, Owen (1977) indicated that there remains a need to make banding operations more efficient by improving capture techniques.

All captured birds were banded with standard U.S. Fish and Wildlife Service bands. In addition, some birds were marked with ponchos (Pyrah 1970), wing tags (Morgenweck and Marshall 1977), fluorescent paint (Keith 1964), or radios (Godfrey 1970). Sexing and aging of flying birds followed methods described by Martin (1964). The combination of feather patterns and molt condition enabled three age classes to be recognized during the summer: birds banded the same year they hatched (hatching year or HY birds), birds hatched the preceding year (second year or SY birds), and birds hatched earlier than the preceding year (after second year or ASY birds). Flightless chicks were aged using techniques suggested by Ammann (1967).

Mist Nets. Although Mendall and Aldous (1943) were frustrated in their pioneering attempts to use "Italian bird nets" to capture woodcock, subsequent studies (Sheldon 1961, Martin and Clark 1964, Gregg 1972, Whitcomb 1974) have demonstrated the usefulness of the technique. Mist netting was the primary capture method employed during the study, with up to 120 nets being deployed by the midsummer peak of capture activities. During the spring, nets were set on singing grounds to capture performing males. Throughout the summer and fall, nets were set in clear-cut areas used by the birds for feeding and roosting. Woodcock use of cutover areas diminished in response to rapid regrowth of vegetation, but construction and maintenance of small openings in these locations extended their usefulness as netting sites (Hale and Gregg 1976).

Spotlights. The combination of strong lights and long-handled nets to capture woodcock has received considerable use on wintering grounds (Glasgow 1958). Use of night lighting to capture woodcock in southern Louisiana represented a revival of "firelighting" and "bec thrashing" techniques used in the early

Mist nets were the primary capture method employed during the study.

Aspen clear-cuts provided attractive feeding and roosting areas for woodcock but rapid regrowth of vegetation limited their usefulness as netting sites to 1 or 2 summers following logging. (Top)

The construction of small openings within a cut-cover area, however, enabled us to continue netting operations for up to 10 or 12 years after logging. (Bottom)

1900's to obtain woodcock for market. Martin and Clark (1964) were first to report using night lighting to capture woodcock for banding on the breeding grounds. But the night hunters' headlights they used were effective only on dark nights, so stronger, hand-held spotlights were developed by Rieffenberger and Kletzly (1967).

Equipment used in the present study was similar to that described by Rieffenberger (1969), except single-beam spotlights were employed instead of a combination flood-spotlight. Night lighting was generally used to capture woodcock in the same situations where mist nets were operated, i.e., on singing grounds during the spring and in clear cuts and other forest openings during the summer and fall. During those years of the study when banding was a priority activity, night lighting and mist netting were used in conjunction throughout the summer. Mist nets were operated during the crepuscular flight period and night lighting was carried out thereafter, with the amount of time spent on a particular evening being dependent upon the availability of suitable openings and the level of capture success.

Funnel Traps. Small cloverleaf traps of the type described by Liscinsky and Bailey (1955) and modified by Martin and Clark (1964) were used to capture woodcock in diurnal habitats. Up to 25 traps were operated in the Hay Creek Study Area each summer during 1978-80. An effort was made to search a potential trapping area before setting out traps to ensure that traps were placed in locations frequented by woodcock. Although most traps were set on woodcock flush sites, some traps were also placed in locations which appeared to contain suitable woodcock habitat.

Bird Dogs. The technique of locating woodcock broods with the aid of bird dogs was first attempted in 1937 by Gustav Swanson and described by Mendall (1938). The capture method was adopted by both Wright (1952) and Liscinsky (1962) and was refined by Ammann (1963, 1977). In Wisconsin, pointing dogs were used to locate broods for banding each spring during 1969-80. Young chicks generally remained motionless when pointed by the dog and could be picked up by hand. Brood hens and flying chicks were captured which short-handled nets. Bill length, weight, and feather development were recorded for captured chicks.

Decoy Traps. Norris et al. (1940) studied the territorial behavior of male woodcock in Pennsylvania by placing mounted decoys on singing grounds. When the reaction of the males was found to be amorous instead of agonistic, traps were designed to capture the birds as they attempted to copulate with the decoys. Sheldon (1967) constructed more complex, automatic decoy traps which he used to capture approximately 800 woodcock in Massachusetts.

Funnel traps were generally placed in moist areas which contained signs of woodcock use, such as splashings or probe marks. (Top)

Single captures were the norm in funnel traps, making the method relatively inefficient in comparison to mist nets. (Bottom)

In the present study, 4 decoy traps were constructed and operated occasionally during two spring seasons. In a few instances the male occupant of the singing ground was attracted to the decoy, but no captures were recorded. Mist nets, on the other hand, were a very effective method for capturing woodcock on their singing grounds, especially when used in combination with taped courtship calls. Because decoy traps were relatively unproductive in comparison to mist nets, little reliance was placed upon them as capture tools.

Radiotelemetry

Information on woodcock movements and habitat utilization was obtained from radio-tagged birds during 1976-78. AVM model SM-1 transmitters were powered with 1.35V mercury cells and equipped with 10-inch-long whip antennas of steel guitar string. The radio package was potted in epoxy and dental acrylic and attached to birds by means of a double loop harness (Dunstan 1972) or elastic wing loop harness (Godfrey 1970). During the initial year, 1.2-g and 2.4-g batteries were used on radio packages for male and female woodcock, respectively, due to the smaller body size of males and evidence of their adverse reaction to radio tagging (Ramakka 1972). The larger batteries were used exclusively during subsequent years, however, because their greater longevity decreased the need to recapture birds to replace transmitters. Use of the larger battery produced a radio package averaging 5.5 g in weight with a calculated life expectancy of 120 days.

AVM model LA-12 receivers were used with both vehicle-mounted and hand-held antennas to locate instrumented birds. Additional aid in locating radio-tagged birds was provided by a directional antenna affixed atop a 60-ft-high portable tower erected in the Hay Creek Study Area in 1977. When birds could not be located from the ground, aerial searching was employed using antennas attached to the wings of the aircraft. Reception distance varied depending upon the density of the vegetation between the transmitter and receiving antenna. Range was maximized as receiving antenna height was increased. Signals could be picked up from the ground using hand-held gear only about 0.25 mile away, but could be heard up to 2.5 miles away using an aircraft.

Birds were monitored on a daily basis. An effort was made to obtain both diurnal and nocturnal locations for each bird, but capture and banding operations often made it impossible to track birds in the evening. For each contact with a radio-tagged bird, the following information was recorded on prepared data forms: time, weather, activity, habitat type, accuracy of the location, and comments on the appearance and behavior of the bird if observed or flushed. Each radio fix was recorded in the field on aerial photos.

The use of radio-tagged birds enabled us to identify those habitats used by woodcock during the summer.

Penned Woodcock

Data on growth, plumage development, and activity patterns were obtained from 17 woodcock maintained in captivity for varying lengths of time during 1972-74. Birds were caged in a 12 ft × 12 ft pen having a ground floor. Three sides of the pen were covered with plastic-coated poultry netting and the remaining side was of plywood. Boards were placed along the bottom of each of the three sides made of netting to provide a visual barrier to the birds and reduce the likelihood of injuries from abrasion. The plywood side was equipped with a small piece of one-way glass which allowed us to view the birds without disturbing them.

To provide a measure of activity, the floor of the pen was gridded into 4 sections with wooden strips. Each time a bird crossed a grid line, it was counted as 1 unit of activity. Birds were color-marked to facilitate their identification. Food and cover, in the form of pans of earthworms and small conifer trees, were provided in each section of the pen. Earthworms were obtained from worm beds maintained by project personnel or purchased from commercial bait dealers.

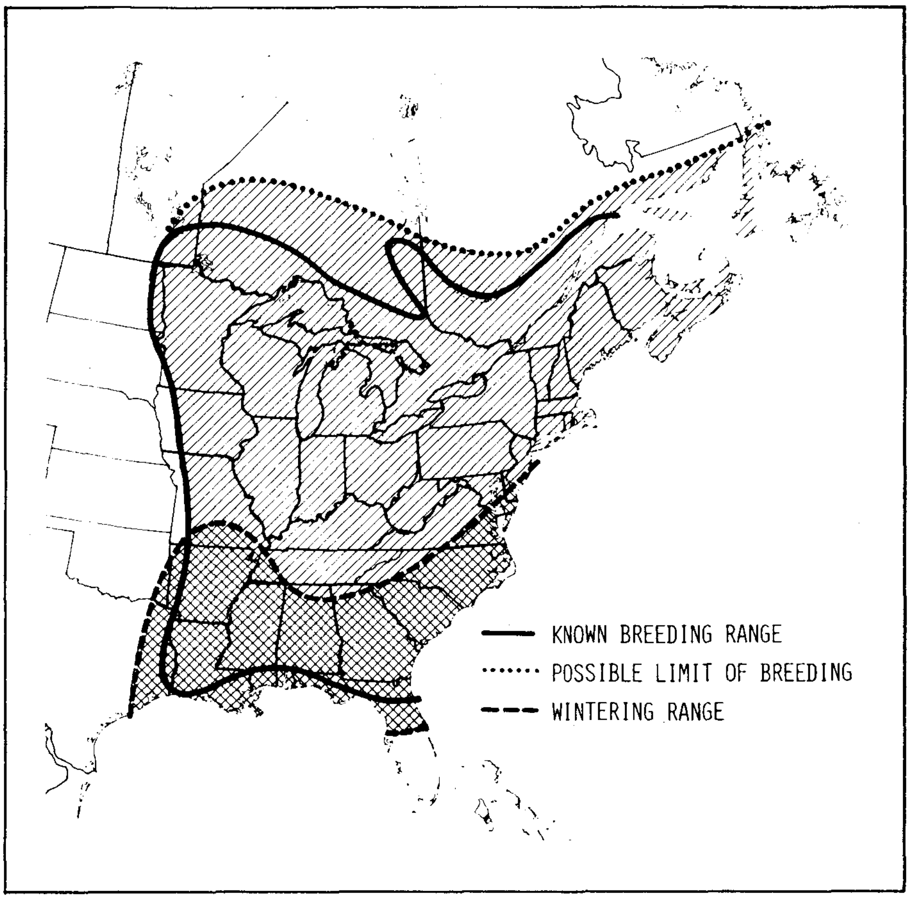


FIGURE 4. Woodcock breeding and wintering ranges (from Sanderson 1977).

General Distribution and Population Status

Except for an apparently unsuccessful transplant of a few hundred birds in California in 1972-73, woodcock are restricted to forested regions in the eastern half of the continent (Fig. 4). Published range maps have differed considerably over the years, but revisions have resulted from increases in available knowledge and not from real changes in distribution. Mendall and Aldous (1943) prepared range maps which reflected their beliefs that optimum breeding habitat occurred only in eastern Maine and the Maritime Provinces and that most woodcock wintered in Louisiana. Sheldon's (1967) winter range map remained unchanged from its predecessor, but additional observations enabled him to extend the accepted northern limits of the breeding range and to recognize that woodcock abundance during the breeding season was not confined to the east. The present "state of the art" range map (Owen 1977), although based on increased information from the singing ground survey and banding analyses, still needs some refinement (Fig. 4).

The distribution of band recoveries from the western and eastern edges of the woodcock's range has revealed two relatively distinct harvest units and migration routes, so Owen (1977) recommended managing woodcock on a flyway basis using two management units, Atlantic and Central. Coon et al. (1977) examined available recovery data to define the most appropriate configuration for the two woodcock management units and suggested the use of the existing boundary between the Atlantic and Mississippi waterfowl flyways. In recent years, woodcock population data from the Atlantic and Central regions have been treated separately since there are indications that the two regions differ in weather patterns, hunting pressure, and trends in land use.

Breeding Range

The breeding range of the woodcock extends along the east coast from southern Newfoundland to northern Florida and west as far as southeastern Manitoba and the eastern edge of Texas. Highest breeding densities occur in the northern portion of the range, including the northern Great Lakes region, northern New England, and Canada. The woodcock is generally considered an uncommon to rare breeder in most southern states, but recent work in Alabama (Roboski and Causey 1981) has revealed that some southern states may make a more important contribution to total annual reproduction than had previously been believed.

Winter Range

Information on woodcock distribution throughout the wintering grounds is scanty. Descriptions by Oberholser (1938) and others of the incredible abundance of woodcock in Louisiana led some subsequent writers to speculate that up to 80% of the continental population wintered there (Duffy 1967, Dalrymple 1970). Louisiana's share of wintering birds was probably overestimated, however, judging by results of a study by Pursglove and Doster (1970) which revealed surprisingly high populations in South Carolina, Georgia, Florida, Alabama, Arkansas, and Mississippi. Furthermore, an analysis of recoveries of Louisiana-banded woodcock (Martin et al. 1969) revealed that most of the birds wintering there were produced west of the Appalachian Mountains and very few were derived from the New England states and Maritime Provinces. A similar examination (Krohn and Clark 1977) of the recovery distribution of woodcock banded in eastern Maine showed that most of those birds wintered in a region extending from southern Virginia to northern Florida.

Wisconsin Range and Status

Historical Accounts. The first published reference to woodcock distribution in Wisconsin was that of Hoy (1853), who said that the species had been increasing rapidly in the Racine area since his first observation there in 1847. Likewise, Barry (1854) reported woodcock sightings in the same area and indicated the species was increasing. Grundtvig (1895) wrote that woodcock were breeding in great numbers near Shiocton in Outagamie County, and Schoenebeck (1902) reported woodcock to be common summer residents in northeastern Wisconsin. Although Kumlien and Hollister (1903) reported woodcock in suitable localities throughout the state, they believed the population was declining from "too close shooting, settlement of the county, and the draining and drying up of its natural resorts." Concern about the status of the bird in southern Wisconsin was also expressed by Cahn (1913), who reported the species as being practically exterminated in Waukesha County, and by Schorger (1929), who advised removing the species from the list of game birds since it was seldom that more than 2 or 3 birds were flushed per day in Dane County.

Settlers began arriving in northern Wisconsin shortly after the Civil War, but no information is available concerning the number of woodcock they encountered. However, an early vegetation map of the state (Hoyt 1860) revealed that dense forests covered much of northern Wisconsin at that time, an indication that woodcock habitat was scarce. The combination of logging, which peaked about 1900, and extensive forest fires, which continued intermittently until the early 1930's, probably created conditions that were more habitable for woodcock than those that had existed prior to settlement, despite Pettingill's conclusion in 1936 that the woodcock was common nowhere in Wisconsin except possibly the northernmost counties.

There was scanty information on woodcock numbers and distribution in the state during the 1930's and 1940's, but the birds were probably abundant in northern and central Wisconsin during that time since other species which shared the woodcock's preference for open, brushy habitats were known to be faring very well. Populations of sharptails (Grange 1948) and deer (Bersing 1956), for example, reportedly reached unprecedented abundance during that period.

Later studies have depicted the species as a common breeder within the forested portion of the state. In western and west central Wisconsin, Buss and Mattison (1955) reported the woodcock as a common resident and migrant in Dunn County as did Kemper (1973) in Chippewa and Eau Claire counties. Faanes and Goddard (1976) listed the species as a common migrant and fairly common nesting bird in Pierce and St. Croix counties. In the northwestern part of the state, Bernard (1967) listed the woodcock as a common migrant and summer resident in Douglas County. In northeastern Wisconsin, Vanderschaegen (1981) considered the species to be a fairly common summer resident in Forest, Vilas, and Oneida counties.

Singing Ground Survey. Results of the singing ground survey revealed an expected relationship between the distribution of woodlands and woodcock in Wisconsin, with birds being heard on nearly every route within the northern forested part of the state and on only a few of the routes within the intensively farmed southern portion of the state (Fig. 5). When examined on a regional basis, the relationship between woodcock breeding populations and forest area was less than perfect due to differences between various forest types in their suitability as woodcock habitat. Nevertheless, a comparison of average number of birds per route with the proportion of forested land in each of the various forest survey units revealed a fairly close association (Table 1).

TABLE 1. *Woodcock singing ground counts and forest land area in Wisconsin.*

Region	Forest Area* (1,000 acres)	Percent State Total	No. Woodcock Routes	Mean No. Woodcock Heard (1968-75)	Percent of State Total
Northwest	5,431	36	29	129	42
Northeast	4,320	29	22	98	32
Central	2,857	19	21	44	14
Southwest	1,512	10	20	8	3
Southeast	825	6	27	29	9
Totals/means	14,945	100	119	308	100

* From Spencer and Thorne 1972.

Despite the fact that no birds were heard on the majority of routes in southern Wisconsin, breeding woodcock are probably now present in suitable habitat in every county. In Dodge County, for example, woodcock were recorded at only 1 of the 40 listening points along the 4 routes within the county, yet several displaying males could be heard each spring in the Horicon vicinity and suitable habitat existed in several other spots within the county. But in regions containing a high percentage of cultivated land, there was little chance that a route would fall in favorable habitat.

Population Trends. The singing ground survey is our best source of knowledge on woodcock population trends, both in Wisconsin and throughout the remainder of the breeding range. Prior to 1968, however, the survey provided relatively little information on statewide population trends due to the small number of routes that were checked annually. With randomization of the survey, the average number of routes surveyed each year increased from 13 during the 1959-67 period to 79 during 1968-82. In addition, those random routes along which no birds were heard for two consecutive years were placed in a "constant zero" category and included in year-to-year comparisons even though not field checked every year. Thus, an average of 87 routes produced counts which were considered comparable from one year to the next during the period 1969-82.

The breeding population index, based on the singing ground survey results, did not change significantly between 1968 and 1982. The index for the Central Region as a whole, however, increased significantly during that same period, with the number of birds heard on comparable routes growing at an average rate of 2% each year (Tautin 1982). Although Wisconsin and Central Region population trends differed in their statistical validity, year-to-year changes in the breeding population indices were very similar (Fig. 6). The apparent synchrony of annual population changes throughout the region indicates that some factor which affected woodcock mortality or recruitment in several states concurrently, such as weather, was responsible for short-term fluctuations.

Wisconsin's woodcock population index fluctuated very little from 1968 to 1976, but increased substantially during 1977-79 and declined during 1980 and 1981. Despite year-to-year changes that were occasionally quite large, our woodcock population index has remained fairly stable over the long run and probably reflects a stable habitat base. A long-term decline in the index, such as has occurred in the Atlantic Region, could be indicative of excessive harvests or declining habitat and should be cause for concern. Although there is no evidence of any problem yet in Wisconsin, our annual woodcock harvests are increasing and habitat quality is declining due to the increasing maturity of our forests. Because constraints upon woodcock population size are probably destined to increase, it behooves us to continue monitoring population changes through the singing ground survey.

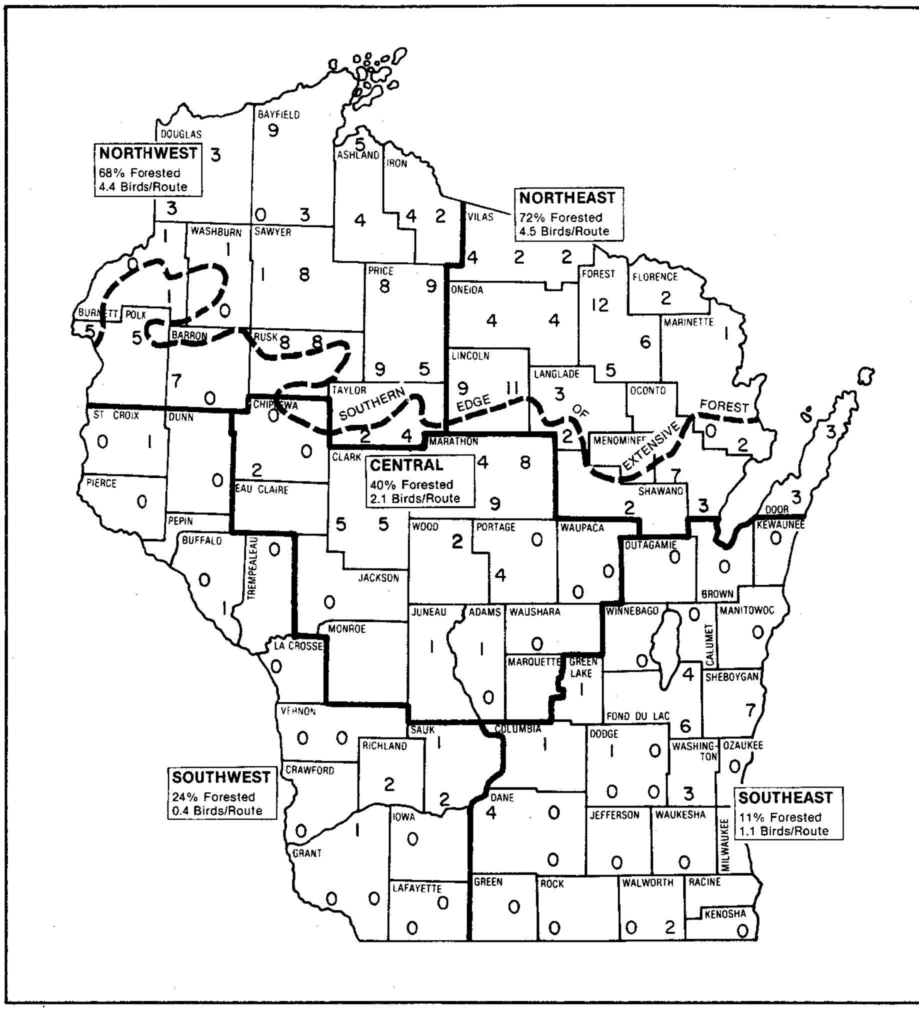


FIGURE 5. Average number of woodcock heard per singing ground survey route and forest land area by Forest Survey Unit, 1968-75.

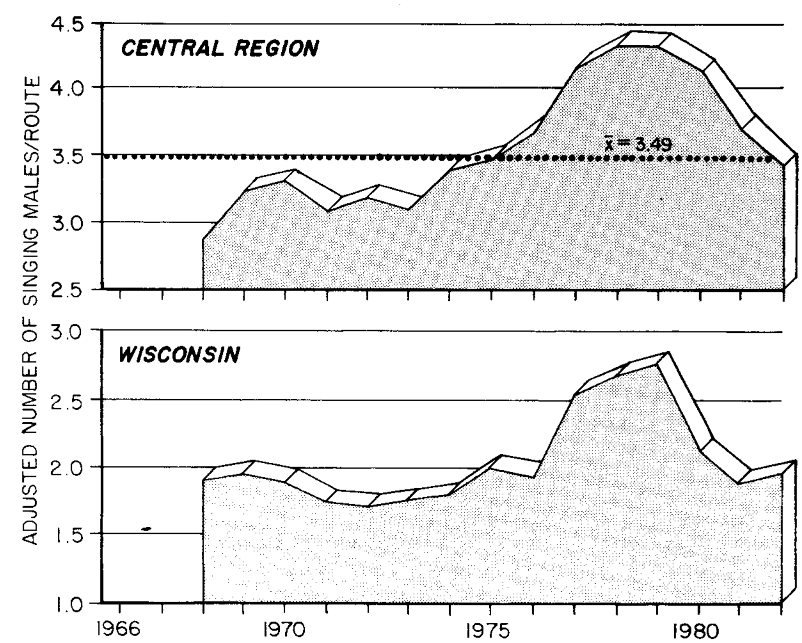
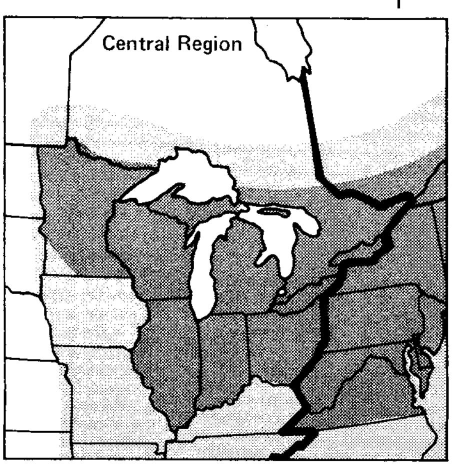


FIGURE 6. Singing ground survey coverage in the Central Region, and approximate breeding range.



Breeding Biology

A variety of forest openings, including some that are very small and ephemeral, can serve as arenas for the male woodcock's courtship displays.

Spring Arrival and Courtship

Although not as widely recognized as a harbinger of spring as the robin, the woodcock is actually a more reliable indicator of spring because it does not overwinter in northern Wisconsin as the robin occasionally does. The woodcock is among the vanguard of spring birds, arriving in southern Wisconsin in early to mid-March and in the most northerly portions of the state by late March or early April. Arrival dates can vary considerably from year to year depending upon the timing of snowmelt. Earliest sightings in the Park Falls area ranged from 13 March to 8 April during the 1973-80 period, with later dates associated with heavy winter snowfalls.

Like other members of the Scolopacidae, such as the long-billed curlew (Allen 1980) and the common snipe (Tuck 1972), male woodcock may arrive on the breeding grounds earlier than females. Indirect evidence for earlier arrival of males was provided by Glasgow (1958) when he found that males departed from the wintering grounds ahead of females. But Modafferi (1967) reported that male and female woodcock arrive on the breeding ground together, and Godfrey (1974) captured a female bird just 2 days after the first male arrival. Because males are vocally obvious during the spring, earlier arrival dates for males could result from their greater conspicuousness rather than from real differences in migration chronology.

Upon arrival in the spring, male woodcock perform daily courtship displays at dawn and dusk in small, open territories called singing grounds. Singing grounds are situated in sparsely stocked woodlands or within forest openings of variable size and character, including old fields, clear cuts, bogs, rights-of-way, and roads. The display, described in detail by Pitelka (1943), consists of intermittent bouts of ground calling (peenting) separated by spiraling flights above the singing ground distinguished by a combination of wing twittering and liquid chirping (flight song). These displays function to advise other males that this particular territory is occupied and also to attract females for mating.

Some adult males fail to obtain a singing ground and appear to function as replacements when a territory becomes unoccupied. One or more nondisplaying males are usually present around perennially used singing grounds, but whether a definite dominant-subdominant relationship exists between these males is unknown. Sheldon (1967) believed that subordinate males were opportunistic drifters, awaiting a chance to claim any vacant territory. Godfrey (1974) demonstrated that the number of subordinate males varied between singing grounds, with a larger number of males associated with grounds that were evidently of higher quality since they were used consistently from year to year. He captured as many as 5 males on a singing ground and reported an average of 1.3 males/singing ground. Whitcomb (1974) obtained a much higher ratio of 2.4 males/singing ground, but his calculations were based upon adult population estimates which were very imprecise.

Mating takes place on the singing ground but has rarely been observed because females tend to arrive on the singing ground when it is quite dark and remain near the edge of the clearing (Mendall and Aldous 1943). Females are also reportedly very wary and ready to take flight at the slightest alarm. Besides hampering efforts to observe courtship, the uneffusive behavior of females nearly precludes their capture during trapping operations on singing grounds. Only 5 hens were captured during singing ground banding activities in Wisconsin which produced 146 captures of males.

The relative scarcity of hens on singing grounds has been reported elsewhere (Sheldon 1967) and has caused some speculation concerning the likelihood of prearrival mating (Godfrey 1974, Couture and Bourgeois 1977). The fact that males are pro-

Although some hens selected nest sites with almost no overhead cover, other hens selected nest sites which provided good concealment. (Top)

The typical woodcock clutch held 4 eggs and none of the 220 nests observed during the study contained more than 4 eggs. (Left)

miscuous and do not form pair bonds tends to support such a contention. In addition, opportunities for females to mate prior to their arrival on their nesting areas do exist since most males are in breeding condition by early February (Roberts 1980) and are actively displaying during migration. But a major argument against this notion is the relatively long time span between first arrival dates and the onset of laying. During 1973-80, the earliest clutches were initiated approximately 2 weeks (range = 9-18 days) after the first woodcock was observed.

Nesting

Nest Site Selection. Since the woodcock breeds across a broad geographic area containing a wide array of climates, it is apparent that the species' nesting habitat requirements can be met by many different plant communities. Several investigators have reported finding nests in a wide variety of cover types and sites, thus hinting that woodcock nesting preferences are rather broad (Sheldon 1967, Liscinsky 1972, Kletzly 1976). Coon et al. (1982) also reported low selectivity in choice of nest sites by woodcock, despite observing a very large difference in nest density between their two search areas. But woodcock nests are notoriously difficult to find and resultant small samples have provided little opportunity for researchers to identify those similarities which exist among nest sites.

The long-term nature of our study, however, enabled us to locate 220 woodcock nests, a sample large enough to provide some awareness of factors influencing the choice of nesting sites by woodcock. But measurements of physical characteristics were taken at only a small portion of our nest sites, so we were unable to use statistical techniques to quantitatively describe nest site requirements. Nevertheless, visual examination of more than 200 nest sites indicated the most important factors in woodcock nest selection to be: (1) security afforded by the proper vegetative structure, and (2) proximity to feeding areas.

Aside from our Wisconsin studies, the only previous study which involved a sizeable number of nests was conducted by Mendall and Aldous (1943), who examined cover types at 128 nests in Maine. They believed that nesting woodcock exhibited definite habitat preferences and stated that "young, open, second growth woodland constitutes the most desirable kind of nesting cover." Their awareness of the importance of the physical appearance, or structure, of nesting cover long preceded widespread acceptance of the theory that birds select habitats based upon structure of the vegetation rather than plant species composition (Emlen 1956, James 1971, Whitmore 1975).

Recent studies of woodcock habitat selection (Kroll and Whiting 1977, Wenstrom 1974, Wishart and Bider 1976) have continued to focus on structural characteristics of preferred habitats, including nesting habitat (Bourgeois 1977, Rabe 1977). Several of these investigations involved the use of relatively sophisticated multivariate statistical techniques to distinguish between good and poor woodcock habitats and between habitats used for nesting and for brood rearing. Both Bourgeois (1977) and Rabe (1977) used discriminate function analysis to determine that nesting hens prefer open habitats characterized by a higher canopy and smaller basal area than habitats used by hens with broods. They concluded that the structure of the understory was the most important feature of woodcock nesting habitat, a conclusion also reached by Gregg and Hale (1977) after analyzing characteristics of 32 nests found during a 2-year portion of the present study. In northern Wisconsin, the forest stands possessing the vegetative structure nesting hens prefer occur primarily in the aspen type.

Although density of the vegetation may be the most important factor in woodcock nest site selection, other habitat features also appear to play a role in determining which areas will be used for nesting. Those features are at least partially independent of structure and include proximity to active singing grounds and availability of earthworms. Mendall and Aldous (1943) determined the average distance between a nest and the nearest singing ground to be 115 yd in a sample of 45 nests. They contended that a close relationship existed between male and female territories, a conclusion supporting their belief that the species was monogamous.

The average distance between a nest site and the nearest singing ground was 130 yd among 46 nests found during 1978 and 1979 in the HCSA and, although measurements were not taken at each nest, all of the 80 nests discovered in that area during 1976-80 were believed to be within human earshot of a singing male woodcock. This apparent relationship between singing ground locations and nest sites was probably not a result of females selecting nest sites within the territories of the males with which they had mated, however, but only a manifestation of the similarity of habitat preferences between male and female woodcock.

Ammann (1970) reported the edges of upland openings to be ideal woodcock nesting habitat. An attempt was made during the present study to quantify the apparent affinity nesting hens showed for edges by measuring the distance between nests and the nearest break in the forest canopy. Measurements were taken during 4 years and included a total of 72 nests. Within that sample, 54 nests (75%) were located within 15 yd of an opening edge and the average distance for all nests was 18 yd.

Woodcock nests were found in habitats ranging from dry to wet, but the nest bowl was usually positioned in a well-drained spot. In the wetter locations, such a spot was often the top of a hummock. Feeding opportunities appeared to exist within a short distance of all nests, even those located in the driest upland sites.

Woodcock often nested near the base of a shrub clump or small conifer (47% of the nests in a measured sample were within 1 ft of a shrub or tree), but some nests were also found having no overhead cover. Although nests in the first category may have been better concealed, the woodcock hen is so effectively camouflaged that even the most open nests were inconspicuous to human eyes. Perhaps the penchant of the woodcock hens to nest near shrubs or small conifers may not be to gain concealment, but may instead be an expression of a widespread tendency among shorebirds to nest near conspicuous objects. Similar behavior has also been reported for the mountain plover (Graul 1975), the killdeer (Bunni 1959), and the long-billed curlew (Allen 1980).

Nest Density. Nest searches were carried out within several 10-acre blocks of the HCSA during 1978 to obtain an estimate of woodcock nest density. Despite a contribution of nearly 300 hours of effort from high school students, coverage was less than expected with only 7 of the 10 areas scheduled for searching being checked and just 3 of those being checked twice during the nesting season. The proportion of simulated nests found by students indicated that their efficiency in finding nests was also less than anticipated. Only 29% of the simulated nests were found during the first pass through a particular covert, and 57% were found after two passes. Although a somewhat higher proportion of real nests than simulated nests may have been found because of the tendency of hens to flush to avoid being stepped on, follow-up searches by project personnel of the areas previously covered by students revealed that a few nests had been missed.

Woodcock nests were frequently associated with an edge or break in the forest canopy.

From 50 to 100 hours of effort were expended in each of the 3 areas which were searched twice, so a high proportion of the woodcock nests in those areas should have been found. Within those 30 acres, a total of 9 nests was found for a density of 1 nest/3.33 acres. This estimate probably represents optimum nesting density, since the search area included the best available breeding habitat in the HCSA. Singing ground counts along the 3 census segments where intensive nest searching occurred averaged more than twice the number found in the remaining 15 census segments (6.25 vs. 2.8 singing males/mile). In addition, our nest density estimate was also inflated because roadside strips contained a large amount of edge cover which nesting hens preferred.

Although our nest density estimate was likely an optimum figure, several records exist of groups of woodcock nests which were indicative of even higher densities. Mendall and Aldous (1943) found concentrations of nests on several occasions in Maine, including 4 broods and 1 nest within 10 acres, 3 nests in 4 acres, and 3 nests in less than 0.5 acre. We also observed instances of nests located in close proximity during our investigation, including 3 nests in less than 0.25 acre in 1977 and 5 nests within 3 acres in 1979. It is possible that such nest clumping resulted because the hens exhibited little territoriality and nesting birds then concentrated in the best coverts. But broods were found in close proximity much less frequently than nests, so it is unlikely that a species which appears to be solitary during brood rearing would be a gregarious nester. Mendall and Aldous (1943) speculated that woodcock actually preferred to nest far apart, but were found together because snow cover had restricted the availability of nest sites or because hens were selecting the edges of their territory for nesting. The latter choice appears most credible, since the brood rearing area of a woodcock hen we radio tagged was known to be on the edge of her summer range and a tendency to select nest sites on the edge of the home range has been documented among hen pheasants (Dumke and Pils 1979).

Although our nest searching was not extensive enough to provide an estimate of average nest density across a broad area, a rough measure of nest density within the HCSA census area could be obtained by adjusting the density estimate for males to arrive at a density figure for females. If we assume that the spring adult sex ratio is similar to that in the fall and further assume that all hens make a single nesting attempt, then nest density could be estimated as follows:

2.1	=	average density of singing males in HCSA (birds/100 acres)
× 1.3	=	expansion factor to account for nondisplaying males
2.73	=	adult male density
÷ 0.61	=	adult sex ratio (M/F)
4.48	=	adult female density (birds/100 acres)
4.48/100	=	1/22.3 acres = average nest density

The above estimate is well below the 1 nest/3.3 acres figure obtained within our nest search areas and is believed to represent a more realistic measure of average nest density. The relatively low rate at which we found nests also indicated the lower estimate of nest density to be more appropriate. The average amount of searching time required to find 1 nest was 9.5 hours, with an hour of searching time often involving the combined efforts of a person and a bird dog. If approximately 1 nest/20 acres was present in our search area and our searches produced 1 nest/10 hours, then our coverage would be 2 acres/hour. The amount of area which can be searched by a person and a bird dog in 1 hour is unknown, but 2 acres appears to be a reasonable estimate.

Egg Laying and Incubation. Woodcock eggs have been described in detail by Bent (1927). The eggs range from pinkish-buff to cinnamon in ground color, are covered with dark spots or blotches, and have a moderate gloss. Our measurements of 44 eggs from 23 different clutches averaged 39.0 × 30.2 mm, significantly larger than the average of 38 × 29 mm reported by Bent (1927). Egg size was also found to differ significantly between clutches. Eggs showed considerable variation in size and shape, ranging from rounded (35.9 × 30.4 mm) to ovate (44.1 × 29.3 mm). Egg weights changed during incubation, declining from 18 to 19 g at the time of laying to approximately 14 to 16 g at hatching.

The hen deposits 1 egg each day until the clutch is completed. The typical complete clutch contained 4 eggs and none of the 220 nests observed in the present study contained more than 4 eggs. Although one report exists of a nest containing 12 eggs (Lincoln 1951) and two reports (Blankenship 1957, Ammann 1969) exist of nests with 6 eggs, at least one of the latter group involved contributions from 2 hens. Incubation was confirmed for several nests containing 2 to 3 eggs; but 89% of all nests, where final clutch size was determined, contained 4 eggs. Mendall and Aldous (1943) found late-season clutches to be smaller, with the majority of their June nests containing only 3 eggs. Although some reduction in clutch size was also observed among late nests in our studies, 10 of 17 June nests still held 4 eggs.

Nests with incomplete clutches were generally found unattended, but some hens were also discovered on their nests during the laying period. Incubation apparently did not begin until after clutch completion, however, since the eggs in an individual clutch hatched at about the same time. Incubation was done solely by the female and required 20 to 22 days for the 7 nests observed from laying through hatching. Two instances of prolonged incubation were recorded during the study. Both cases involved infertile clutches which were attended by the hen for at least 36 and 38 days, respectively.

Incubating hens are very reluctant to flush from their nests and several reports exist of birds being touched or even picked up while on a nest. When flushed from a nest, hens occasionally performed distraction displays which involved very slow, laborious flights made as close to the ground as vegetation allowed. In flight, the tail was slightly fanned and bent forward and the legs were dangling conspicuously. After alighting, the hen would often feign wing injury and utter characteristic whining calls. The frequency and intensity of such displays were apparently dependent upon the stage of the nesting cycle. Hens in early incubation only rarely performed distraction displays while hens with broods did so consistently.

Nesting hens found during the present study were only occasionally flushed upon discovery, which then necessitated a subsequent check when the hen was off the nest to determine number of eggs and stage of incubation. Such checks were usually made at dusk when, as Ammann (1967) reported, the hen is most likely to be off the nest. No consistent departure times were observed during daytime hours, with hens rarely being found absent during the several hundred nest checks performed throughout the study.

Feeding areas used by incubating hens had characteristically large excrement, or splashings, probably a result of long periods spent on the nest. Although probe marks and splashings were never found in the immediate vicinity of a nest, signs of feeding were occasionally found as close as 30 ft distant and commonly observed within 150 ft of a nest. The presence of large splashings thus provided clues to the whereabouts of an incubating hen and thorough searches of those areas often produced a nest. If intensive searches around feeding areas failed to result in discovery of a nest, the location could be monitored at dusk to determine the direction from which the hen arrived. In one such case, an observer was able to hear the hen take flight when she departed from the nest to feed which made locating the nest on the following day a simple matter.

Nest Success. Most nests were discovered during nest searches, but several were located by DNR personnel during routine field activities. Since nest searches were conducted throughout the breeding season, the sample likely contained both initial and renest clutches. The total consisted of 148 nests which were active at the time of discovery and 72 which had already been terminated. Inactive nests were included since there was little problem distinguishing between nests that had hatched and those that had been disrupted.

TABLE 2. *Fate of 220 woodcock nests found in Wisconsin, 1969-80.*

Year	Nests Hatched No.	(%)	No. Nests Destroyed by: Predation	Human Interference	Desertion	Unknown	Total Nests
1969	4	(67)	1	1			6
1970	9	(60)	4	1	1		15
1971	9	(41)	10	2		1	22
1972	5	(50)	2	3			10
1973	6	(46)	4	2		1	13
1974	11	(55)	7		2		20
1975	10	(53)	8	1			19
1976	5	(33)	5	3	2		15
1977	10	(59)	6	1			17
1978	19	(53)	17				36
1979	11	(37)	17		1	1	30
1980	5	(29)	10		2		17
Totals/(%)	104	(47)	91 (42)	14 (6)	8 (4)	3 (1)	220

TABLE 3. *Woodcock nest success as indicated by various methods of estimation, 1975-80.**

Year	Traditional	Mayfield	Total Nests
1975	56	51	56
1976	29	26	38
1977	89	84	63
1978	69	48	53
1979	42	31	38
1980	50	40	29
Means	55	43	47

* Traditional = proportion of active nests which hatched; Mayfield = overall nest survival rate; Total nests = proportion of active and inactive nests which hatched.

Annual nest success, or the percentage of nests hatching at least 1 egg, varied from 29 to 67% and averaged 47% over the 12 years of study (Table 2). Eliminating the 14 nest losses which were attributable to human interference or study activities brought the average success rate to 50%, still well below the comparable figure of 67% reported by Mendall and Aldous (1943). But their calculated success rate was biased upward because it did not take into account the fact that nest mortality is a function of time. Mayfield (1961, 1975) pointed out the problem and proposed a method of estimating nest success which removed that bias through using information only from the period during which a nest was under observation. Because the Mayfield method has been recognized as necessary for the proper interpretation of nesting studies (Miller and Johnson 1978), success rates were also calculated based on "nest days". Estimates of nest success derived from total nests (47%) compared reasonably well with estimates based on Mayfield's method (43%) (Table 3) and also showed smaller year-to-year fluctuations than estimates based solely on active nests (55%), probably due to larger sample sizes.

Predators destroyed 42% of all nests, making predation the major cause of nest loss. The appearance of egg shells indicated mammalian predation in a number of cases, but sign was generally insufficient to identify the species responsible. The time-lapse movie camera failed to provide any information on predator identity because it was constantly malfunctioning. The camera was used at about 6 nests, 1 of which was destroyed by a mammalian predator the day after the camera was removed for repairs. The potential for capturing mammalian nest predators on film was limited at the outset, however, by the need for daylight. Skunks were common in the study area and were believed responsible for some nest losses. Coyotes, weasels, red squirrels, and thirteen-lined ground squirrels were seen less frequently, but were also potential egg predators. In several instances, predators left nothing but an empty nest. In at least one such case, a crow was known to have taken the eggs.

Because predators destroyed 7 of the 11 active woodcock nests observed in 1971, a dummy nest study was undertaken the following spring to obtain an index to predator activity. The proportion of simulated nests destroyed by predators in the study was surprisingly low (14%), yet identical in both study areas. Predation losses were lower among April nests (6%) than among May nests (22%), but that difference might have resulted from variations in level of nest concealment rather than from increased predator activity in late spring. In an effort to compensate for the lack of herbaceous cover during the early spring, a higher proportion of early simulated nests may have been inadvertently placed in more secure sites, such as beneath conifers. Nevertheless, the higher predation rate on late nests should be considered a minimum estimate of predator activity, since fewer visual and olfactory clues were available at dummy nests than at real nests.

One factor contributing to a high rate of predation among woodcock nests could have been the concentration of nests along edges. In a recent study of several open-nesting passerines, Gates and Gysel (1978) reported a highly significant positive correlation between fledging success and increasing distance from the field-forest edge. The high predation rate along edges was attributed to the higher number of nests and greater activity of potential nest predators in those vicinities. They concluded that such habitat discontinuities functioned almost as "ecological traps" by concentrating nests and thereby increasing density-dependent mortality.

Although predators were responsible for the destruction of eggs in many nests, the fate of some of those nests might have already been sealed. Because the woodcock is a very early nester, inclement weather conditions, including cold temperatures and significant snowfalls, are not unusual during the nesting season. Such adverse weather has been known to result in deserted clutches when eggs are frozen or buried under snow. Before the nest searching crew could discover such nests, however, predators had often scavenged the eggs. Thus, although weather conditions caused the loss of many nests which were then subsequently destroyed by predators, it was seldom possible to document such losses.

During the 1979 nesting season, however, a late snowstorm provided an opportunity to gain information on the effect of weather on nesting success. A 6-inch snowfall within the study area on 5 May was judged to have forced hens to abandon those nests having little or no overhead cover. Of 17 nests under surveillance at the time of the storm, 9 were found inactive upon inspection 8 May. The eggs were missing from 6 nests, shells from eggs destroyed by predators remained in 2 nests, and abandoned but intact eggs were found in only 1 nest. There is little doubt that the impact of this storm was unusually severe because snow depth was sufficient to cover nearly all of the ground vegetation surrounding the nests, thus making the hen or the eggs very visible to passing predators. Nevertheless, the rapid disappearance of the eggs from those nests points up the difficulties involved in discriminating between weather and predation as causes of nest losses.

The total of 8 nests lost to desertion probably underestimated the true level of abandonment because some deserted clutches were unknowingly charged as predation losses. Reasons for nest abandonment were not always identifiable, but infertility was a factor in some cases. At least 4 of the 8 deserted nests were known to contain infertile eggs. Deserted nests also contained fewer eggs than other nests, with the 8 nests holding only 19 eggs. The small clutch size among deserted nests was likely an indication that yearling hens were involved in the desertions, since females among other species lay fewer eggs when breeding for the first time (Crawford 1977) and desert more readily than older birds (Geis 1956, Brakhage 1965). Although the ages of woodcock hens which deserted their clutches were unknown, a recent report (Dwyer et al. 1982) that yearling woodcock hens fledge fewer chicks leads to speculations that differences in breeding biology known to exist between yearling and older females in some birds also exist among woodcock.

Egg Success. Fate of individual eggs in completed clutches was dependent upon environmental factors, such as weather and predators, and also upon intrinsic factors such as fertility. Egg success, or the percentage of eggs that are successful, was tabulated in addition to nest success since it provided a more precise picture of the various causes of reproductive losses.

Sixty-one percent of the 585 eggs contained within 152 completed clutches hatched (Table 4). Predation was the primary cause of eggs failing to hatch, accounting for 25% of the total number of eggs in completed clutches and 65% of all egg losses. Although the proportion of infertile eggs (4%) was higher than the 1.6% infertile eggs reported by Mendall and Aldous (1943), egg failure did not appreciably reduce woodcock productivity during most years. Infertility and embryonic weakness combined accounted for only 6% of all eggs, but some variation occurred between years. Yearly differences in overall egg quality would not be unusual, since Koenig (1982) reported that a variety of factors can influence hatchability of eggs.

Renesting. Renesting in the woodcock has not been documented through the use of marked birds, but available evidence indicates that renesting can occur if the initial nest is destroyed. On several occasions during the course of our study an incubating hen was found only a short distance from a nest which had already been destroyed. Mendall and Aldous (1943) reported similar observations in Maine and indicated that the hen had probably laid a replacement clutch within her original territory. Diminishing clutch size late in the nesting season has also been interpreted as evidence for renesting (Mendall and Aldous 1943), but Tuck (1972) demonstrated that small clutches among late nesting yearling birds, not renesting, were responsible for this phenomenon in the common snipe.

Data collected during this study revealed that the woodcock's response to nest disruption may be similar in some cases to that described by Klomp (1970) for the lapwing, another shorebird which lays a normal clutch of 4 eggs. If a lapwing nest containing either 1 or 2 eggs was disrupted, the bird laid another nest (continuation nest) and incubated 3 or 2 eggs, respectively. If a nest was destroyed at the 3-egg stage, the bird would lay 1 egg in a new site and then desert it and lay another clutch of 4 in a new nest (continuation - desert). When a 4-egg nest was interrupted, the bird generally renested.

Although several woodcock nests were found disrupted at the 2-egg stage, little evidence was found of the existence of 2-egg continuation nests among woodcock. Among all clutches known to be in the incubation phase, only 2 contained 2 eggs. Single egg clutches were more common, indicating a possible similarity between woodcock and lapwing response to disruption of nests at the 3-egg stage. Woodcock hens appeared reluctant to incubate a single egg, however, and most 1-egg nests were soon deserted. Of 5 occasions that a woodcock hen was found attending a single egg, the hen was again present on the subsequent check in only 1 case and in that case the egg was found deserted on the following nest check. Likewise, only 1 example was observed of a chick successfully hatching from a 1-egg nest, and 3 eggs were known to have disappeared from that particular nest sometime during incubation. On a few occasions, single, intact eggs were found which were not in a nest, but it was impossible to determine whether such eggs represented continuation - desert nests or were eggs dropped by birds which had failed to construct a nest.

Most references to renesting in the American woodcock have involved replacement clutches, with only a smattering of speculation about raising 2 broods in 1 year (Pettingill 1936). The European woodcock, however, was reported by Steinfatt (1938) to regularly breed twice a year. Although that conclusion has been cited by many over the years (Pitelka 1943, Mendall and Aldous 1943, Sheldon 1967) and is still being published in British and European handbooks, Shorten (1974) pointed out that no real evidence exists on which to base such an assumption. A recent article (Rabe 1979) has again suggested the possibility of our bird raising 2 broods in a year. The evidence for double-broodedness involved a hen which had been collected in company with a brood. The development of the hen's reproductive system indicated she was progressing toward another nesting attempt. Although 2 broods are surely conceivable, such an occurrence is not likely since the hatching date for the envisaged second nest would have been late June, somewhat later than the latest known hatching dates observed in Maine, Massachusetts, and Wisconsin.

Hatching. We observed pipping periods of 24-48 hours and near synchronous hatching of the eggs in an individual clutch, which was in agreement with the findings of Mendall and Aldous (1943). The hatching process and unique lengthwise splitting of woodcock eggs have been described in detail by Wetherbee and Bartlett (1962).

Although many other shorebirds carry hatched egg shells away from the nest, similar behavior was never observed at woodcock nests. After hatching, the chicks remain in the nest and are brooded until dry. While observing a woodcock nest 1 day prior to hatching, Ammann (1970) heard the hen give a series of low, guttural calls "as if talking to the chicks." The bird was apparently responding to embryonic sounds which have been documented to occur among many species. Such vocalizations are believed important in imprinting young birds and in facilitating parental care by synchronizing the hatch (Lack 1968, Graul 1974).

Hatching chronology was determined from ages of chicks in 262 broods, including 89 which were the products of known nests (Table 5). Hens began initiating clutches in early April in all but the latest springs, making the woodcock the earliest ground nesting bird in northern Wisconsin. The earliest hatching date of 17 April was backdated to a 25 March nest initiation date. The peak hatching period was the second week of May, when about 35% of all nests hatched. Hatching phenology appeared to be about 1 week earlier in northern Wisconsin than in eastern Maine (Mendall and Aldous 1943), despite the fact that both areas are at the same latitude. Only 34% of the nests in Maine had hatched by 15 May, while 57% of the nests in our study areas had hatched by that time. The latest hatching date we observed was 15 June.

Broods

Development and Fledging of the Young. Precise hatching dates were known for less than 10% of the 308 broods observed during the present study and relatively few chicks were recaptured, so opportunities to determine growth rates by recapturing known-age chicks were relatively scarce. The amount of data collected during the investigation, however, was believed adequate to describe the growth pattern of the woodcock. In addition to data from wild chicks, information was also obtained from 2 broods which were raised in captivity.

Weights of newly hatched chicks ranged between 9 and 16 g, with the average weight of 42 chicks less than 1 day old being 13 g. Woodcock chicks may lose weight during the first day as has been reported for other shorebirds (Forsythe 1973, Hussel and Page 1976). The contents of the yolk sac were believed to provide the major nourishment for the chicks during the first day, since the chicks were brooded for a good share of the time and little evidence of feeding was observed.

Weights increased rapidly during the fledging period (Fig. 7). Most chicks tripled their hatching weight during the first week and had attained a 5- to 6-fold increase by the end of the second week, at which time they were approximately half adult size. Female chicks were occasionally 10 to 20 g heavier than their male broodmates at this age, but weights were not always reliable indicators of sex. The rapid growth rate slowed after the third week, with most chicks reaching adult size at 5 to 6 weeks of age. Captive chicks grew more slowly than wild chicks. Although occasional food shortages occurred, stress from confinement and fre-

TABLE 4. *Fate of woodcock eggs in completed clutches found in Wisconsin, 1969-80.*

Year	No. Nests	Total Eggs	Avg. Clutch Size	Hatched	Human Interference	Destroyed by Predators	Nest Deserted	Infertile	Dead Embryo
1969	3	12	4.0	12					
1970	10	38	3.8	29		4		4	1
1971	12	46	3.8	30		11	4		1
1972	7	27	3.9	18	4	4			1
1973	11	44	4.0	24	10	10			
1974	17	63	3.7	36		19		4	4
1975	17	67	3.9	38	4	23		1	1
1976	10	38	3.8	14		15	8	1	
1977	12	43	3.6	33	3	4		3	
1978	25	98	3.9	66		28		4	
1979	20	78	3.9	36		23	11	5	3
1980	8	31	3.9	19		8		4	
Totals	152	585	3.9	355	21	149	23	26	11
Percent of total eggs				61	4	25	4	4	2

TABLE 5. *Woodcock hatching dates in northern Wisconsin.*

	April		May					June		
Year	17-23	24-30	1-7	8-14	15-21	22-28	29-4	5-11	12-18	Total
1969		1	2	1						4
1970			9	7	8	7	2	2		35
1971			8	8		3	3			22
1972				7	5		3			15
1973	1	1	7	7	3	1	2		2	24
1974			7	14	14	12	1	1		49
1975				19	5	6	1			31
1976		5	4	4	1		2		1	17
1977		2	1	3	3	1				10
1978		1	7	8	8	1			1	26
1979				4	4	1	4			13
1980			1	10	3	2				16
Totals	1	10	46	92	54	34	18	3	4	262
Percent of totals	0.4	4	18	35	21	13	7	1	2	

quent handling was believed more important than malnutrition in causing retarded growth. Whitcomb (1974) found that growth rates among wild chicks were depressed due to frequent recaptures.

Although both of the published studies (Pettingill 1936, Whitcomb 1974) on woodcock chick weights involved broods located on islands, the results were quite disparate. Pettingill reported weights of chicks from 1 brood on a very small island which were considerably lower than those observed by Whitcomb on a large island where feeding opportunities would not have been constrained. Pettingill's chicks weighed only 55 g when 2 weeks old, while Whitcomb reported chicks of that age to weigh in the range of 80-90 g.

Bill lengths of 6 chicks which still retained an egg tooth averaged 13.8 mm. Culmen growth was similar to growth in body weight, with a rapid increase during the first 3 weeks and a slower increase over the following 2 to 3 weeks. Bill lengths increased at an average rate of about 2 mm/day during the first 2 weeks, a rate Ammann (1977) used to develop a simple formula for aging flightless chicks:

$$\text{age in days} = \frac{\text{bill length} - 14}{2}$$

Feather development also progressed at a rapid pace, with primary feather sheaths evident only 2 days after hatching. Wing coverts began emerging from their sheaths at 5 days of age and juvenile flight feathers were protruding about 2 mm beyond their sheath at 1 week of age. At 2 weeks of age, the dorsal surface of the wing and the humeral tract were well feathered and the rectrices had emerged from their sheaths. By this time, the longest primaries were unsheathed for more than half of their approximate 50 mm length and some chicks could be sexed by the width of their outer primaries, a technique first described by Greeley (1953). At 3 weeks of age, juvenile plumage covered most of the body, and the natal down remained conspicuous only in the regions of the head and legs.

Chicks could flutter short distances when 2 weeks old, but were strong fliers at 3 weeks of age. Chicks more than 18 days old were difficult to capture and most would be considered fledged if fledging is defined as the ability to sustain flight for at least 300 ft. The fledging period of 18-19 days for the woodcock is similar to the 19-20 day period reported by Tuck (1972) for the common snipe.

Brood Care and Behavior. Hens which were flushed from their broods consistently performed distraction displays. Sheldon (1967) believed the dangling legs and peculiar flight of a "broody" hen could give an observer the impression she was carrying something. He concluded that many of the accounts of hens transporting young were only hens performing distraction displays. But the evidence is too great to conclude that all such incidents were imaginary, since included among the numerous reports of hens carrying young were some from reliable naturalists (Grinnel 1922, Schorger 1929). Those incidents must occur very rarely, however, since none of our observers witnessed the act during several hundred brood encounters in Wisconsin. Likewise, Mendall and Aldous (1943) flushed brooding females on

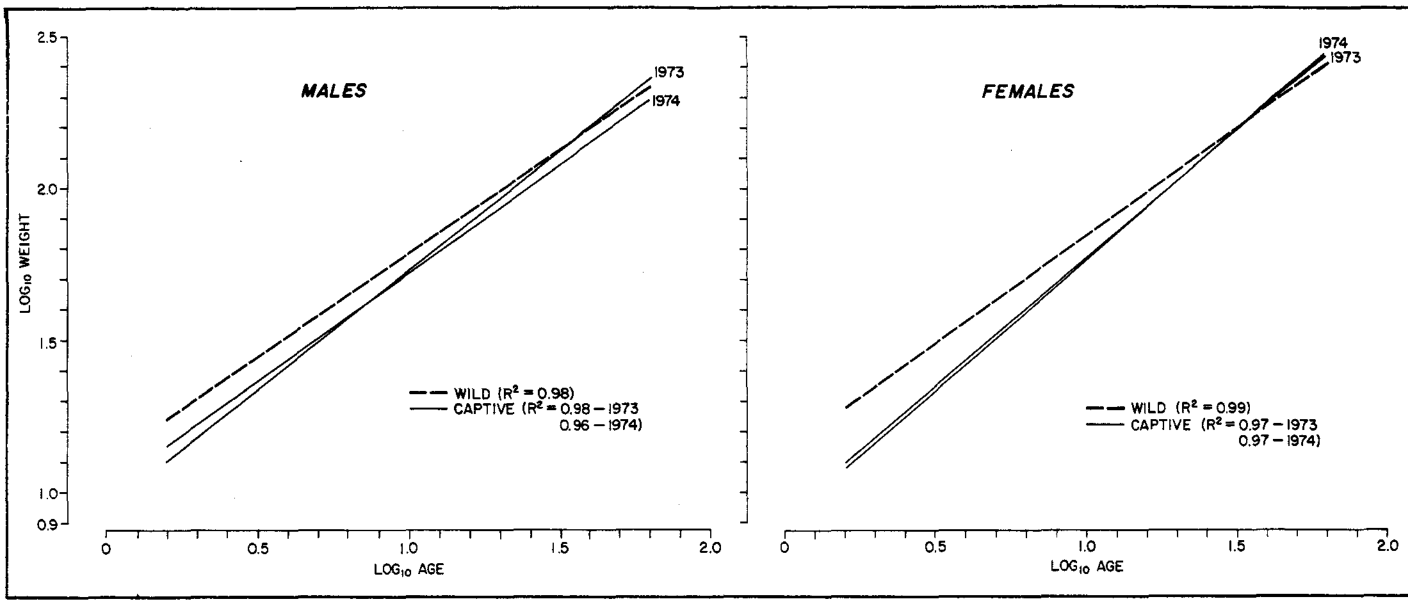


FIGURE 7. Relationship between body weight and age for immature woodcock.

more than 400 occasions without observing such behavior. Andy Ammann, a veteran of more than 20 years of woodcock brood banding, never actually observed the phenomenon but did report (Ammann 1966, 1974) circumstantial evidence of hens carrying chicks. Sheldon (1967) also reported circumstantial evidence of a hen carrying a chick and mentioned his own observation of a ruffed grouse hen accidentally air-lifting one of her chicks. Conceding that such an event is possible, it most certainly would be inadvertent and might resemble an observation recorded during the present study where a hen accidentally "carried" an egg for a short distance when flushed from her nest.

When threatened with danger, a woodcock hen and her chicks usually became motionless. The response of the hen and the brood to disturbance seemed dependent upon the age of the chicks, however, with "freezing" being the common defense when the chicks were small and flushing becoming more frequent when the chicks were capable of flight. Hens with very young chicks appeared even more reluctant to flush than incubating hens, sometimes failing to flush when a net was placed over them. Although such behavior was most common among hens brooding chicks, on 2 occasions a hen also sat tight while each of her 4 chicks were individually picked up, banded, measured, and returned to their position near the hen. Day-old chicks generally did not move until picked up or touched and made little effort to escape when captured. When a few days older, however, chicks would attempt to escape by running as soon as one chick was picked up and began peeping.

Young chicks were dependent upon the hen for both food and protection. Sheldon (1967) assumed that woodcock hatchlings fed themselves as soon as their egg yolk was resorbed. Wenstrom (1974) also assumed that radio-tagged chicks were feeding on litter insects because their signal indicated little or no probing, failing to consider that hens were capturing earthworms for their chicks. But observations during the present study were in agreement with Pettingill (1936) who believed that chicks needed parental assistance to obtain food. Feeding behavior of woodcock chicks was very similar to that reported for the common snipe (Tuck 1972). Young chicks would crowd around the feeding adult and take earthworms from her bill. Although bills of young chicks often evidenced mud from probing activity, the hen continued to feed the chicks long after they began obtaining food on their own. Even chicks which appeared fully grown were occasionally seen begging or obtaining food from the hen. The time span during which chicks were dependent on the hen for food could not be precisely determined, but probably lasted until they were at least 1 week old. Tuck (1972) believed that snipe chicks were dependent upon adults for food until their bills had grown to half their adult length at about 10 days of age.

Earthworms comprised the primary food of young woodcock, based on limited data collected during the study. A young brood enclosed within a lawn edging fence and observed from a blind consumed nothing but earthworms, which were captured by the hen during intermittent observations over a 2-day period. Superficial examinations of the stomach contents of approximately 10 of the 32 chicks killed accidentally during brood banding operations also revealed only earthworms and grit. Similarly, Mendall and Aldous (1943) reported that earthworms accounted for 88% of the food items found in 6 stomachs of chicks less than 3 weeks old.

Habitat

Summer and Fall Use

Woodcock habitat use during the spring season was discussed in an earlier section of this report, so the following analysis is limited to habitats used for daytime feeding during the summer and early fall. Information on habitat use was obtained from both trapping and telemetry activities, but our trapping efforts were concentrated in only a few habitat types and thus did not provide a valid measure of habitat use. Relatively few birds were captured in diurnal habitats and relatively few habitats were represented among catches made with funnel traps since traps were concentrated in the best habitats. Telemetry data, on the other hand, were believed to represent an unbiased measure of habitat use because radio-tagged birds had access to a variety of cover types. Habitat use was quantified by summing for each major cover type the number of daily locations obtained from radioed birds. Major cover types were classified as aspen, alder, conifers, and mixed covers. Mixed covers included combinations of aspen and other hardwoods, or aspen and conifers where no individual tree species was prevalent.

A summary of use of the major cover types by radioed birds is provided in Table 6. During 1976-78, a total of 934 locations were accumulated from 38 birds during 1,012 tracking days, but only 604 fixes were considered sufficiently precise to permit assignment to a cover type category. Aspen received the greatest use by radio-tagged woodcock, accounting for nearly half of all locations. The majority of daytime locations occurred in aspen stands during both 1977 and 1978, but use of alder surpassed aspen during 1976. Drought conditions prevailed through north central Wisconsin in 1976, however, so it is very unlikely that normal patterns of habitat use were in effect. Annual precipitation during 1976 was 25% below normal at Park Falls, which may have forced woodcock to move to lowland sites in order to obtain earthworms.

TABLE 6. *Diurnal habitat use by radio-tagged woodcock in Wisconsin during the summer and early fall period, 1976-78.*

	Woodcock-days of Use*				
Year	Aspen	Alder	Mixed	Conifers	Total
1976	69	90	40	6	205
1977	124	71	18	2	215
1978	99	46	39	0	184
Totals	292	207	97	8	604

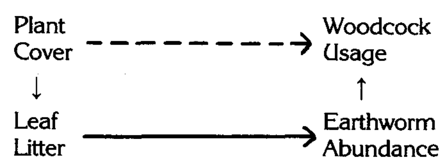
* One daytime location of one radioed woodcock.

Although aspen was the cover type receiving the greatest use by woodcock, there were a number of aspen stands within our study areas which were never used. Much of the woodcock use recorded in aspen occurred in stands that were either very young or, from a forester's point of view, very poor. Many of the latter stands would probably be considered off-site due to prevailing unfavorable moisture conditions. In addition to selecting only certain types of aspen stands for use, woodcock also used only small areas within those chosen stands, often that portion along an upland-lowland ecotone. Many of the aspen stands used by radio-tagged woodcock contained alder as an associate or understory species, so use of alder was understated in the present analysis. The presence of a shrub component, such as alder or hazel, appeared to be a prerequisite to woodcock use of many aspen stands that were in large sapling or older age classes (10+ years).

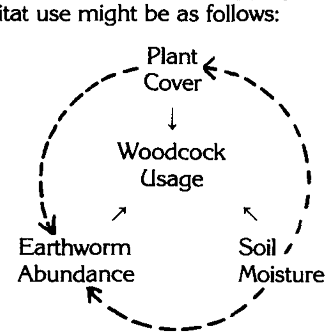
As was true in the case of nest site selection, the structure of a stand, more than its floristics, largely determined its attractiveness to woodcock. Results of some studies have indicated vegetative structure to be even more important than food availability in determining woodcock habitat use. Although he could find no single habitat component which guaranteed woodcock usage, Liscinsky (1972) ranked cover type first, soil drainage second, and food supply third in order of importance. Wishart and Bider (1976) sampled earthworm populations within woodcock habitats in Quebec and reported no statistical differences in numbers or biomass of worms between good and poor habitats. Likewise, Kroll and Whiting (1977) found earthworms present in soils in both used and unused habitats on the Texas wintering grounds.

But Reynolds et al. (1977) reported a direct and significant relationship between the number and biomass of sampled earthworms and the intensity to which woodcock used cover types. They analyzed factors which affected earthworm abundance and found striking similarities between woodcock and earthworms in habitat preferences. Alder and aspen covers were most heavily used by both woodcock and earthworms, whereas conifers were rarely used. This relationship was explained on the basis of earthworm food preferences, with a leaf palatability scale for earthworms being: alder = aspen > birch = maple = cherry = elm > conifers. Thus, they concluded that woodcock use of covers was related to earthworm abundance which was in turn influenced by vegetation providing earthworms with their preferred foods.

Reynolds et al. (1977) recognized, however, that earthworm numbers were influenced by factors other than food, such as soil moisture and temperature. Despite that recognition, their diagrammatic representation of woodcock cover selection failed to include the effect of soil properties:



But Liscinsky (1972) examined the results of several earthworm studies and concluded that soil drainage was more important than any other factor in determining soil suitability for earthworm production. Thus, a more appropriate illustration of woodcock habitat use might be as follows:



Habitat Trends

Although there exists a general consensus as to what constitutes ideal woodcock habitat, we still do not know how much habitat is available in the United States or even within a single state such as Wisconsin. There have, however, been several recent attempts to classify woodcock habitat and to develop a numerical measure of habitat changes associated with succession

Within blocks of good habitat, the essential ingredients of woodcock cover are generally available within a small area. Birds were known to nest, rear broods, feed and roost within 100 yards of this Hay Creek study area singing ground.

Old homesteads characteristically provide openings and edges which are valuable components of woodcock habitat.

Ecotones between aspen and alder received considerable use by woodcock as daytime cover.

Alder stands were used extensively by woodcock because the plants' site requirements and structure served to assure the birds with earthworms and security during foraging.

Habitats which lacked a shrub component, such as this northern hardwood stand in the Hay Creek study area, were not used by woodcock.

and varying patterns of land use. One such attempt (Cushwa et al. 1977) involved the use of published timber inventory data as an index to woodcock habitat trends. Cushwa et al. used the sum of three forest area statistics—unproductive forest land, seedling/sapling stands, and nonstocked areas—as an estimate of potential habitat within each state. They believed that changes in area of potential habitat should be more closely correlated with changes in woodcock populations than changes in total area of forest land. Their analysis revealed a loss in potential habitat in Wisconsin between 1963 and 1970 which exceeded 3 million acres. Forest succession was the major cause of habitat loss, with many stands growing out of the seedling-sapling size class. Michigan supposedly lost even more habitat than Wisconsin, with 38% of the potential habitat in the two states being lost between 1963 and 1970.

Based upon their estimate of habitat changes, Cushwa et al. (1977) speculated that woodcock populations should decline in Michigan and Wisconsin and should increase in states like Ohio and Maine, which both posted gains in potential habitat exceeding 3 million acres. But a recent analysis (Tautin 1982) of long-term trends in the singing ground survey revealed that those predictions have not come to pass and have, instead, been contradicted by woodcock population changes. Breeding population indices have undergone small, however statistically insignificant, increases between 1968 and 1982 in Michigan and Wisconsin, while significant declines have occurred in both Maine and Ohio. Thus, it is apparent that the parameters selected in that investigation did not provide an accurate measure of woodcock habitat.

But results of other studies have revealed that land use and timber resource statistics do have potential value as indicators of woodcock habitat quantity and trends in habitat availability. In a previous report (Gregg 1982), a significant correlation was found between the number of singing grounds and the amount of area occupied by aspen, upland brush, and lowland brush within each of 18 segments of our HCSA census strip. Gutzwiller et al. (1982) examined published land use data for Pennsylvania and found changes to be consistent with the apparent decline in the breeding woodcock population in that state. They reported declines in land categories potentially beneficial to woodcock—such as pastureland, sapling-seedling stands, and nonstocked forest areas—while sawtimber, and urban and built-up areas not suitable to woodcock increased.

An examination of available land use statistics for Wisconsin indicates that many of the changes in land use that are occurring in Pennsylvania are also happening in our state, but not to the same extent. Wisconsin and dairy farming have always been synonymous, but farmland area in the state is decreasing through diversions to other causes, especially urban development (Table 7). Urbanization probably does not represent as great a threat to woodcock habitat in Wisconsin as it does in many eastern states, but even here has contributed to a significant loss of forest land. In a seven-county region in the southeastern corner of the state, nearly 50,000 acres of land representing 3% of the region were converted from rural to urban uses between 1963 and 1970 (Wisconsin State Board of Soil and Water Conservation Districts 1980).

On a statewide basis, however, forest land area is changing slowly enough to indicate a fairly stable woodcock habitat base. The aspen-birch forest type, an important component of that base, also appears to have a solid future in Wisconsin. Aspen-birch forests are shrinking very slowly and still comprise the largest area of all forest types in the state. Because aspen is a species of significant economic importance in Wisconsin, the future outlook for woodcock habitat is much brighter here than in those states where forest industries demand mostly softwoods.

Up-to-date information on the status of lowland brush, the other major component of our woodcock habitat base, is unavailable but is also believed to be secure. Although lowland brush communities are successional in nature, Curtis (1959) pointed

TABLE 7. *Wisconsin land use data and recent trends.*

Land use Category*	1,000 acres	(year)	Trend
Farmland	19,300	(1975)	Declining: 10% loss since 1965
Urban/builtup	2,900	(1977)	Increasing: especially in southeastern Wisconsin
Commercial forest land	14,478	(1977)	Declining slowly: 1% loss since 1968
Aspen-birch type	4,202	(1977)	Declining slowly: 1% loss since 1968
Seedling-sapling stands	4,489	(1968)	Declining: 20% loss since 1956

* Data from Wisconsin State Board of Soil and Water Conservation Districts (1980) and Spencer and Thorne (1972).

out that they may persist in unchanged condition for long time periods. He suggested that cessation of mowing wet meadows had contributed to an expansion of the lowland brush type in Wisconsin, at least on state-owned lands. The type is not presently threatened by any large-scale conversion attempts, although the initiation of streambank brushing projects during recent years caused some concern about loss of woodcock habitat. If removal of woody vegetation were to occur along all of the nearly 9,000 miles of trout streams in the state, then the technique would indeed represent a significant threat to woodcock habitat. In a recent evaluation of the technique, however, Hunt (1979) indicated that only small, heavily shaded streams were likely candidates for brushing and recommended that brushing proceed with caution until more thoroughly evaluated. Evidence that his recommendation is being followed was a tabulation of trout habitat improvement projects which revealed a total of 42.8 miles of stream bank brushed during 1977-82. Assuming that brush was cut back the normal 30 ft on each bank, then the total area treated during the 6-year period was only 310 acres.

Although the quantity of woodcock habitat may be changing little in Wisconsin, habitat quality may be in greater jeopardy. The progressive maturation of our forests is evidenced by a 20% decrease in seedling-sapling area and a 51% increase in sawtimber area between 1956 and 1968 (Spencer and Thorne 1972). Besides growing older, the composition of our forests is changing due to succession and tree planting, causing maple-beech-birch, spruce-fir, and red pine types to all increase. These changes toward an older, more stable forest community will necessarily reduce the value of that forest to woodcock. In addition, management intensity is expected to increase on forest land in the future, which could bode both good news and bad about woodcock habitat in our state. The good news is that harvest operations may involve an increased emphasis on clearcutting and rotations may be shortened. The bad news is that forests may lose diversity as even-aged stands become better stocked and more homogeneous.

Gutzwiller et al. (1982) pointed out problems that have hindered every effort to relate land use and woodcock habitat: (1) securing reliable and comparable sources of land use data over time, and (2) obtaining data with sufficient detail to relate to the specific habitat requirements of woodcock. Even within the relatively small HCSA, we had difficulty using available forest inventory data as a measure of woodcock habitat because of differing systems of forest type classification on federal and state lands. Most of the decline in woodcock habitat in Wisconsin reported by Cushwa et al. (1977) resulted from a reduction in nonstocked area from an excess of 2.5 million acres in the 1956 forest inventory to only 370,000 acres in the 1968 survey. However, some of that reduction was not real physical change and only came about because of a change in sampling procedures between surveys. Unfortunately, as pointed out by Spencer and Thorne (1972), the changed procedure precludes making meaningful comparisons of nonstocked areas between surveys. Because small problems can be multiplied when expanding data to a statewide or nationwide basis, considerable care is required in attempting to sift woodcock habitat from land use figures.

Perhaps the reason that forest inventory statistics fail to serve as reliable indicators of woodcock habitat is that vegetation represents only one of the three components of woodcock habitat use. Woodcock not only require plant cover of the proper form to permit foraging and provide protection from predation, but further require that those plants grow in sites having moist soils harboring earthworms. Of the various systems used to classify forests, most include a category which could be considered preferred by woodcock above other categories, but no system includes a category which could easily be equated with woodcock habitat. For example, if using a system where forests are classified by type, the area of aspen would be included as woodcock habitat and the area of red pine would be excluded. If using a system of stand size classes, then area of seedling-sapling stands would be included as woodcock habitat, while area of sawtimber would be excluded. But woodcock do not restrict their activities to the aspen type or to very young stands, so these statistics are difficult to translate into woodcock habitat. In addition, most forest inventory figures do not include area estimates for alder or lowland brush, a forest type of equal importance to aspen as an indicator of woodcock habitat.

Because of the woodcock's need for moist soils and the importance of the aspen-alder connection, wetland inventories could logically be coupled with forest inventories to come up with a measure of woodcock habitat. There are about 10 million acres of wet soils in Wisconsin and more than 40% of that area is forested (Johnston 1976). A sizeable share of the 4 million acres of wet forests consists of lowland brush, with estimates varying from 815,000 acres (Jahn and Hunt 1964) to slightly more than 1 million acres (Stone and Thorne 1961). Recognizing that woodcock use other forest types in addition to aspen and alder, if we use the area of aspen-birch forests and lowland brush as a rough indicator of woodcock habitat, then the total in Wisconsin amounts to about 5 million acres. Another index to available woodcock habitat could be produced by using density and habitat estimates from the HCSA and projecting them to a statewide figure. Singing male density within the HCSA census strip, where 31% of the land area consisted of forest types attractive to woodcock, was about three times higher than the average on all singing ground survey routes. Expanding the density:habitat ratio from the study area to the entire state would indicate that only 10% of total forest land area, or about 1.5 million acres would be classed as woodcock habitat.

It should now be apparent that currently available land use or timber statistics provide a very imprecise measure of woodcock habitat in Wisconsin. If future demands on woodcock populations require a more accurate determination of habitat availability, then the best way to proceed might be to purposefully conduct a woodcock habitat inventory. Kletzly (1976) indicated that such an inventory is underway in West Virginia through the use of aerial photographs and on-ground inspections. Dobell (1977) was successful in using aerial photography to assess woodcock habitat changes in Canada. He developed a habitat index based on the extent of forest crown closure and found a significant relationship between that index and the number of singing males on New Brunswick woodcock routes. The U.S. Fish and Wildlife Service is presently involved in a similar effort to relate counts of singing male woodcock and habitat changes along some U.S. woodcock routes. Use of aerial photos and even satellite imagery in wildlife habitat assessments is growing and photography will probably provide the basis for any future attempts to classify or inventory woodcock habitat. A statewide wetlands inventory is now underway in Wisconsin which should provide us with a considerable amount of information on woodcock habitat.

Movements

Spring Migration

Woodcock are very early migrants, beginning their northward migration during February in most winters. A comparison of recovery locations for the Wisconsin-banded birds which were reported shot in January or February indicated that some woodcock are on the move during that time span. The median latitude for 37 January recoveries was 31°N while 19 February recoveries averaged 32°N, about 70 miles farther north (Fig. 8). Woodcock hunting seasons in most southern states close by mid-February, however, so shot recoveries fail to show the full extent of movement during the month. The median latitude of 4 Wisconsin-banded woodcock which were recovered in February by means other than hunting was 35°N, on a parallel with the northern boundary of Mississippi and central Arkansas. Glasgow (1958) reported that most birds had abandoned southern Louisiana by the middle of February in normal winters and by the end of February in cold winters.

Only 3 recoveries have been reported during March, so little information is available to track migration farther north. The 3 recoveries all occurred during the first half of March and were obtained in northern Alabama, northern Arkansas, and central Missouri.

Woodcock generally arrive in southern Wisconsin during middle to late March and reach the most northerly sections of the state during late March and early April. Robbins (1970) reported the earliest arrival date among records of the Wisconsin Society for Ornithology was 8 March, but the exceptionally mild winter of 1980-81 provided new record arrival dates for several species, including a woodcock in the Milwaukee area on 19 February (Lange 1981).

Brood Movements, Breakup and Dispersal

Information on brood movements was obtained by monitoring the location of 1 radioed brood hen and relocating marked broods with the aid of bird dogs. Woodcock chicks were capable of travel at an early age, enabling the hen to move her brood rather long distances within a short time after hatching. The mobility of woodcock chicks has been described by Mendall and Aldous (1943), who reported a brood of 1-day-old chicks traveling through 25 yd of exceedingly dense cover in 20 minutes, and by Wenstrom (1974), who reported a brood moving 59 yd away from the nest within hours after hatching.

Some hens also promptly moved their broods away from the nest during the present study, perhaps responding to anxiety caused by our frequent visits. Mendall and Aldous (1943) recognized the potential influence of disturbance on brood movements and excluded broods that were repeatedly flushed from their analysis of brood movements. Despite the exclusions, however, they found broods at steadily increasing distances from the nest throughout the first brood week. Conceding that broods totally free from disturbance might show less movement, they concluded that brood movements were governed primarily by the presence of satisfactory food and cover. Similarly, the substantial variation in both magnitude and timing of brood movements observed in the present study indicated that some factor other than our harassment, such as habitat quality, determined brood wanderings. For example, 1 brood was relocated 9 days after hatching only 40 yd from the nest while another brood had moved more than 200 yd from the nest by the second day after hatching.

Although broods were capable of moving long distances, their day-to-day movements were generally not lengthy. Daily linear movements averaged 80 yd for the single brood we followed and 90 yd for 5 broods monitored by Wenstrom (1974). The total area traversed by a hen and her chicks during the brood period was also not very extensive, averaging 15.7 acres for the 3 broods Wenstrom followed until breakup. Our radioed brood, consisting of chicks which were 6 days old when first located, occupied a minimum home range of 11 acres throughout the 26-day remainder of the brood period.

Whitcomb (1974) reported that woodcock broods remained intact until 29 days of age and in a subsequent paragraph stated that broods "dispersed about 30 days after hatching," implying that breakup and dispersal were synonymous. But data collected in the present study and in Alabama (Horton and Causey 1981) have indicated that the terms probably refer to behavioral activi-

TABLE 8. *Dispersal of woodcock banded as flightless chicks in northern Wisconsin, 1971-80.*

Year	No. Chicks Banded	Number and Sex of Chicks Recaptured Within Various Distances (miles) from the Banding Site: < 1	1.1-3	3.1-5	> 5	Birds Recaptured: M	F	Both
1971	64	1M 1F	1F			1	2	3
1972	38							
1973	63	2M 3F	1M			3	3	6
1974	125							
1975	96	5M 2F		1F		5	3	8
1976	42	5M 4F				5	4	9
1977	29	3M				3		3
1978	87	8M 8F		1F	1F	8	10	18
1979	45	1M 3F	1M			2	3	5
1980	44	1M 1F				1	1	2
Totals	633	26M 22F	2M 1F	2F	1F	28	26	54

ties which are separated in time. Published estimates of the length of the woodcock brood period have varied considerably, ranging from a low of 24 to 26 days (Wenstrom 1974) to a high of 6 to 8 weeks (Sheldon 1967). The weight of the evidence, however, indicates that most broods break up about 4 to 5 weeks after hatching. Brood breakup is then followed eventually by dispersal defined by Kendeigh (1961) as the movement of individuals away from their homesites.

In Wisconsin, information on dispersal was obtained through recaptures during the summer of birds banded as flightless chicks. Data were available on 63 recaptures of 54 individuals from among the 633 locals (flightless young) banded during the springs of 1971-80 (Table 8). Some chicks began visiting forest openings during the dusk flight period very soon after brood breakup. The youngest known-age chick captured in a mist net was 34 days old and a member of a brood that had broken up 2 days earlier. Apparently, males began participating in evening flights at an earlier age than females, since only 4 females were included among the 18 chicks captured in nets before they had attained 6 weeks of age. Because all 18 chicks were recaptured within 1 mile of the original capture site, it appears that most movements made during the first week or two following breakup involve short distances.

Although only a small proportion of banded chicks were recaptured during the summer, the available data indicated that most birds remain in the same general area where they were hatched. Only 10% of recaptured chicks had moved more than 1 mile from their original capture site. The timing of dispersal movements could not be precisely determined, since birds had been residing in their new location for an unknown period of time before they were captured. Thus, the 43-day-old bird recaptured 2 miles from its original banding site may have been somewhat younger when the actual dispersal flight occurred. The 6 recaptures of birds which had moved more than 1 mile were spread over the entire June through September trapping season, however, which indicated that woodcock disperse individually over a lengthy time span. Such dispersal contrasts sharply with the explosive, synchronized dispersal pattern exhibited by young ruffed grouse occupying the same habitats (Godfrey and Marshall 1969).

The proportion of banded chicks that was recaptured during the summer varied considerably between years (Table 8), providing some indication that dispersal pressure might also vary annually. But our small volume of data made it impossible to identify causes of dispersal or the relationship between dispersal and population densities. Although of uncommon occurrence, long-distance dispersal was observed among both male and female birds and in all compass directions. The longest movement by a banded chick involved a bird recaptured on 31 July some 15 miles from where it had hatched on 7 May, an indication that woodcock dispersal in northern Wisconsin does not approach the situation which evidently prevails in Alabama. In that state, Horton and Causey (1981) found that dispersal activity among their radio-tagged woodcock chicks was initiated during the third week following brood breakup and continued through the eighth week. Dispersal movements usually occurred during the dawn crepuscular period and most birds were believed to have moved at least 10 miles, since it was generally impossible to reestablish radio contact with the bird after it had moved. Dispersal movements were felt to involve a large proportion of the population, since intensive searches of their study area revealed woodcock to be very scarce by late summer. Although the magnitude of the woodcock exodus from Alabama was not determined, an example of its potential extent was provided by the direct recovery in Michigan of a chick banded in northern Alabama (Causey et al. 1979).

Summer Movements and Activity Patterns

Information on woodcock activity patterns and movements was obtained incidentally to annual preseason (June through September) banding operations. During 1971-80 our trapping operations resulted in nearly 10,000 woodcock captures which included 1,235 repeats (Table 9). Although moves of 0.25 to 0.5 mile were common among repeat captures, only 49 movements exceeded 1 mile and just 3 of those were longer than 5 miles. These findings support those of other authors who have found summer movements to be predominantly local, generally constituting sallies between diurnal and nocturnal cover.

Mendall and Aldous (1943) believed that woodcock were so remarkably sedentary on the breeding grounds that any significant movement prior to migration would be noteworthy. They reported 3 cases in which birds were recovered north of the point of banding and speculated that those birds had engaged in summer or early fall wanderings. But because the timing of the moves was unknown, they categorized such movements as "vagrant migration". Movements by Michigan-banded woodcock which Ammann (1978) termed premigratory wanderings also probably belong in the vagrant migration category, since a review of the recovery dates (Ammann 1969, 1972, 1976, 1978) revealed that migration could have been underway in nearly every case.

Although Sheldon (1967) recaptured birds in his Massachusetts netting fields that had moved up to 2 miles from the original banding site, and Kletzly and Rieffenberger (1969) reported some local movements by woodcock within their West Virginia study area, the vast majority of all their recaptures occurred near the original capture site, a situation which also prevailed during banding operations in Maine (Krohn and Clark 1977).

Immature males were the most mobile group, being responsible for 41 of the 49 moves which exceeded 1 mile. An immature female woodcock, however, which was banded in Sawyer County on 3 July and recaptured about 45 miles ESE in Lincoln County on 14 September, made the longest move recorded during the study.

Although uncommon, long distance movements evidently occurred throughout the summer, since recaptures of birds which had moved more than 1 mile were made during every month of the trapping season. The likelihood of recapturing a bird outside the original banding site increased somewhat during the summer, however, with the percentages of repeats that were taken more than 1 mile from the previous site being 2, 3, 4, and 7 in June, July, August, and September, respectively. Although the small increase could be interpreted as an indication of heightened activity levels in early fall, it might also be a reflection of the progressively longer time span during which a move could occur. The interval between banding and recapture was generally much shorter for birds recaptured in June or July than among those recaptured late in the summer. For those birds which moved more than 1 mile, average elapsed times between capture and recapture were 6, 20, 34, and 60 days for June through September repeats, respectively.

Because records of woodcock movements obtained from recapturing marked birds could not often be assigned to specific time periods, additional information on summer activity patterns was obtained by analyzing catch rates and monitoring the behavior of radio-tagged or captive birds. Capture success varied considerably between methods, owing largely to the extent to which a particular capture method was employed but also to differences in vulnerability to capture between birds of different sex and age (Table 10). Immatures outnumbered adults in each capture method employed, but were particularly abundant in catches

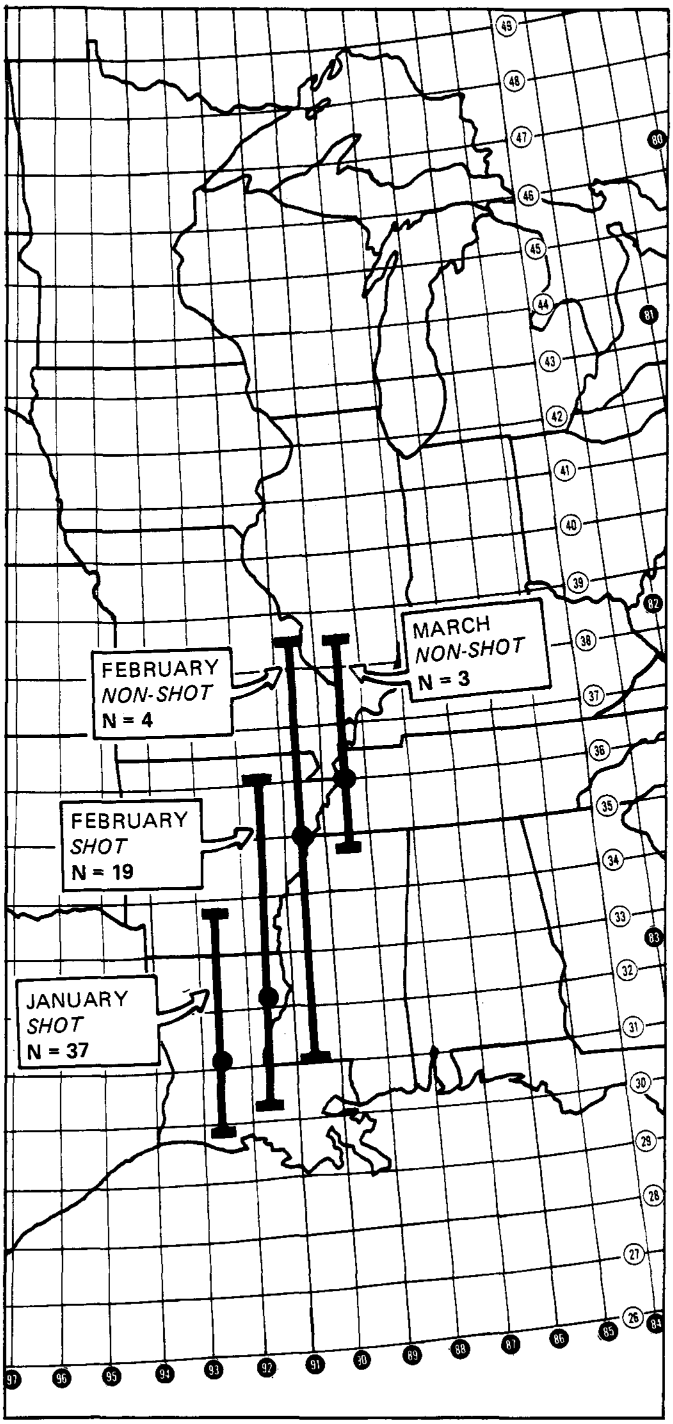


FIGURE 8. Spring migration of woodcock as indicated by recovery locations of Wisconsin-banded birds, 1968-80.

made with mist nets and spotlights. This preponderance of young birds, especially males, among samples of woodcock captured in fields or other forest openings at night has been widely reported (Sheldon 1961, Kletzly and Rieffenberger 1969, Krohn 1971, Whitcomb 1974) and led Sheldon to conclude that sex- and age-related differences in activity levels were responsible. But Dunford and Owen (1973) found no difference in the use of fields by immature males and female radio-equipped woodcock, and suggested that the higher percentage of males caught in fields may be related more to ease of capture than to differences in usage of fields. In our captured samples, immature males outnumbered immature females by approximately a 2 to 1 margin with little difference noted between years or between mist netting and spotlighting catches. Thus, a real difference between young males and females in usage of northern Wisconsin forest openings does appear to exist.

Observations of captive birds in 1972 and radio-tagged birds during 1976-78 also revealed immatures, especially males, to be more active than adults during the summer. The number of times that penned birds crossed grid markers during each 1-hour observation period averaged 6, 9, 15 and 10 by adult male, adult female, immature male and immature female birds, respectively. Greater mobility of immature birds within our radio-tagged cohort was also evidenced by the higher proportion of young birds which moved away from the neighborhood where they had been captured. Contact was lost with 6 of 17 radioed immature birds prior to the time that transmitter failure was likely to occur and 3 of those birds were subsequently relocated 1.3 to 5.4 miles away. In contrast, none of the 7 adult birds tracked during the summer was known to move away from the capture site.

The difference in movement patterns between adult and immature woodcock caused problems in defining the boundaries for summer home ranges and made it difficult to compare home range sizes between birds of different age. Comparisons were further complicated by differences in duration of the tracking period which averaged more than twice as long among adults than immatures. Home range sizes are provided in Table 11 for all birds having an adequate history of locations but sizes were not calculated for several immature birds which dispersed during the tracking period, since the total area they traversed was not believed to be a valid estimate of home range. For example, an immature male tagged on 29 June 1976 was relocated from the air 5.4 miles south and 4.7 miles southeast of his previous location on 12 July and 21 July, respectively. Connection of his successive daytime locations would include an area several square miles in extent and provide an inflated measure of the total area the bird actually used. Although capable of long distance moves, most woodcock confined their movements to small areas during the summer with daytime locations of 16 birds encompassing an average of only 32 acres. Even within these relatively small areas, successive daytime locations were often within 50 yds of each other which would indicate that woodcock spend most of their time in activity centers which are less than an acre in extent.

Although woodcock activity levels appeared to be related to the sex and age of the bird, variations in capture success occurred each summer which indicated that activity levels may also be dependent upon season. Only mist-netting captures were

TABLE 9. *Summer movements of woodcock in northern Wisconsin, 1971-80.*

Age/Sex	No. Birds		Times Recaptured					Distance Between Capture Sites (miles)			
Group	Captured	Recaptured	1	2	3	4	Total	< 1	1.1-3	3.1-5	> 5
Ad. males	712	36	34	2			38	38			
Ad. females	637	26	25	1			27	27			
Imm. males	4,725	747	651	87	7	2	854	813	32	7	2
Imm. females	2,444	288	261	26	1		316	308	6	1	1
Totals	8,518	1,097	971	116	8	2	1,235	1,186	38	8	3

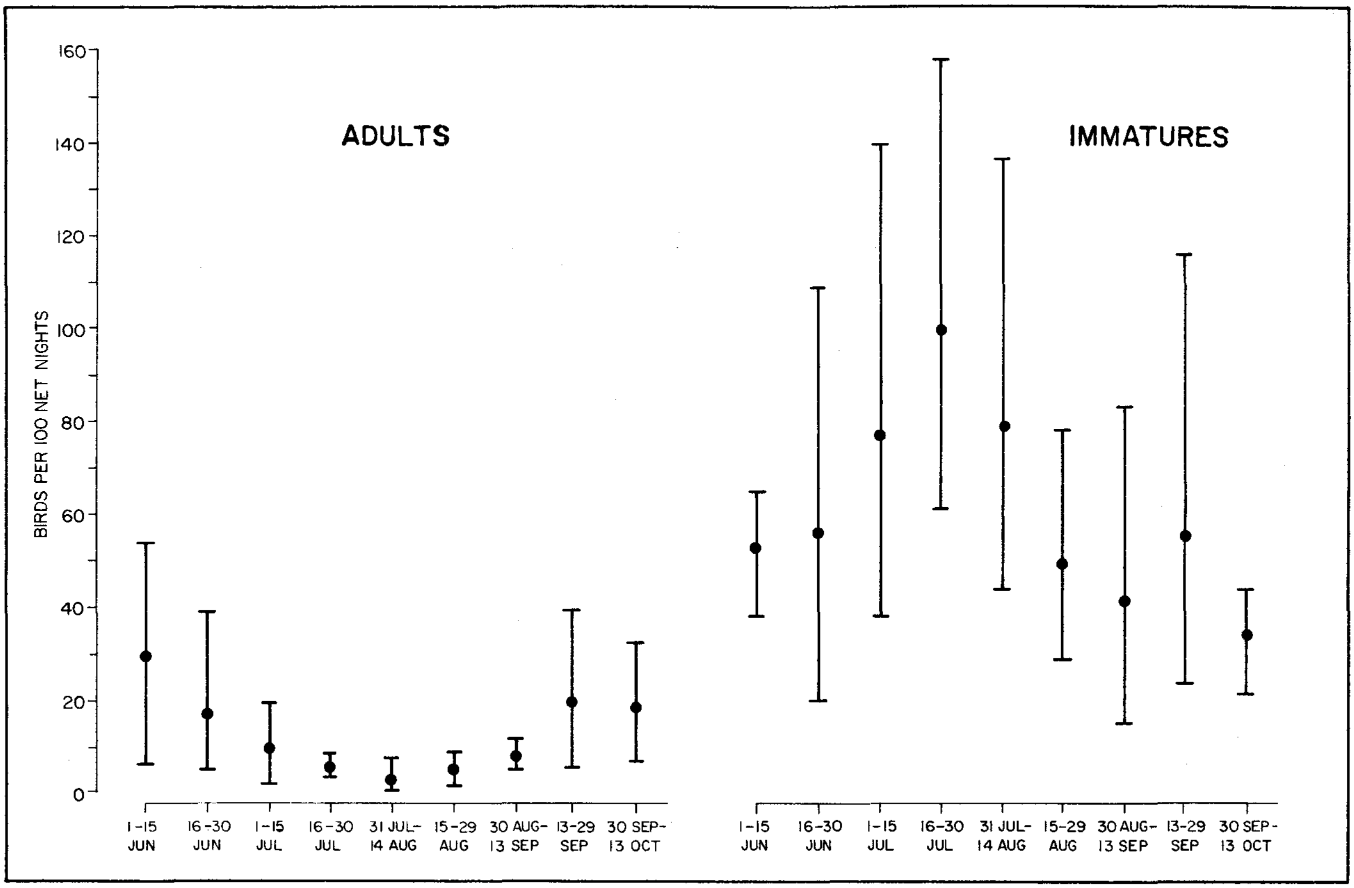


FIGURE 9. Trends in adult and immature catch rates in mist nets throughout the summer (11-year average).

used to detect seasonal trends in capture success, since nets were employed for the duration of the summer while other capture methods were used only intermittently. When the numbers of adult and immature woodcock captured each summer in mist nets were segregated into 15-day time periods, catch rate patterns were surprisingly similar from year to year (Fig. 9). Immature capture rates generally increased from early June to a peak in July, probably coinciding with the increase in the number of broods that had broken up. The rate then decreased in August and rebounded somewhat during September. Adult capture rates, on the other hand, were highest in June, declined to a very low level during August, and then increased during September.

The pattern of adult catch rates was very similar in shape to the adult summer weight curve described by Owen and Krohn (1973). They reported that adult woodcock experienced a period of weight loss which was presumably related to energy demands of plumage replacement since the timing coincided with the peak of the molt. Even though Owen and Morgan (1975) found no relationship between molt and activity levels of adult radio-tagged woodcock, our results suggest that increased energy demands have an impact on capture success by reducing the frequency with which adults participate in crepuscular flights. The postjuvenile molt of immatures, being incomplete, probably demands less energy than the postnuptial molt of adults, but might also influence activity levels. Hints of a relationship between molt condition and activity levels among immature woodcock, also existed in the pattern of catchability. The decline in the immature catch rate occurred later and was less dramatic than that for adults, coinciding with the later and less intense molting peak of immatures.

Fall Migration

Although some early writers speculated that woodcock began their southward movements in August or September, data collected in the present study indicate that in Wisconsin woodcock migration occurs in October (Table 12). Mendall and Aldous (1943), too, found little evidence of migration in Maine before the first of October. Of 35 direct (first-year) recoveries of Wisconsin-banded birds that were reported shot during the month of September, all except 1 were recovered within 10 miles of the banding area. The single exception was an immature male shot on

TABLE 10. *Number of woodcock captured during the summer and relative catchability of birds of different age and sex, 1970-80.*

		Woodcock Captured					Birds/Unit Effort*				
Capture Method	Capture Effort	Ad. Male	Ad. Female	Imm. Male	Imm. Female	Total	Ad. Male	Ad. Female	Imm. Male	Imm. Female	Total
Nets	10,542	502	464	4,868	2,390	8,224	5	4	46	23	78
Lights	1,069	148	159	902	474	1,678	14	15	84	44	157
Traps	4,749	17	36	21	47	121	0.4	0.8	0.4	1.0	0.3

* Unit effort = 100 net-nights, 100 man-hours, and 100 trap-days for nets, lights, and traps, respectively.

TABLE 11. *Tracking data from 36 woodcock monitored in northern Wisconsin, 1976-78.*

Tagging Date	Age-Sex		Tracking Days	Locations	Home Range (acres)	Final Status
25 May 76	Ad	F	50	65	48	Prob. transmitter failure - 14 Jul
16 Jun 76	Ad	F	74	98	98	Prob. transmitter failure - 30 Aug
24 Jun 76	Imm	M	6	7	-	Transmitter removed due to faulty harness - 29 Jul
29 Jun 76	Imm	M	23	12	-	Contact lost due to dispersal movements - 21 Jul
9 Jul 76	Imm	F	29	40	14	Predator killed - 6 Aug
9 Jul 76	Imm	M	12	18	10	Transmitter failed - 21 Jul
19 Jul 76	Ad	M	21	28	14	Transmitter failed 9 Aug; shot 26 Sep
3 Aug 76	Imm	M	17	27	31	Contact lost - 20 Aug
13 Aug 76	Imm	F	7	9	-	Prob. transmitter failure - 20 Aug
19 Aug 76	Ad	M	17	15	7	Killed by avian predator - 3 Sep
24 Sep 76	Ad	M	34	38	26	Migrated - 27 Oct
24 Sep 76	Imm	F	17	11	-	Migrated - 10 Oct
1 Oct 76	Imm	F	29	28	-	Transmitter removed due to faulty harness - 29 Oct
1 Oct 76	Imm	M	33	45	-	Transmitter removed due to faulty harness - 2 Nov
22 Jun 77	Imm	F	43	26	12	Contact lost due to dispersal movements - 4 Aug
23 Jun 77	Ad	F	101	53	58	Harness broke or hunter removed - 3 Oct
30 Jun 77	Ad	M	10	9	-	Transmitter failure - 12 Jul
30 Jun 77	Imm	M	4	3	-	Carcass in water, cause of death unknown - 20 Jul
22 Jul 77	Imm	M	13	6	-	Contact lost - 28 Jul
22 Jul 77	Imm	F	21	9	58	Killed by avian predator - 11 Aug
22 Jul 77	Imm	M	11	8	-	Predator killed; harness involved - 2 Aug
4 Aug 77	Imm	F	45	25	78	Shot by hunter - 17 Sep
23 Aug 77	Imm	F	32	14	-	Contact lost - 26 Sep
26 Aug 77	Imm	M	21	11	-	Contact lost - 20 Sep
29 Aug 77	Imm	M	5	5	-	Contact lost - 6 Sep
27 Sep 77	Ad	M	22	19	-	Migrated - 18 Oct
30 Sep 77	Imm	F	41	48	-	Premigratory moves on 4 and 5 Nov; departed 9 Nov
30 Sep 77	Ad	F	25	28	-	Migrated - 25 Oct
19 Jun 78	Imm	F	12	12	9	Transmitter failed - 1 Jul
6 Jul 78	Ad	F	89	75	20	Transmitter removed - 2 Oct; recaptured 1979
19 Jul 78	Imm	F	25	21	10	Found dead; harness involved - 14 Aug
25 Jul 78	Imm	F	38	38	26	Killed by predator - 6 Sep
10 Aug 78	Imm	F	6	6	-	Predator killed; harness involved - 15 Aug
14 Aug 78	Imm	F	26	21	-	Transmitter removed due to broken harness - 8 Sep
16 Aug 78	Imm	F	32	29	-	Contact lost 18 Sep
16 Aug 78	Imm	F	26	24	-	Found dead; harness involved - 11 Sep

TABLE 12. *Distribution and chronology of hunting season recoveries for woodcock banded in Wisconsin, 1968-80.*

Time Period	Number of Direct Shot Recoveries by Degrees of Latitude*									
	46°-44°	44°-42°	42°-40°	40°-38°	38°-36°	36°-34°	34°-32°	32°-30°	30°-28°	Total
11-20 Sep	17									17
21-30 Sep	18									18
1-10 Oct	27									27
11-20 Oct	25	2								27
21-31 Oct	13	1								14
1-10 Nov	4	2	1	1						8
11-20 Nov				2	1					3
21-30 Nov					1		1			2
1-10 Dec						4		1		5
11-20 Dec						1	2	3		6
21-31 Dec					1	1	1	4	1	8
1-10 Jan							1	4	2	7
11-20 Jan							2	4	1	7
21-31 Jan							1	3	2	6
1-10 Feb							2	2		4
11-20 Feb								1		1
Totals	104	5	1	3	3	6	10	22	6	160

* REFERENCE POINTS: 45° - Wausau, WI; 43° - Madison, WI; 41° - Peoria, IL; 39° - St. Louis, MO; 37° - Dexter, MO; 35° - Memphis, TN; 33° - Lexington, MS; 31° - Tylertown, MS; 29° - Delta/gulf.

29 September about 35 miles southwest of the banding site. Although this bird may have begun migrating, occasional long-distance movements were also known to occur throughout the summer.

Band recovery data indicated that, in most years, a relatively small proportion of resident woodcock depart from north central Wisconsin before 10 October (Table 12). Our birds are only beginning to deposit premigratory fat reserves in early October, thus being similar to Maine woodcock which were physiologically unprepared for migration before mid-October (Owen and Krohn 1973). But recovery locations demonstrated that some woodcock began their fall migration in early October when fat deposits were still relatively light. Several immature birds were recovered during the first half of October at points up to 100 miles from the banding site. No adults were recovered at long distances from the banding site during that same period, however. Thus, fall departure dates appeared more closely related to age classes rather than weight classes of birds with immatures leaving ahead of adults. An analysis of October recovery locations revealed that the bulk of our immature birds were in transit by late October while many adults still remained in their summer ranges (Table 13).

In addition to variation between birds of different age, woodcock departure dates also fluctuated from year to year with changes in prevailing weather conditions. Severe cold snaps forced nearly all birds out of northern Wisconsin by 1 November in some years, but continued mild weather in other years enabled birds to remain surprisingly late. A few reports exist of woodcock sightings in northern Wisconsin as late as mid-November, with the latest observation in the Park Falls vicinity being 25 November. Precise migration dates were obtained for 5 radio-tagged birds, 2 in 1976 and 3 in 1977, which were monitored until their departure. Radio-tagged birds were often among the last birds to depart in the fall and it is possible that stress from capture and tracking caused the birds to have difficulty in attaining the physiologic state needed to trigger migration. In 1976, 2 of our radioed birds were recaptured in late October and early November when it was believed that all other woodcock had departed. A new harness design had been used on these birds which had evidently been too tight, resulting in a sore spot on the birds' backs and a failure to show normal fall weight gains. Although other investigators have not reported delayed departure of radioed birds, the problem may not have been unique to our investigation. Coon et al. (1976) commented that their Pennsylvania birds may not have been unduly late in beginning migration despite departure dates that were well beyond the 24-25 November period when Liscinsky (1972) reported fall movement out of the state to be complete. Similarly, Godfrey (1974) did not report the 2 November departure of his radioed bird to be unusually late, but did indicate that no birds remained in his Minnesota study area on the following day. Migration dates differed for each bird and did not always coincide with weather patterns most suitable for migration. Godfrey (1974) reported that woodcock in Minnesota characteristically departed between the retreat of a low pressure system and the entrance of a high pressure center, when winds were most favorable for southerly flight. Two of the 5 radioed birds made premigratory flights similar to those reported by Coon et al. (1976) in Pennsylvania. One bird moved 1.75 miles southwest of her normally used area 4 days prior to departure and another bird moved 2.5 miles and 4 miles on 2 consecutive nights and then made her final departure 5 days later.

Because the bulk of northern Wisconsin woodcock do not begin their southward migration until mid-October, most birds have accomplished only a small share of their journey by the end of the month. Only 1 of 74 direct recoveries reported as shot during October was obtained from outside the state and that particular bird was recovered 50 miles north of Wisconsin's southern border in northeastern Iowa. Relatively few Wisconsin-banded birds were reported shot during November, but recovery locations reveal that our birds travel a considerable distance during the month. While early November recoveries occurred in Wisconsin and northern Illinois, birds were shot later in the month as far south as Oklahoma and northern Mississippi. Our birds probably complete the last leg of their 1,000-1,200 mile trip during Decem-

TABLE 13. *Distance between banding and recovery locations for adult and immature woodcock shot during October, 1968-80.*

Time	Number of Direct Recoveries by Distance From Banding Site					
	Immatures			Adults		
Period	0-10 miles	11-50 miles	50+ miles	0-10 miles	11-50 miles	50+ miles
1-10 Oct	18	1	2	4	1	0
11-20 Oct	17	2	4	4	0	0
21-31 Oct	1	1	7	4	0	1

TABLE 14. *Minimum homing rates among woodcock of different age and sex as indicated by the number of returns and indirect recoveries which occurred near the banding area.*

Banding	Immature						Adult						Average Total
	Male			Female			Male			Female			Return
Year*	Recaptured*	Shot*	Total	Recaptured	Shot	Total	Recaptured	Shot	Total	Recaptured	Shot	Total	Rate (%)
1970	1	2	3	2	3	5	1	1	2	2	1	3	3.6
1971	4	2	6	3	4	7	2		2	3		3	3.4
1972	4	3	7	2	2	4	1	1	2	1	1	2	1.5
1973	5	9	14		4	4	2	1	3	2	2	4	1.5
1974	3	4	7	2	3	5	4		4	2	3	5	1.3
1975	3	5	8	3	4	7	2		2	1	1	2	3.5
1976					1	1							0.3
1977	7	5	12	9		9	2		2	1	2	3	3.5
1978	5		5	2	3	5	2	1	3	3	4	7	2.0
1979	5	1	6	4	1	5	4	1	5	4	4	8	4.7
Totals	37	31	68	27	25	52	20	5	25	19	18	37	
Avg. return rate (%)	0.8	0.7	1.5	1.1	1.0	2.1	3.1	0.8	3.9	3.1	2.9	6.0	

* Birds that were tagged in the year indicated and shot or recaptured in a subsequent year.

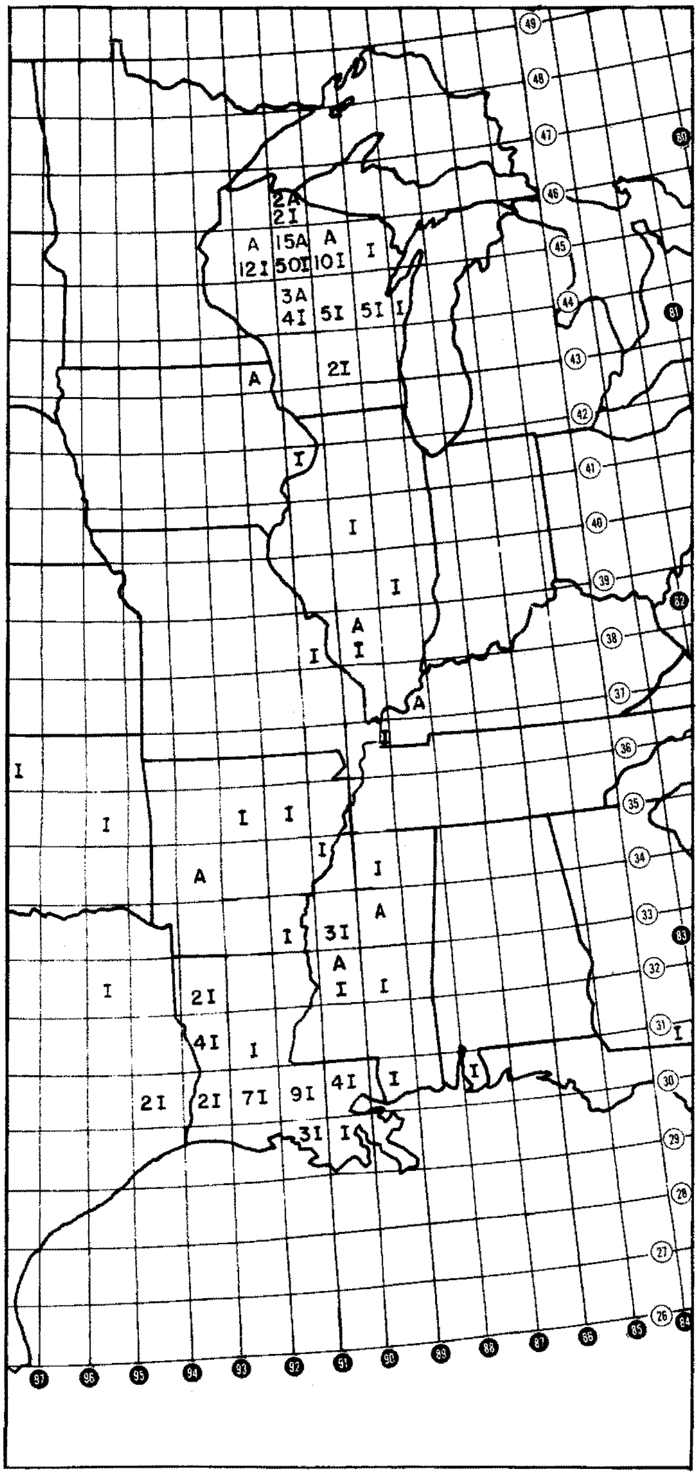


FIGURE 10. Distribution of direct recoveries of adult and immature woodcock banded in Wisconsin, 1968-80.

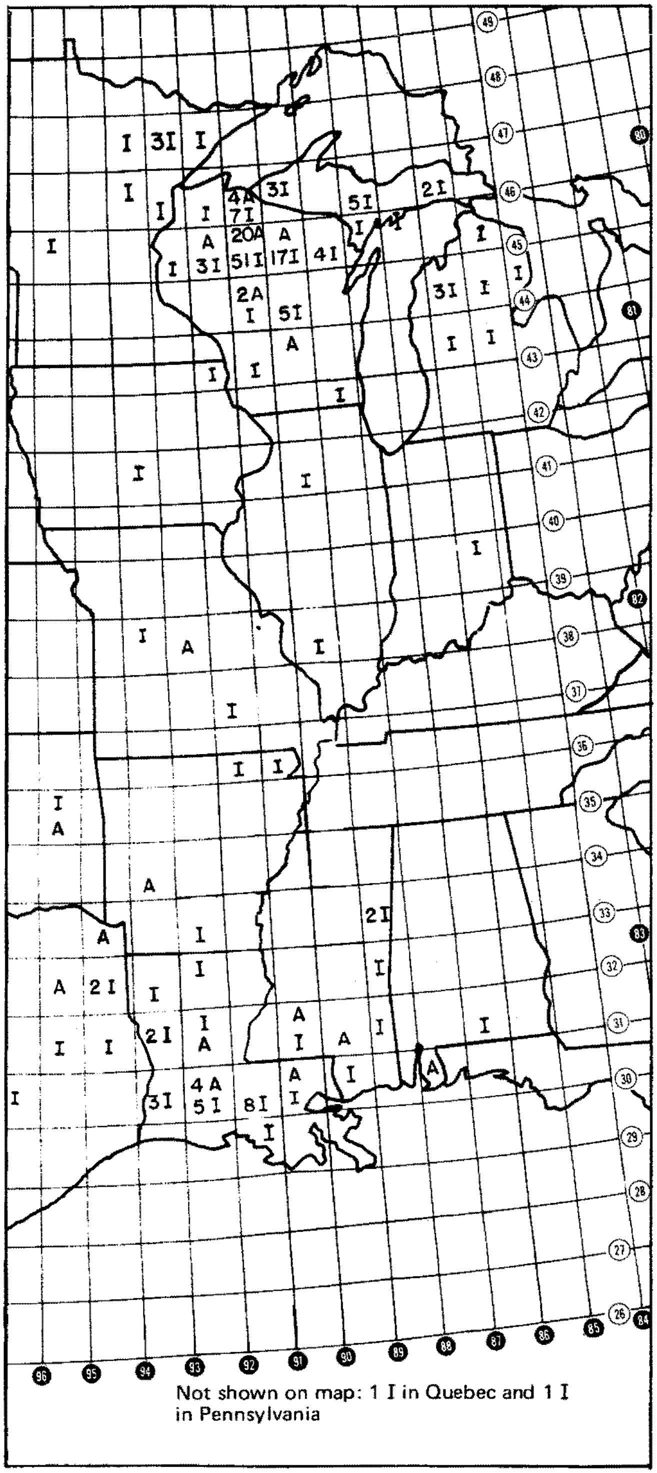


FIGURE 11. Distribution of indirect recoveries of adult and immature woodcock banded in Wisconsin, 1968-80.

ber, since a progressively southward orientation of recoveries continued until at least the middle of the month.

Sheldon (1967) provided a map of woodcock migration routes but states that the reader "may be required to use his imagination to see the continuity of routes". Despite the additional recoveries which have accumulated since that time, it remains difficult to describe the migration pathway Wisconsin birds follow because recoveries have been concentrated near the banding areas and on the wintering grounds (Fig. 10). A map of direct recovery locations reveals that fall migration from Wisconsin is oriented strongly southward, however, with no direct recoveries having been reported from either Minnesota or Michigan. The narrow recovery pattern resulting from woodcock bandings differs dramatically from the broad distribution of recoveries reported for other migratory birds banded in Wisconsin, such as the mallard (March and Hunt 1978).

Homing

Because substantial numbers of male woodcock have been banded on their singing grounds, the largest volume of data on

TABLE 15. *Distribution of shot recoveries from woodcock banded in Wisconsin during 1968-80.*

State or Province	Direct* No.	Direct* Percent	Indirect* No.	Indirect* Percent	Total No.	Total Percent
Northern breeding ground						
Ill.	4	2.2	2	0.9	6	1.5
Ind.		.0	1	0.5	1	0.3
Iowa	2	1.1	2	0.9	4	1.0
Ky.	2	1.1			2	0.5
Mich.			21	9.7	21	5.3
Minn.			8	3.7	8	2.0
Mo.	1	0.6	3	1.4	4	1.0
Penn.			1	.5	1	0.3
Wis.	117	64.3	123	56.9	240	60.0
Que.			1	0.5	1	0.3
Wintering ground						
Ala.	1	0.6	2	0.9	3	0.8
Ark.	5	2.7	4	1.9	9	2.3
Ga.	1	0.6			1	0.3
La.	35	19.2	31	14.4	66	16.6
Miss.	9	4.9	7	3.2	16	4.0
Okla.	2	1.1	2	0.9	4	1.0
Tex.	3	1.6	8	3.7	11	2.8
Totals	182	100.0	216	100.0	398	100.0

* Direct = first year; indirect = after the first year.

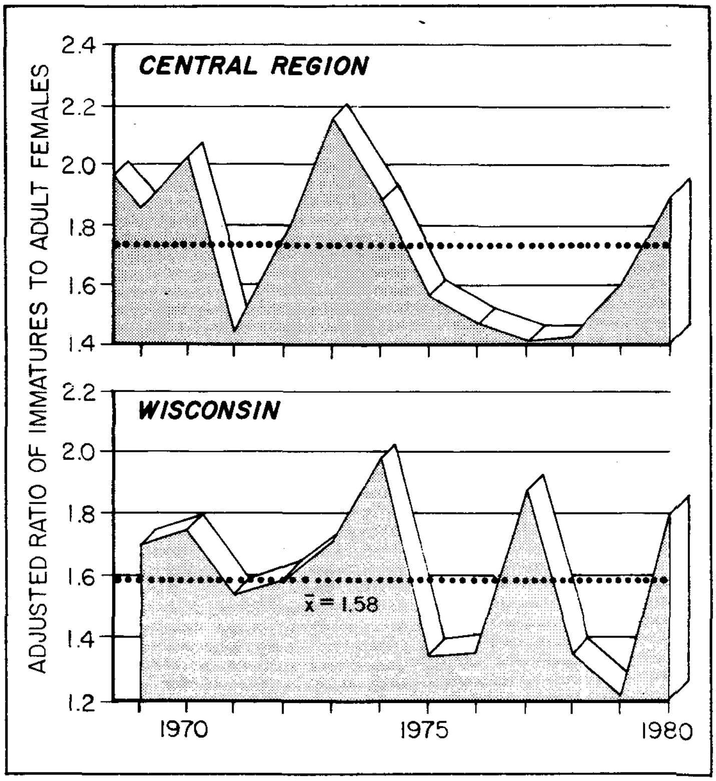


FIGURE 12. Annual woodcock recruitment in Wisconsin and the entire Central Region as indicated by the wing survey.

homing concerns adult males. Banding studies by Sheldon (1967) and Godfrey (1974) revealed that relatively few adult males returned to the same singing ground where captured in the previous year, but most birds returned to the vicinity of their breeding areas. A high degree of fidelity for their breeding areas was also evidenced by 20 returns of Wisconsin-banded adult males. Among 18 returns which had been originally captured during summer banding operations, 16 were recaptured during a subsequent summer at the same site and 2 others were retaken on singing grounds within 1.5 miles of the original capture site. Two returns were recorded from among males which were originally banded on singing grounds, 1 on the same singing ground and another on a different ground 0.75 mile distant.

Although data on homing among adult females is more limited, available evidence indicates that most surviving hens also return year after year to the same nesting areas. We recorded 19 returns by adult females in Wisconsin (Table 14). One hen was known to return to the HCSA in 1979 despite being frequently flushed and recaptured during a 3-month period in 1978 in which she had been radio-tagged. In addition to Wisconsin-banded birds, an adult female that had been banded on the Louisiana wintering grounds in 1965 was captured on the HCSA in both 1968 and 1969. Ammann (1978) also reported the capture of previously banded hens in Michigan.

Data collected during the present study revealed homing tendencies to be considerably higher among adults than among juveniles, although Sheldon (1967) believed that most woodcock of each sex and age group returned to their original rearing grounds. Although adults accounted for only 14% of the banded samples during 1970-79, they were responsible for 36% of the 112 returns obtained from those bandings (Table 14). Return data were scarce and all homing rates were underestimated, however, because mist nets were the primary capture method employed in Wisconsin and adult vulnerability to capture with mist nets was low. Birds banded as either flightless young or flying immatures showed similar return rates, with both groups returning at a rate well below that shown by adults. Location of return captures also indicated greater homing precision by adults, since all returns of birds banded as adults were within 2 miles of the original capture site, while several returning juveniles were captured 2 to 20 miles away from the point of banding.

In addition to the low return rate from summer trapping, indirect hunting season recoveries (after the first year) have also provided proof that not all young woodcock return to their natal areas. Several woodcock banded as juveniles in Wisconsin have been shot in subsequent hunting seasons in other northern breeding ground states (Table 15 and Fig. 11). The existence of several Wisconsin-banded birds in the bogs of Minnesota woodcock hunters caused Marshall (1982) to suggest a fall movement of birds from Wisconsin to Minnesota. But the fact that no direct recoveries have been recorded in that state indicates that our birds do not reach such areas during their first summer or fall, and instead arrive there on their first northward migration. Once a bird has completed its migration cycle and has bred in a particular area, it is apparently quite capable of returning to that area in subsequent breeding seasons since none of the birds banded as adults were recovered in adjacent breeding ground states.

Little difference in homing tendency between birds of different sex was observed in the present study, but a review of published band recovery information leads to a conclusion that homing instincts of juvenile males are greater than those of juvenile females. Mendall and Aldous (1943) reported that woodcock recoveries throughout North America totaled 46 by 1942, but only 3 recoveries of juvenile birds provided information pertinent to homing. Two of those birds, a male and a bird of unknown sex, were recovered near the point of banding while the remaining bird, a female, was recovered during the second fall after banding about 60 miles north of her natal area. The only exceptions Sheldon (1967) found to homing included a juvenile female and another female of unknown age which were recovered about 60 miles northwest and 350 miles northeast of their respective banding sites. Although Sheldon speculated that the latter bird may have been a migrant when banded, the 1 September banding date makes such a conclusion highly unlikely. Finally, Krohn and Clark (1977) reported that 11 woodcock banded in Maine were recovered 2 or more hunting seasons after marking in central New Brunswick, with 8 of those birds being immature females when banded.

Information obtained from more than 10,000 bandings added to our understanding of woodcock movements and mortality.

Population Dynamics

Population Density

Though normally a solitary or even asocial species, woodcock concentrate at various times both on their breeding and wintering grounds, causing Sheldon (1967) to compare woodcock densities to the "crests and troughs of ocean waves." Counts recorded at concentration sites may be impressive, but spring counts of displaying males (= occupied singing grounds) remain the accepted measure of population density.

We located 40 singing grounds (2.7/100 acres) within our 1,500-acre KCSA census block during the spring of 1976. Although the census area encompassed both suitable and unsuitable woodcock habitat, some of it constituted choice singing ground cover since it included an extensive intermixture of brush and openings. In comparison, the 1,300-acre area censused within the HCSA during that same spring included only a small amount of good habitat and produced only 16 singing grounds (1.2/100 acres). Subsequent census efforts within the HCSA were expended in a 2,880-acre strip which included a more representative mix of good and poor habitats. Forest types attractive to woodcock, including aspen, alder, and upland brush, accounted for 31% of the census strip, fairly similar to the 37% that such types accounted for within the HCSA as a whole. An average of 2.1 singing grounds/100 acres was found within the census strip during 1977-80.

Additional information on relative breeding densities is also available from the singing ground survey now that routes are distributed randomly. If we assume that a survey participant hears all peenting male woodcock within a 220-yd radius of each of the 10 listening points along each route, an area of about 300 acres would then be censused on the entire route. Thus, the average of 2.0 singing males/route heard during 1968-81 on Wisconsin's survey routes (Tautin 1982) might also be interpreted as an average statewide density of 0.67 singing males/100 acres for that same period. Such a density appears rather conservative, perhaps an indication that our estimate of area coverage along each route may be too high. Conservatism is preferable in this case, however, because roadside counts of singing male woodcock are probably biased toward overestimating true densities in most situations, since many of the forest openings used by displaying males (logging areas, homesteads, trails) are juxtaposed to roads.

Published estimates of breeding woodcock density have varied considerably (Table 16), but some of that variation was probably due to differences in size and conformation of census areas rather than solely to differences in habitat quality. Odum and Kuenzler (1955) recognized that density indices were much higher in small islands of prime habitat than in larger blocks of average quality habitat and categorized those respective measures as specific and crude densities.

Densities as high as 8 singing grounds within a 72-acre tract have been reported in isolated pockets of breeding habitat (Goudy et al. 1977), but counts made within the primary nesting range reveal maximum density over sizeable blocks of good habitat to be 4-5 singing grounds/100 acres. Densities of slightly more than 4 singing grounds/100 acres were counted in the best breeding habitats in Pennsylvania (Norris et al. 1940) and Maine (Mendall and Aldous 1943). Sheldon (1967) also reported 4-5 singing grounds/100 acres in known woodcock habitats in Massachusetts.

Estimates of crude woodcock density, or that density existing within blocks of land containing both suitable and unsuitable habitats, have been in the range of 1-2 singing grounds/100 acres (Table 16). Sheldon (1967) estimated 2 singing grounds/100 acres for the entire 88,000-acre Quabbin Reservation in central Massachusetts, but failed to provide any data in support of that estimate.

If the singing ground survey provides a valid, though somewhat inflated, estimate of relative population density across the major breeding range of the woodcock, then densities in Wisconsin are quite similar to those existing in Minnesota and several New England states, but below these prevailing in New Brunswick and southern Ontario. Michigan's density index is also slightly higher than our own, probably because forested land is more extensive and broadly distributed there than in Wisconsin. Michigan's land area is 52% commercial forest and only 2 counties are less than 10% forested (Chase et al. 1970), whereas Wisconsin's land area is 42% commercial forest and 10 counties have less than 10% of their area in forests (Spencer and Thorne 1972).

Population Structure

Summer trapping and the fall wing-collection survey both provide information on woodcock population composition, but the sex-age data of captured samples are biased, as has been reported in other studies (Sheldon 1961, Kletzly and Rieffenberger 1969). A comparison of the sex-age structure of captured and shot samples of Wisconsin woodcock revealed a preponderance of immature males among captured birds (Table 17). Immatures, especially males, were captured at a much higher rate than adults in summer roosting areas, making it impossible to draw inferences about population structure from samples of birds caught with mist nets or spotlights. Sex and age ratios of birds captured in the daytime habitats by use of funnel traps appeared more realistic than those recorded in roosting areas, but our funnel-trapping catch of 137 birds was too small for a meaningful comparison.

Besides containing an unrealistically high proportion of immatures, captured samples also varied in composition throughout the summer and early fall (Table 18). Adults were especially scarce in August samples when their participation in crepuscular flights was presumably suppressed by energy demands of the molt. Despite such seasonal variations in activity levels, the sex-age structure of our captured samples was quite similar from year to year. Immatures comprised 81 to 91% of the catch, with adults accounting for the remaining 9 to 19%. Males and females were nearly equal in abundance among adults, but immature males outnumbered immature females by a 2:1 margin.

In contrast to the preponderance of immature males observed in our captured samples, shot samples contained an abundance of adult females (Table 17). Adult females accounted for nearly one-third of all wings submitted by Wisconsin woodcock hunters, contributing to a lopsided adult sex ratio of 0.61 males/female. A sex ratio that far removed from equality appears to be unusual among birds, but Wisconsin's estimate has remained consistent from year to year and is similar to the rangewide average of 0.67 males/female reported during recent seasons (Artmann 1975). The woodcock sex ratio is also unusual in that it favors females, since published references on disparate sex ratios among waterfowl (Aldrich 1973), snipe (Tuck 1972), and ruffed grouse (Dorney 1963) all involved surpluses of males.

Causes for the distorted adult sex ratio remain unclear, but it appears that equal numbers of each sex are produced since the sex ratio among a small number of chicks accidentally killed and among banded chicks recaptured during the summer was close to 50:50. The sex ratio evidently remains even throughout the first fall, because equal numbers of juvenile males and females have been recorded in the wing survey during recent years (Table 19). Therefore, if differing survival rates between males and females are responsible for the disparate adult sex ratio, their effect is not evident until after the first fall. Although recovery data from Wisconsin-banded birds were insufficient to test for differences between survival of adults and immatures, a recent analysis (Dwyer and Nichols 1982) of regional recovery data indicated that survival rates of adult woodcock tend to be higher than those of young. That difference was greater among male birds in the Eastern unit, where young males had very low survival rates, but was greater among female birds in the Central unit. Nevertheless, information on woodcock survival rates obtained through banding analyses does tend to confirm the existence of the greater number of adult females in the population.

But Martin et al. (1965) examined data from the wing survey and concluded that adult males may not be taken in proportion to their actual numbers in the population. They found the proportion of adult males among wings submitted by hunters in northern states increased during the season which suggested a later migration of adult males. Sheldon (1967) analyzed wing survey data and suggested that adult males were moving through many areas after the peak of hunting pressure had passed, thus reducing the likelihood of their being taken by hunters. An examination of wing survey data for Wisconsin tended to support Sheldon's conclusion. The proportion of adult males among wings submitted by Wisconsin hunters was highest during the November portion of recent hunting seasons, when weekly wing receipts were at their lowest level (Table 19). In addition, direct recovery rates among Wisconsin-banded adults were considerably higher for females than males which, providing summer mortality rates were similar between the sexes, indicated that adult males were less likely to be shot than were adult females. But the reason our banded hens were shot at a higher rate was not because they had migrated into areas of heavier hunting pressure, since most direct recoveries of both males and females occurred near the banding area. Thus, it appears that some behavioral difference besides migrational timing must contribute to the greater vulnerability of adult females to shooting.

In addition to a potential weakness in measuring the adult sex ratio, some concern has also been expressed regarding the age ratio data resulting from the wing survey. Martin et al. (1965) reported seasonal changes in the age ratios for several states, with the proportion of immatures increasing during the season in Maine and New Jersey and decreasing in Michigan. An examination of Wisconsin wing survey data revealed our age ratio tends to be similar to Michigan's, with the proportion of immatures declin-

TABLE 16. *Estimates of breeding woodcock density.*

Location	Year(s)	Reference	Size of Tract (acres)	Description of Tract and Count	Density Index*
Maine	1939	Mendall and Aldous	1,500	Peak year for census area	4.2
Penn.	1939	Norris et al.	950	Moist (best) area in barrens	4.2
Minn.	1947-49	Dangler and Marshall	640	Portion of Cloquet forest	2.6
Mass.	1951	Sheldon	88,000	Estimate of Quabbis Reservation	2
Penn.	1950-60	Liscinsky	—	Large blocks of suitable habitat	1
Minn.	1967-70	Godfrey	3,875	Portion of Cloquet forest	0.7
Mich.	1968	Whitcomb	1,300	Suitable habitat on High Island	3.3
Wis.	1976	This study	1,500	Good habitat in KCSA	2.7
Wis.	1976	This study	1,300	Poor habitat in HCSA	1.2
Wis.	1977-80	This study	2,880	Belt transect through HCSA	2.1

* Singing grounds/100 acres.

TABLE 17. *A comparison of age-sex composition between samples of woodcock captured during the summer and shot during the fall in Wisconsin, 1970-80.*

	Captured in Summer							Shot in Fall						
		Age-Sex Composition (%)				Sex Ratios			Age-Sex Composition (%)				Sex Ratios	
Year	Sample Size	Ad. Male	Ad. Female	Imm. Male	Imm. Female	Ad. Male/ Ad. Female	Imm. Male/ Imm. Female	Sample Size	Ad. Male	Ad. Female	Imm. Male	Imm. Female	Ad. Male/ Ad. Female	Imm. Male/ Imm. Female
1970	372	6	7	55	32	0.9	1.7	1,435	20	29	27	24	0.7	1.1
1971	589	9	10	54	27	0.9	2.0	1,655	17	33	24	26	0.5	0.9
1972	1,130	9	7	57	27	1.3	2.1	2,382	19	32	25	24	0.6	1.0
1973	1,877	5	6	60	29	0.8	2.0	2,739	18	31	25	26	0.6	0.9
1974	1,768	7	7	57	29	1.0	2.0	2,845	18	28	28	26	0.7	1.1
1975	581	6	7	56	31	0.8	1.8	3,073	20	34	24	22	0.6	1.1
1976	460	4	5	61	30	0.9	2.0	2,105	23	33	24	20	0.7	1.2
1977	850	4	5	64	27	0.8	2.3	2,658	17	29	29	25	0.6	1.2
1978	1,164	8	6	55	31	1.3	1.8	1,888	21	34	22	23	0.6	0.9
1979	702	8	8	54	30	1.1	1.8	1,689	22	35	20	23	0.6	0.8
1980	538	8	6	57	29	1.2	2.0	1,658	19	29	26	26	0.6	1.0
Totals/ avg.	10,031	6.5	6.5	58	29	1.0	2.0	24,127	19	32	25	24	0.6	1.0

TABLE 18. *Age-sex composition of woodcock captured in Wisconsin according to 30-day trapping periods, 1970-80.*

	Age-sex Composition (%)				
30-day Period	Ad. Male	Ad. Female	Imm. Male	Imm. Female	Sample Size
1 Jun - 30	13	14	48	25	963
1 Jul - 30	6	5	59	30	4,182
31 Jul - 29 Aug	4	5	61	30	3,092
30 Aug - 28 Sep	11	9	53	27	1,713
29 Sep - 30 Oct	14	17	48	21	247
Summer and Fall	7	7	57	29	
Number	694	691	5,866	2,946	10,197

TABLE 19. *Seasonal changes in sex-age composition among samples of woodcock wings submitted by Wisconsin hunters to the federal wing collection survey, 1976-80.*

		Age-Sex Composition (%)				Sex-Ratio		Age Ratio
10-day Period	Sample Size	Ad. Male	Ad. Female	Imm. Male	Imm. Female	Ad. Male/ Ad. Female	Imm. Male/ Imm. Female	Imm./Ad. Female
11-20 Sep	787	18	32	27	23	0.55	1.15	1.59
21-30 Sep	1,111	21	29	25	25	0.71	0.96	1.74
1-10 Oct	2,737	18	32	25	25	0.58	1.01	1.62
11-20 Oct	2,944	19	33	24	24	0.58	1.02	1.45
21-31 Oct	1,927	23	32	25	20	0.71	1.27	1.43
1-10 Nov	403	26	35	18	21	0.74	0.86	1.08
11-20 Nov	42	26	36	12	26	0.73	0.45	1.07
Season totals/avg.	9,951	20	32	25	23	0.62	0.96	1.51

ing during the last few weeks of the season (Table 19).

Among other species of birds, declining age ratios during the hunting season have been attributed to a progressive reduction of immatures caused by their greater vulnerability to shooting. But no evidence has been found of age-specific differences in vulnerability to shooting among woodcock, so age ratio trends apparently result from differences in migrational timing.

Tuck (1972) believed that juveniles preceded adults in the fall migration of snipe and the same situation apparently prevails among woodcock. Wing survey data have indicated that adult males are the last birds to depart in the fall and it is logical to assume that adult females might also exhibit a greater site tenacity than juveniles. Furthermore, the proportion of direct recoveries occurring within the state is higher among adults (76%) than immatures (62%), another indication that adults remain longer in the state.

Despite the potential biases which hamper any sampling effort, the wing survey appears to provide a fairly good measure of woodcock population structure. Age and sex ratio data have been remarkably consistent and conclusions about woodcock population dynamics based on wing survey data have generally been supported by information obtained through banding analyses. But recovery data do indicate that adult males may be underrepresented in the wing survey. If the 0.6 male:female ratio from the wing survey represents the true ratio for the hunting season period, then the ratio the following spring would be even lower since adult male mortality should exceed that among females during the spring migration and courtship period. Furthermore, since some adults are subdominant and do not possess a singing ground, the ratio of singing grounds to adult females would be in the range of 1:3 or 1:4. But results of our spring field work indicate that estimate to be unrealistic and the ratio of 8 singing grounds to 13 nesting females reported by Goudy et al. (1977) appears more comparable to the situation existing within our study areas. Even if females outnumbered males by a 2:1 margin in the spring, the shortage of males should not hinder reproduction since woodcock do not form pair bonds and the male has no involvement in nesting or brood rearing.

Recruitment

Compared to most other Wisconsin game birds, the woodcock's reproductive potential is very low. The hen woodcock's clutch of 4 eggs is only 1/2 to 1/3 the size of the average clutch for the pheasant, mallard, or ruffed grouse. Because the woodcock's production is inherently limited and because annual harvests are expanding, it is important that we have some measure of the productivity of the species. Such a measure has been available since 1959, when the federal wing collection survey was implemented. The ratio of immatures to adult females among wings submitted by hunters serves as an index to annual reproductive success. Although some bias may result from the manner in which samples of wings are obtained, the survey is our best indicator of changes in woodcock productivity. During the present study, information on annual production was also obtained as a result of nesting investigations and summer banding. Relationships between these various measures of productivity were examined to determine their comparative value as indicators of annual reproductive success.

Nesting Studies. Disregarding the small number of nests which were disrupted due to study operations, overall nesting success during the course of the study averaged 50% (Table 20). Annual nest success ranged from 29 to 80%, but small sample sizes contributed to the extremes. Nevertheless, variations in annual nesting success did occur as a result of changes in weather conditions and predation pressure. But only in a few cases could nesting success be directly related to a single factor. One such case was the poor nesting success in 1979 which resulted from a severe late spring snowstorm. Even the lowest level of success observed among woodcock nests, however, would be considered a moderate to above average level of nesting success among other game birds, indicating that high nesting success has compensated to some degree for the woodcock's small clutch size. Because a high proportion of woodcock nests are successful, renesting may play only a minor role in determining annual recruitment levels. Although evidence of renesting was found during the present study, replacement clutches were not believed to make a major contribution to production in most years.

In addition to excellent nesting success, woodcock also appeared to experience low chick mortality during the brood period. Average size of the 301 broods in which chick counts were believed complete was 3.1 chicks. Since successful nests produced an average of only 3.5 chicks, chick mortality between hatching and the time the broods were discovered was evidently quite low. A more precise estimate of chick mortality during the brood period was provided by the decline in average brood size which accompanied an increase in brood age. The number of chicks in broods less than 1 week old averaged 3.2, while broods more than 2 weeks old averaged 2.7 chicks. If we arbitrarily assign an age of 3 weeks (about midway between flight capability and brood breakup) to those older broods, then chick mortality during the first 3 weeks of the brood period would average only 0.04 chick/day.

Year-to-year variations in average brood size were smaller than those recorded for nesting success, but were still large enough to indicate that chick survival varied between years (Table 20). Annual variations in weather conditions were believed to be primarily responsible for observed differences in brood size, but an examination of weather records provided little evidence of a relationship. If weather conditions during some years caused a large number of hens to lose their entire brood, however, such losses would not necessarily be reflected in smaller average brood sizes during those years since it is impossible to identify the proportion of hens which had lost their brood.

In addition to weather conditions, brood size may also be dependent upon the age structure of the nesting population. Dwyer et al. (1982) reported that broods of hens in their first breeding season averaged 2.9 chicks, while broods of older hens averaged 3.5 chicks. But their tests of the effect of the year and hen age on brood size revealed year effects to be more important in determining brood size and chick survival.

Summer Banding. If the number of immature woodcock using summer roosting sites is a function of the production of young in that area, then it follows that the immature catch rate should provide a measure of annual woodcock productivity. Capture success can also be influenced by factors other than abundance of birds, such as weather conditions and the proficiency of the banding crew. The impact of those variables on year-to-year capture rates should have been minimal, however, due to the duration of our capture efforts and the low turnover rate among project personnel.

A comparison of the mist netting catch rate of immature birds with production indices obtained from nesting studies revealed inconsistent results (Table 20), which might be expected because of the small samples involved. But the similarity of the indices in some years indicated they may have some value in assessing annual productivity. Although nest success, brood size, and immature capture rates were in general agreement only half the time, it does appear possible to distinguish between good and poor production years. Thus, 1974, 1977, and 1978 appeared to be years of above-average woodcock production in north central Wisconsin, while 1971, 1979, and 1980 were believed to be poor production years.

Wing Collection Survey. Wisconsin's fall woodcock age ratio has averaged 1.6 immatures/adult female and has remained quite stable, fluctuating in a range of $\pm$ 25% during 1969-80 (Table 20). The consistency of the productivity index is surprising when one considers that the woodcock is among the earliest nesters and frequently encounters severe weather conditions during the nesting and brood rearing period. Fluctuations in the productivity index derived from the wing survey coincided with changes in the other production indices only about half the time, a level which could be expected on the basis of chance alone. But

TABLE 20. *Estimates of annual woodcock productivity in Wisconsin, 1969-80.*

Year	Nest Success*		Brood Size		Immature Capture Rate**		Fall Age Ratio	
	No. Nests	Percent	No. Broods	Mean Size	No.	I/100 NN	No.	I/AF
1969	5	80	6	3.2	145	56	1,081	1.7
1970	14	64	39	3.1	341	60	1,435	1.7
1971	20	45	24	3.1	382	42	1,655	1.6
1972	7	71	15	2.8	770	59	2,382	1.6
1973	11	55	32	3.2	1,134	73	2,739	1.7
1974	20	55	55	2.9	1,082	79	2,845	1.9
1975	18	56	39	3.2	451	69	3,073	1.3
1976	12	42	19	2.7	424	70	2,105	1.4
1977	16	63	11	3.2	771	94	2,658	1.9
1978	36	53	28	3.4	971	84	1,888	1.4
1979	30	37	15	3.1	584	56	1,689	1.2
1980	17	29	18	2.7	445	43	1,658	1.8
Totals/ avg.	206	50	301	3.1	7,500	68	25,208	1.6

* Proportion of total nests which hatched 1 or more chicks, excluding nests disrupted by study activities.

** Number of immature woodcock captured/100 net-nights of effort during preseason banding operations.

TABLE 21. *The number of woodcock bandings and direct recoveries by age and sex group in northern Wisconsin during 1968-80.*

Age and Sex	Preseason Period			All Seasons		
	Number Banded	Direct Recoveries	Recovery Rate	Number Banded	Direct Recoveries	Recovery Rate
Local unknown				748	11	0.015
Immature male	4,725	71	0.015	5,176	87	0.017
Immature female	2,436	48	0.020	2,680	54	0.020
Adult male	500	2	0.004	765	10	0.013
Adult female	523	17	0.033	680	19	0.028
Totals	8,184	138	0.017	10,049	181	0.018

the age ratio among woodcock wings collected in the state presumably reflected the productivity of the entire region contributing to Wisconsin's fall flight, while the other indices represented the productivity of a small area in north central Wisconsin. Although there appeared to be little correlation between the various production indices over the long term, there was good agreement during a few years. An example was 1979, when an unusually late snowfall evidently impacted production within our study area and also over a large portion of northern Wisconsin. Nest success, immature catch rate, and the fall age ratio were all well below average that year (Table 20).

The effect of that storm was unusual, however, not only because of its extent, but also because it occurred while many hens were in mid- to late incubation when the likelihood of renesting is low. Since such a storm would have to be considered a rare event, the chance that a single weather phenomenon might reduce woodcock productivity over a region encompassing several states is probably remote. It is far more likely that annual production fluctuates independently in response to environmental conditions which differ from region to region and state to state. That annual woodcock production in Wisconsin is not closely related to productivity in other states is evident in a comparison of age ratios from Wisconsin and the entire Central Region (Fig. 12).

Survival

Recovery and Survival Rates. The number of preseason woodcock bandings and resulting recoveries are provided in Table 21. Direct recovery rates were low, averaging less than 2%. Because of the low recovery rates and the relatively small number of adult bandings, our data were not well suited for use with recently developed models of Brownie et al. (1978). A scarcity of adult recoveries made it impossible to analyze adult and immature data separately, so age-specific differences in recovery or survival rates could not be identified. The analysis of our recovery data was provided by the Migratory Bird and Habitat Research Laboratory in Laurel, Maryland. Hypotheses about differences in recovery or survival rates between birds of different sex were tested by using z-test statistics (Brownie and Robson 1974, Brownie et al. 1978).

The mean recovery rate for females (.026) was higher than that for males (.018), but small samples failed to provide a significant test statistic. The higher recovery rate for females could result either from their greater vulnerability to hunting or from lower survival of males than females during the interim between marking and the hunting season. Although available data are not sufficient to permit a choice between these two possibilities, it would not be unreasonable to assume that both might contribute to the observed difference. Female woodcock have slower average flight speeds (Godfrey 1974) which, coupled with their substantially larger size, could make them an easier target and thus more vulnerable to shooting. On the other hand, males are much more active than females during their first year of life which would put them at a greater risk of death through natural mortality. In addition, adult males are actively displaying in the spring which would make them more vulnerable than females to predation.

Estimated mean survival rate was also slightly higher for females than males (Table 22), but the test statistic indicated no significant difference between the sexes. Results of earlier studies in Louisiana (Martin et al. 1969) and Maine (Krohn et al. 1974) revealed that females tend to have higher survival rates than males. Although our limited data did not permit us to draw the same conclusion, some evidence was produced which indicated that females did live longer than males. Despite the preponderance of males among Wisconsin-banded woodcock, females outnumbered males among recoveries made 3 or more hunting seasons after banding. Females comprised the major share of elderly woodcock, since 10 of the 14 recoveries made 6 or more hunting seasons after banding were females.

TABLE 22. *Mean survival and recovery rates for woodcock banded in Wisconsin and the entire Central Region.*

Reference Area	Age/Sex	Recovery Rate Mean	Recovery Rate SE	Survival Rate Mean	Survival Rate SE
Wisconsin	Male	0.018	0.24	0.524	0.041
	Female	0.026	0.38	0.542	0.048
Central Region*	Adult male	0.031	0.007	0.40	0.15
	Adult female	0.047	0.008	0.525	0.096
	Immature male	0.025	0.004	0.356	0.124
	Immature female	0.032	0.006	0.313	0.094

* Dwyer and Nichols (1982).

Longevity. Estimated mean life spans for Wisconsin woodcock were 1.5 and 1.6 years for males and females, respectively. These estimates were derived from a banding analysis performed in 1980 by personnel of the Migratory Bird and Habitat Research Laboratory which did not incorporate data on several old-age birds recovered during recent hunting seasons and thus may understate average longevity. The estimates also appear to underestimate differences between the sexes, since 10 of the 14 recoveries made 6 or more hunting seasons after banding were females.

The oldest male bird observed during the study was banded near Park Falls as an ASY bird on 26 June 1974 and recaptured in the same area and on the same date in 1980 when he was at least 8 years old. The oldest female, on the other hand, was banded near Park Falls as an immature bird on 30 June 1971 and was shot in Oconto County on 2 October 1982 at the age of 11 years 5 months. This bird established a new record for woodcock longevity by exceeding the 9 years 4 months life span reported by Clapp et al. (1982).

Causes of Mortality - Hunting. Annual estimates of Wisconsin's woodcock harvest are available for 1933-80 from voluntary returns of hunter report cards and from DNR mail surveys (Fig. 13). Resulting kill estimates are not adjusted for sampling biases and thus serve only as indices to harvest levels. The woodcock harvest index derived from this survey has surpassed 200,000 during recent hunting seasons, but the index is believed to exceed true harvest levels due to response biases. March and Hunt (1978) found DNR harvest estimates for ducks to be approximately 25% greater than U.S. Fish and Wildlife Service figures, but neither survey could be considered free of response bias.

Another index to Wisconsin's annual woodcock kill is provided by the federal waterfowl harvest questionnaire. This survey requests information from duck stamp buyers about the number of waterfowl and other migratory birds they bag. The survey revealed that those Wisconsin hunters who purchased federal duck stamps bagged an estimated 125,000 woodcock during the 1976-77 hunting season (Martin 1979). The proportion of the annual woodcock kill that is accounted for by hunters who pursue both waterfowl and woodcock is unknown, but federal duck stamps in Wisconsin have averaged about 30% of small game license sales in recent years. Clark (1972) reported less than 50% of the woodcock harvest could be attributed to waterfowl hunters in several states having reliable small game kill surveys. He believed doubling the woodcock harvest reported by waterfowl hunters would provide a conservative estimate of total U.S. woodcock harvest. If Clark's assertion is correct, the woodcock kill of

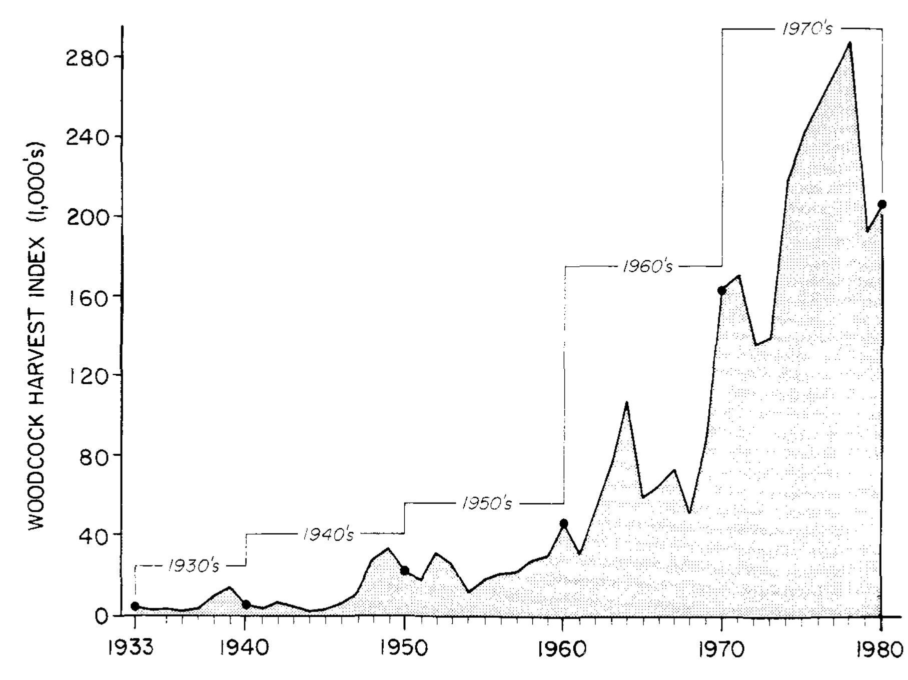


FIGURE 13. Woodcock harvest trends as indicated by DNR small game harvest survey, 1933-80.

Owls were believed to be the major predators of woodcock within our Wisconsin study areas.

Because woodcock are among the earliest ground nesting birds in Wisconsin, they risk the loss of nests to spring snowstorms.

822,000 reported by duck stamp purchasers during the 1976-77 season (Martin 1979) could then be projected to a total kill of 1.6 million birds.

Despite the imprecision of harvest estimates, surveys were in agreement concerning the importance of Wisconsin as a harvest area and the increasing interest in woodcock hunting. Wisconsin ranked fourth among all states in both estimated annual kill (Owen 1977) and number of woodcock bagged by waterfowl hunters (Martin 1979). Federal surveys have revealed that the proportion of waterfowl hunters who also hunt woodcock increased significantly between 1964 and 1975, with the increase averaging about 3%/year rangewide and 7%/year in Wisconsin (Martin 1979). In addition, the woodcock harvest index derived from our small game kill survey has more than doubled during every decade since the 1930's. Changes have been most dramatic during the past two decades, however, as evidenced by the 10-fold increase in the index between the late 1950's and the late 1970's (Fig. 13). Increased woodcock harvests are the probable result of growing hunter interest and cannot be attributed to an expanding woodcock population. It is, in fact, likely that increased harvests have occurred in the face of woodcock population declines, since successional changes have contributed to a reduction in habitat quality.

Although the harvest of woodcock in Wisconsin appears to be increasing, low recovery rates of Wisconsin-banded woodcock suggest that hunting is not a major cause of overall annual mortality. Recovery rates differed considerably between cohorts banded in northern and central Wisconsin, however, indicating that levels of hunting mortality varied between regions. Direct recovery rates for small numbers of woodcock banded during 1978-80 in ruffed grouse trapping operations at Navarino and Sandhill Wildlife areas averaged 7.9 and 8.2%, respectively, while recovery rates for birds banded in northern Wisconsin sites during those same years averaged 2.1%. The direct recovery rate for another group of birds banded in 1975-76 near Stevens Point during a graduate research investigation (Haasch 1979) was 21.4%, more than 10 times higher than the 1.8% average recovery rate for northern Wisconsin bandings during the same years.

But regional differences in recovery rates and hunting mortality may be overstated if band reporting rates differ between areas. Such a situation was probable, since a mandatory hunter check station is operated at Sandhill and some band collecting activity apparently occurred in the Stevens Point study. Although such activities certainly resulted in a higher proportion of recovered bands being reported, the great disparity in recovery rates between birds banded in northern and central Wisconsin indicates that a regional difference in level of hunting mortality exists.

No estimates of band reporting rate for woodcock are available. Factors which have been suspected to reduce waterfowl band reporting rates, though, such as restrictive hunting regulations and band commonness (Martinson 1966), should have little effect on woodcock band reporting rates since regulations have remained relatively stable during recent seasons and only about 70,000 woodcock have been banded. Nevertheless, band commonness was a potential problem during the present study due to the relatively large volume of bandings in some of our perennially used netting areas. In 1974, for instance, more than 40% of total rangewide bandings occurred in northern Wisconsin and a few of the netting sites utilized that year had already been in use for several consecutive summers. But if the intensity of our banding effort caused reporting rates to be depressed near banding sites, it would be reasonable to assume that the fraction of total recoveries coming from the vicinity of the banding sites should have declined over the years. An analysis of the 1970-79 recovery data, however, revealed little change over the years in the relative proportion of recoveries which occurred near the banding site. The low recovery rate was, therefore, believed to be an accurate reflection of very light hunting pressure.

Hunting accounted for only 2 of the 11 deaths recorded among our radio-tagged cohorts, another indication that most woodcock die from causes other than shooting. An adult male radio-tagged on 19 July 1976 in the KCSA was subsequently shot near the capture site on 26 September. The bird was in good condition judging by his weight of 160 g and was still carrying his transmitter which had ceased functioning in August. An immature female bird radioed on 4 August 1977 in the HCSA was also eventually shot in the same general area on 17 September. The bird had lost weight during the monitoring period, going from 195 g at capture to 171 g at recovery, but behaved normally when last flushed on 15 September.

Another radioed adult male bird was expected to become a hunting season casualty because his normally used cover was adjacent to a hunting trail located within a portion of the study area which received above average hunting pressure. During a monitoring session on 25 September 1976, a woodcock hunter was known to pass within 15-20 yd of the bird. The bird showed no reaction to the hunter's presence and remained inactive until I flushed him later to pinpoint his location. Despite his continued use of the same general area, the bird survived and departed on migration on 27 October.

Collisions. Deaths from causes other than shooting represented only 6% of all recoveries, but there is little chance of a banded woodcock that died of natural causes being found and reported. Eleven of the 24 nonshot recoveries involved deaths from collisions, including birds struck by motor vehicles, found dead on highways, or killed by flying into objects. Woodcock make frequent use of dirt or gravel roadways, especially during the crepuscular flight period, and have been observed courting, bathing in puddles, and probing for earthworms while on roads. During an earlier study in Michigan (Gregg 1972), woodcock were encountered on roads with sufficient frequency that our vehicle was equipped with a platform which supported a person during attempts to net the birds as they flushed.

Besides the several recoveries resulting from collisions with vehicles, 1 young male bird banded near Park Falls was recovered the following spring about 70 miles northwest of the capture site when he struck a guy wire on a radio tower. Collisions with wires or other stationary objects were also known to have caused death or serious injury to several unbanded birds. One bird apparently survived an encounter with a tree, and was still carrying a piece of wood embedded in his breast muscle when captured. Another bird, an unbanded adult male, had evidently broken a leg by colliding with a telephone wire. The bird was found directly beneath the wires during nest/brood searching operations and was very near death judging by his weight of 88 g. Although wires and towers were known to cause some mortality, they probably posed less hazard for woodcock than for many other nocturnal migrants. No woodcock have been reported among the several thousand birds killed by television towers in Wisconsin (Kemper 1958, Kemper et al. 1963, Sharp 1971, Weise 1971).

Predation. The relative importance of predation as a cause of woodcock deaths is difficult to gauge, but most researchers have agreed that predation plays a minor role in woodcock population regulation. Only 3 of our 24 nonshot recoveries, or about 1% of all recoveries, could be attributed to predation. One bird was reportedly caught by a cat, another by a dog, and a third by a hawk or owl. All of these animals had been previously implicated in woodcock mortality, but only the house cat has been considered a serious threat (Mendall and Aldous 1943).

Among wild predators, owls probably take the most woodcock. Sheldon (1967) reported seeing a great horned owl hunting near a singing ground and finding the remains of several woodcock in a horned owl nest. Owls were also known to take woodcock in our study areas and 1 family of long-eared owls appeared to be selectively preying on woodcock. During the 1975 summer, 1 or more of the owls was observed flying back and forth over a section of logging road which was being used by a large number of woodcock each evening. The owls were using the area prior to the initiation of our netting efforts and probably continued to do so after we left, even though we captured up to 4 of them in our nets.

Besides long-eared owls, potential predators captured in our nets included several saw-whet owls, and a small number of barred owls and sharp-shinned hawks. Both barred owls and saw-whet owls were known to attack woodcock in our nets, but were probably attracted by the birds struggling in the nets since a woodcock would be an unlikely prey species for the tiny saw-whet. Despite the suspected attractiveness of our netting sites to predators, very few birds were killed by predators due to the short period of time they were in the nets. In 1974, for example, only 6 of the 1,235 woodcock captured in mist nets were killed by predators.

Predators accounted for 6 of the 11 woodcock deaths recorded among our radio-tagged cohort, but in 2 cases transmitter harness difficulties predisposed the birds to predation. The remaining 4 instances of predation did not appear to be equipment related, however, and were believed to represent normal instances of predation. The 4 birds were killed an average of 26 days after tagging (range = 17 to 38) and all had appeared healthy when last observed. One bird was killed by a small mammal, as evidenced by tooth marks on the harness and the caching of the carcass remnants beneath a large stump. The carcass of another bird had nearly all the breast muscle consumed and the skeleton intact, indicating that a raptor was involved. Evidence in the remaining 2 cases was insufficient to identify the predator.

Weather. Although several records of woodcock mortality resulting from cold waves exist for the wintering grounds, such losses are more difficult to detect on the breeding grounds. Within our study areas, inclement weather caused significant losses of nests and occasionally even young chicks, but was believed to be a much more important mortality factor than indicated by any carcass counts.

Alison (1976) observed some mortality among adult male woodcock during an early spring snowstorm in Ontario and we recorded two instances of weather-related starvation among males in the spring. Males, because of their smaller body size and associated greater heat loss, are less well equipped than females to withstand cold weather. They also appear to fare poorer than females during periods of nutritional stress, since males among our captive birds succumbed more quickly to food shortages than did females. During the first year of our penned woodcock studies, when earthworm supplies were the least reliable, all 4 of the captive male birds died before either of the 2 females perished. Average survival period among captive males was approximately 1 month, while females survived for at least 8 months.

Body weights of adult males are at their lowest point during the spring courtship period, and energy reserves in the form of body fat would not be available to sustain them if food became unavailable. Thus, any mortality resulting from severe spring weather would involve primarily male birds and could be a factor in maintaining the preponderance of females among adult woodcock.

Management Considerations

Harvest Management

Woodcock hunting is regulated by the U.S. Fish and Wildlife Service, with results of singing ground and wing surveys forming the basis for hunting season frameworks. The current framework dates are 1 September and 28 February, and individual states can set their hunting seasons within that period. Hunting regulations have been liberalized over the years, the daily bag limit increasing from 4 to 5 birds in 1963 and season length expanding from 50 to 65 days in 1967. Wisconsin's mid-September opening date and 65-day season have remained stable since 1967.

The liberal seasons and bag limits have been justified by the very low band recovery rate which indicates that hunting is not a major cause of mortality. But the low recovery rate may be misleading if band reporting rates for woodcock are low. No estimate is available on the band reporting rates and little data exist on woodcock crippling loss, so it is impossible to measure harvest rates. Even if kill rates were known, however, the true importance of hunting to woodcock would depend upon a knowledge of the extent to which hunting mortality replaces, or compensates for, natural mortality.

Although regulations can be used to affect the size of the harvest, fluctuations in annual harvests from about 50,000 birds to more than 250,000 birds under the same season framework indicate that our present regulations exert little control over the size of the harvest. As hunting interest continues to grow, however, hunting regulations can be expected to become a more useful management tool. Increased harvests may soon even force a reappraisal of the benefits of earlier hunting seasons. Results of the wing survey have indicated that September woodcock harvests have remained relatively small since the earlier season was adopted in 1967. But that situation is expected to change in 1983 with the concurrent opening of the ruffed grouse season in mid-September, providing an increased incentive for hunters to be afield early. In Michigan, where for several years woodcock and ruffed grouse hunting seasons have opened concurrently in mid-September, wing survey data indicate that a relatively high proportion of the annual woodcock harvest occurs early in the season. During the 1972 through 1975 hunting seasons, for example, from 26-35% of all wings submitted by Michigan hunters were collected during the first two weeks of the season, while only 13-19% of the Wisconsin wing receipts occurred during that same period (Artmann 1977).

Since very few migrant woodcock are believed present in the state during September, hunting pressure during that period is directed almost exclusively at local birds. Large harvests during the September portion of the season could conceivably reduce subsequent breeding populations. Although there is no evidence that hunting has yet had any effect on woodcock populations, a continued growth in annual harvests will increase our need for a better understanding of the relationship between hunting and population size.

Habitat Management

Harvest regulation alone will not guarantee a continued abundance of woodcock, since habitat conditions ultimately determine population size. If suitable habitat declines, woodcock numbers will decline whether hunting occurs or not. Because our forests are naturally growing older, woodcock populations will decrease without an effective program of habitat management.

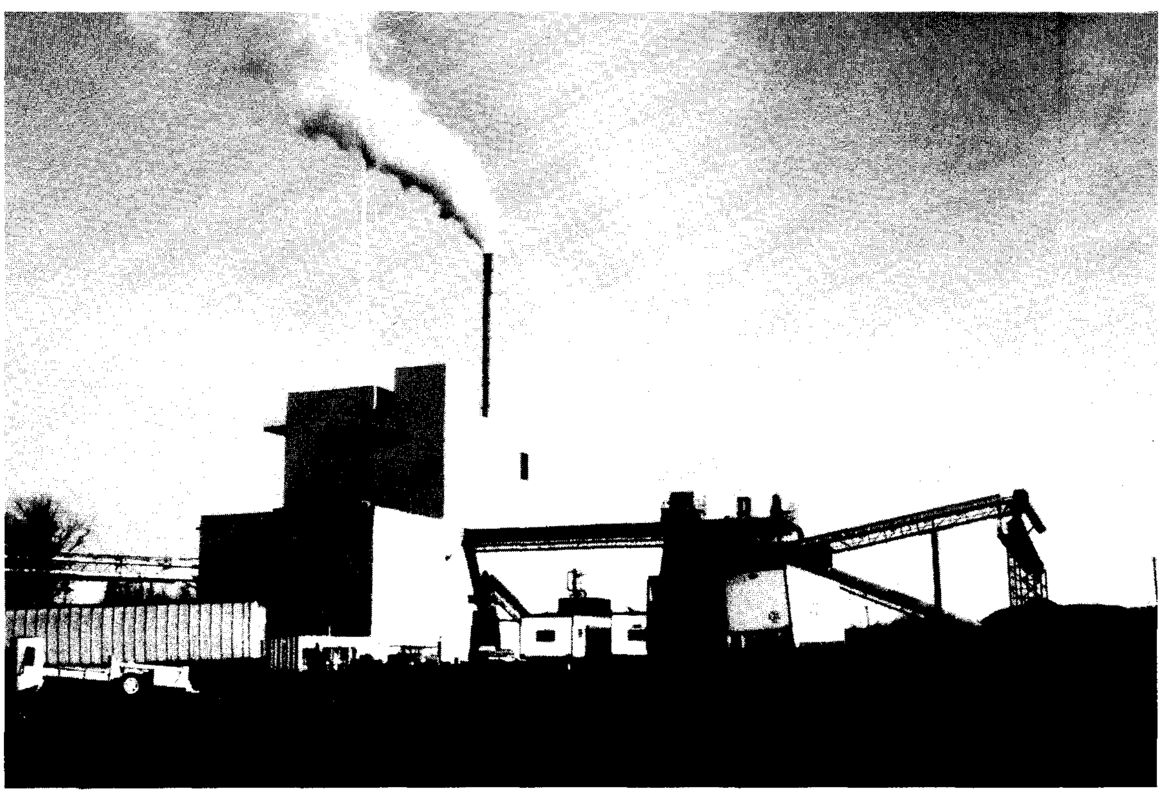
Habitat Factors. Woodcock abundance is dependent upon the amount of habitat containing both food, in the form of earthworms, and cover of the proper structure to provide foraging opportunities and protection from predators. Earthworm biomass and woodcock numbers in a particular locale are determined to a great degree by soil conditions, but it is not feasible to alter or regulate soil conditions on an extensive basis to benefit woodcock. Management of soil conditions is possible in small areas as evidenced by the European gamekeeper's creation of artificial snipe beds, where soil moisture and texture are controlled by mixing the proper portions of mud, reed stubble, and pig manure. Reynolds et al. (1977) suggested that soil habitats could be improved for earthworms and woodcock if an inexpensive irrigation or weir system could be established to regulate soil moisture or water table height.

Although difficulties in attempting to modify physical characteristics of the soil are apparent, Reynolds et al. (1977) pointed out that earthworm abundance is also dependent upon the existence of their preferred foods. Thus, they believed that any efforts aimed at improving woodcock habitat should focus on aspen and alder instead of softwoods or mixed cover since the latter types sustain relatively few earthworms.

A variety of plant species has been observed within habitats used by woodcock, but aspen and alder are by far the most important forest types to woodcock in Wisconsin. These plants apparently provide the vegetative structure that is best suited to the woodcock's foraging strategy. Both species are representative of the pioneer stage of forest succession and are typical of the youthful forests woodcock prefer. The leaves of both species also provide choice food for earthworms. Furthermore, aspen stands characteristically contain openings and brush which are important components of woodcock habitat. Aspen also has a short cutting rotation, which ensures that a young forest is frequently available. Maintenance of both aspen and alder is believed essential to the continued abundance of woodcock in Wisconsin.

Specific Cover Requirements. Woodcock habitats have been categorized in various fashions during investigations of cover preferences. Mendall and Aldous (1943) recognized four distinct classes of cover according to seasons they were used. They were (1) breeding cover, (2) summer cover, (3) early fall cover, and (4) late fall cover. Forest types receiving the greatest use during those seasons were alder, young hardwoods, and young hardwood-conifer stands. Mixed stands were preferred in the spring and alder was the preferred type during the remainder

Commercial forestry operations will continue to play a key role in determining the amount of woodcock habitat available in Wisconsin.



Increased use of wood, such as the 20 semi-trailer loads of wood chips burned each day in the new steam generating plant in Park Falls, should benefit woodcock by an increased availability of young forests.

of the year. But considerable overlap was observed in seasonal habitat use, since preferred types often existed within the same general cover. Sepik et al. (1981) also identified four distinct types of habitat which were believed essential to meet the woodcock's biological needs. Specific habitats were required for (1) singing grounds, (2) nesting and brood rearing, (3) daytime feeding, and (4) roosting. Habitat types which fulfilled those requirements were (1) clearings, (2) young, second growth hardwoods, (3) alders or young hardwoods on moist soils, and (4) large fields.

But, just as a particular habitat can be used by woodcock from spring through fall, so can a particular type serve more than a single purpose. In our study areas, at least, a few forest openings served as both courtship sites and roosting areas, and some forest stands were used for both nesting and feeding. Thus, it appears that the four categories recognized in the previously cited studies could logically be lumped into three types — aspen, alder, and openings. Regardless of whether habitat needs were classified by season or function, these types could be considered essential.

Extensive Habitat Management. The most practical way to manage woodcock habitat throughout Wisconsin's extensive northern forest is by means of commercial forestry operations. Because our timber resource is largely aspen and because the state's timber economy is oriented toward pulpwood, Wisconsin's forests should continue to produce woodcock along with a variety of other wood products. Pulpwood sales will probably continue to be the major habitat management tool in Wisconsin for several years to come.

Maintenance of the aspen type will not be sufficient to guarantee woodcock abundance, however, since young aspen stands appear to be much more productive of woodcock than are older stands. If woodcock habitat quality is directly related to the availability of young aspen stands, then we can expect a decline in habitat quality during the 1990's. Computer projections carried out by DNR Forest Management staff on the 964,000 acres of aspen on public lands indicated only 6,000 acres to cut per year throughout the 1990's because of heavy cutting in the 1970's and 1980's to harvest overmature stands. That figure is only 28% of the acreage that should be cut to reach age class regulation and represents a real scarcity of young aspen in the near future. A move to shorter rotations would certainly improve the outlook for woodcock habitat in Wisconsin and might also be good forestry, since Einspahr (1972) indicated that total annual volume could be doubled by adopting 10 to 20 year rotations and complete tree harvesting.

But not all forest management practices benefit woodcock and some, such as the planting of forest openings, are detrimental. Coordination of forestry and wildlife management programs is now a required procedure on all public lands in Wisconsin, however, so opportunities exist for integrating woodcock habitat needs with the forest management program. To some extent, this integration has been ongoing in Wisconsin since 1970, when guidelines were established that set priorities for forest management activities.

These guidelines identify habitat types important to several forest game species and provide recommendations on the amounts of various types necessary to maintain deer densities at specified levels. For example, a minimum of 45% of the area should consist of intolerant (sun-loving) forest types, including 3-5% permanent openings and 25% aspen in order to maintain a deer herd at a level of 20/mile^2 in the fall. Although the relationship between forest composition and population densities is not as well defined for woodcock as for deer, the abundance of both species hinges upon the presence of intolerant forest types. Not all intolerant types are equally valuable to deer and woodcock, however, since most scrub oak and jack pine forests are poor places to find earthworms. But in regions where loamy soils predominate, the 25%, 45%, and 65% levels of intolerant types required to maintain low, medium, or high deer densities appear to be very similar to the proportion needed to maintain low, medium, or high densities of woodcock. When those compositional guidelines were applied to the various segments of the HCSA census area, corresponding densities of singing males averaged 1.1, 2.4, and 4.1/100 acres, respectively.

Since woodcock abundance is closely tied to the abundance of intolerant forest types, successional changes represent a major threat to the future existence of woodcock habitat. Succession has not impacted all woodcock habitat components equally, however, because the abundance of alder appears to have changed little during recent years. Acreages of aspen and openings, on the other hand, have undergone substantial reductions and these declines are expected to continue. But an ongoing program of openings and aspen maintenance on our public forest lands provides some assurance of the future availability of those habitat components. In the case of openings, however, maintenance efforts alone were found to be inadequate to meet the recommended 3-5% openings goal and additional openings are being constructed to supplement relict openings. Although intensively used by deer, a recent examination of constructed openings revealed little use by singing male woodcock (McCaffery et al. 1981). Most of the constructed openings were situated in young stands having an ample supply of smaller openings suitable for singing grounds, however, and woodcock use is expected to shift to constructed openings as forest stands mature and smaller openings close out.

Because deer, ruffed grouse, and woodcock all share the need for a young, diverse forest, management recommendations designed to improve the habitat of one species will generally benefit the others. There is some evidence that large-scale programs designed to maintain the intolerant stage of forest succession may benefit woodcock earlier, and perhaps to a greater degree, than either deer or ruffed grouse. On 6 experimentally clearcut areas in Michigan, Bennett et al. (1982) found that woodcock demonstrated a greater response to habitat treatments than either deer or ruffed grouse.

Intensive Habitat Management. Habitat management is also feasible for the small landowner who wants to improve his property for woodcock. Not every piece of land is suited for woodcock management, however, and areas that are dominated by droughty soils or heavily forested with conifers would make poor candidates for a woodcock management program. The general rule in any habitat management venture is that it is more economical to improve existing habitat than to create habitat where none presently exists. Before work on the land begins, a landowner must decide whether woodcock habitat is his exclusive goal or whether he would prefer to see a variety of wildlife on his land. Land intensively managed for woodcock will receive little use by those wildlife species which prefer mature forests. A landowner should also seek professional advice from a forester or wildlife manager in developing a management scheme for his property. With professional assistance, a landowner might be able to accomplish a good share of his management objectives through commercial forestry operations.

Several techniques are available for managing vegetation once a landowner has determined his goal and developed a management plan. Specific management techniques, including clear cutting, burning, mowing, and herbiciding can be used to create singing grounds and roosting areas and rejuvenate feeding areas. Sepik et al. (1981) recently produced an excellent guide to woodcock habitat management which included several examples of actual management situations. They recommended managing feeding covers by clear-cutting alder in narrow strips over a 20-year cutting cycle. Singing grounds can be created by clear-cutting strips through aspen stands or by constructing several 1/4- to 1/2-acre openings throughout those stands. A smaller number of openings (1/100 acres of forest) at least 3 acres in size should be established to provide roosting areas. Singing grounds and roosting areas can be maintained by periodic burning or herbiciding.

Summary and Conclusions

The woodcock occurs throughout Wisconsin, with its distribution being associated with the distribution of forested land across the state. Little information is available on the historical abundance of the species in Wisconsin, but the bird was presumably scarce in the mature forests that existed in the state prior to settlement. The more youthful forest that resulted from the logging and fire era probably enabled the species to increase in numbers. Although no estimate of woodcock population size is available, a reliable index to the size of Wisconsin's woodcock breeding population has been available since 1968 when the existing singing ground survey was reorganized and expanded. Despite an increase in Wisconsin's woodcock population index during 1977-79 and a decline during 1980 and 1981, the long-term trend appears to be stable.

The woodcock is an early migrant, normally arriving in northern Wisconsin during late March or early April. Males probably arrive ahead of females and select an open area, or singing ground, in the forest for their dawn and dusk courtship displays. These displays function to defend the territory against other males and also to attract females for mating. Mating takes place on the singing ground, with the promiscuous male having no involvement in nesting or brood rearing.

Woodcock are the earliest nesters among the ground nesting birds found in northern Wisconsin, with most nests being initiated in April. Hens lay 1 egg/day and the normal clutch contains 4 eggs. Incubation lasts for about 21 days. Nests are frequently associated with an edge or break in the forest canopy. Examination of 220 nest sites indicated that the structure of the vegetation, especially the shrub layer, and proximity to feeding areas constituted the primary factors in nest site selection. Estimates of nest density obtained from nest searches may have been inflated because searching was concentrated in the best coverts, but the small number of nests found in marginal habitats indicated that nests were not distributed randomly. Nest density within a 30-acre block of good habitat was about 1 nest/3 acres, while nest density within a much larger block of average quality habitat was estimated to be 1/20 acres.

Nest success averaged approximately 50%, with predation being the leading cause of nest failure. Late snowstorms were known to cause significant loss of nests during some springs, but the true importance of weather was difficult to discern because of the interrelationship of weather and predation. Some evidence of renesting was observed, but no indication of second broods was recorded. Hatching dates for northern Wisconsin woodcock nests ranged from mid-April to mid-June with the second week in May being the peak period. Woodcock chicks were precocial and left the nest soon after hatching, but remained dependent upon the hen for food until at least 1 week old. Earthworms comprised the major food item for chicks and adults alike. Chicks grew rapidly and were about half grown and capable of short flights at 2 weeks of age. Chicks were well feathered and strong fliers when 3 weeks old, but the broods generally remained intact for 4 to 5 weeks after hatching.

Aspen was the cover type receiving the greatest use by woodcock. The shrub component, such as alder or hazel, appeared to be a prerequisite to woodcock use of many aspen stands after they reached about 10 years of age.

Forest land area is changing slowly enough in Wisconsin to indicate a fairly stable woodcock habitat base. Quality of that habitat, however, may be in greater jeopardy due to forest maturation and changes in composition.

Although hens were capable of moving their broods long distances, day-to-day movements were not lengthy and broods appeared to remain in an area of about 10 to 15 acres during the

brood period. Even after brood breakup, most chicks remained in the same general area where they had hatched. Summer movements were predominantly local and consisted of sallies between daytime covers and nocturnal roosting areas. Immatures were more abundant than adults in summer roosting areas and accounted for 85% of the approximately 10,000 captures recorded during preseason banding operations. Differences in capture trends between adults and immatures throughout the summer indicated that physiological differences between birds of different age may have influenced activity and thus catchability levels.

Band recovery data revealed that, in most years, relatively few woodcock depart from northern Wisconsin before the middle of October. Departure periods depended upon weather conditions, direction, since no direct recoveries have been recorded in either Minnesota or Michigan. Woodcock migration from Wisconsin also appears to be leisurely, with recovery data indicating that our birds do not complete their trip until December. The birds' residence on the wintering grounds is relatively short, since spring migration begins in late January during mild winters and in February during cold winters.

Estimates of woodcock density existing within blocks of land containing both suitable and unsuitable habitats range from 1-2 resulting in an abundance of birds in early November during mild falls and an absence of woodcock by that time in other years. Fall migration from Wisconsin is oriented very much in a southerly singing grounds/100 acres, which, if expanded to account for females and nondisplaying males, would result in estimated spring densities of 20-40 woodcock/mile^2.

Data from preseason banding and the federal wing collection survey were analyzed for information on the composition and dynamics of Wisconsin's woodcock population. Some inferences about population dynamics can be drawn from existing data, even though captured and shot samples may both be biased. More adult females than males are shot each year because they are more abundant or more vulnerable to shooting, or because both factors are operating. Even though more adult females are shot each year, it appears that females survive at a higher rate because hunting is not the most important factor in total annual mortality. But hunting is becoming increasingly more important since our annual harvest indices have demonstrated a 10-fold increase over the past two decades. Although there is no evidence that hunting has yet had any effect on woodcock population, a continued growth in annual harvests will increase the need for a better understanding of the importance of hunting on woodcock population dynamics. But regulation of the harvest will not guarantee a continued abundance of woodcock, since habitat conditions ultimately determine population size. In Wisconsin, habitat types important to woodcock were aspen, alder, and openings. Maintenance of these types is believed essential to woodcock abundance and an assessment of habitat trends and recommendations for habitat management are provided.

Literature Cited

Aldrich, J. W.
1973. Disparate sex ratios in waterfowl. Pp. 482-89 *in* D. S. Farner, ed. Breeding biology of birds. Nat. Acad. Sci., Wash., D.C.

Alison, R. M.
1976. Late snowstorm causes woodcock mortality. Ont. Field Biol. 30(1):51-52.

Allen, J. N.
1980. The ecology and behavior of the long-billed curlew. Wildl. Monogr. 73. 67 pp.

Ammann, G. A.
1963. Methods of capturing woodcock hens and chicks on their breeding grounds. Mich. Dep. Conserv. Game Div. Rep. 2414. 5 pp.
1966. Woodcock banders' newsletter, No. 1. Mich. Dep. Conserv. Game Div. Inf. Circ. 143. 3 pp.
1967. Woodcock banders' newsletter, No. 2. Mich. Dep. Conserv. Game Div. Inf. Circ. 145. 5 pp.
1969. Woodcock banders' newsletter, No. 4. Mich. Dep. Nat. Resour. Game Div. Inf. Circ. 156. 6 pp.
1970. Suggestions for spring woodcock banding. Mich. Dep. Nat. Resour. Game Div. Inf. Circ. 160. 3 pp.
1972. Woodcock banders' newsletter, No. 6. Mich. Dep. Nat. Resour. Wildl. Div. Inf. Circ. 164. 4 pp.
1974. Woodcock banders' newsletter, No. 8. Mich. Dep. Nat. Resour. Wildl. Div. Inf. Circ. 170. 4 pp.
1976. Woodcock banders' newsletter, No. 10. Mich. Dep. Nat. Resour. Wildl. Div. Inf. Circ. 180. 7 pp.
1977. Finding and banding woodcock broods using pointing dogs. Mich. Dep. Nat. Resour. Wildl. Div. Rep. 2780. 8 pp.
1978. Woodcock banders' newsletter, No. 12. Mich. Dep. Nat. Resour. Game Div. Inf. Circ. 184. 8 pp.

Artmann, J. W.
1975. Woodcock status report, 1974. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. 189. 39 pp.
1977. Woodcock status report, 1976. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. 209. 21 pp.

Barry, A.
1854. Ornithological fauna of Wisconsin. Proc. Boston Soc. Nat. Hist. 5:1-13.

Bennett, C. L., Jr., D. L. Rabe, and H. H. Prince
1982. Response of several game species, with emphasis on woodcock, to extensive habitat manipulations. Proc. Woodcock Symp. 7:97-105.

Bent, A. C.
1927. Life histories of North American shore birds — Part 1. U.S. Natl. Mus. Bull. 142:61-78.

Bernard, R. F.
1967. The birds of Douglas County, Wisconsin. Passenger Pigeon 29(2):3-36.

Bersing, O. S.
1956. A century of Wisconsin deer. Wis. Conserv. Dep. Publ. 353-66. 272 pp.

Blankenship, L. H.
1957. Investigations of the American woodcock in Michigan. Mich. State Univ., E. Lansing, PhD Thesis. 217 pp.

Bourgeois, A.
1977. Quantitative analysis of American woodcock nest and brood habitat. Proc. Woodcock Symp. 6:107-18.

Brakhage, G. K.
1965. Biology and behavior of tubnesting Canada geese. J. Wildl. Manage. 29(4):409-19.

Brownie, C. and D. S. Robson
1974. Testing for equality of the annual survival rates in the SRY model for band return data. Biom. Unit, Cornell Univ., Ithaca. BU-515M. 18 pp.

Brownie, C., D. R. Anderson, D. P. Burnham, and D. S. Robson
1978. Statistical inference from band recovery data — A handbook. U.S. Fish and Wildl. Serv. Resour. Publ. 131. 212 pp.

Bunni, M. K.
1959. The killdeer, *Charadrius v. vociferous* Linnaeus, in the breeding season: Ecology, behavior and the development of homiothermism. Univ. Mich., Ann Arbor, ScD Thesis.

Buss, I. O. and H. M. Mattison
1955. A half century of bird changes in the lower Chippewa River. Milw. Pub. Mus. Publ. in Ornithol. No. 1. 319 pp.

Cahn, A. R.
1913. The birds of Waukesha County, Wisconsin. Bull. Wis. Nat. Hist. Soc. 11:113-49.

Causey, K., G. Horton, J. Roboski, R. Johnson, and P. Mason
1979. American woodcock hatched in Alabama killed in Michigan. Wilson Bull. 91(3):463-64.

Chase, C. D., R. E. Pfeifer, and J. S. Spencer, Jr.
1970. The growing timber resource of Michigan, 1966. North Cent. For. Exp. Stn., St. Paul, Minn. Resour. Bull. NC-9. 62 pp.

Clapp, R. B., M. K. Klimkiewicz, and J. M. Kennard
1982. Longevity records of North American birds: Gaviidae through alcidae. J. Field Ornithol. 53(2):81-124.

Clark, E. R.
1972. Woodcock status report, 1971. U.S. Bur. Sport Fish and Wildl., Spec. Sci. Rep.—Wildl. 153. 47 pp.

Coon, R. A., P. D. Caldwell, and G. L. Storm
1976. Some characteristics of fall migration of female woodcock. J. Wildl. Manage. 40(1):91-95.

Coon, R. A., T. J. Dwyer, and J. W. Artmann
1977. Identification of potential harvest units in the United States for the American woodcock. Proc. Woodcock Symp. 6:147-53.

Coon, R. A., B. K. Williams, J. S. Lindzey, and J. L. George
1982. Examination of woodcock nest sites in central Pennsylvania. Proc. Woodcock Symp. 7:55-62.

Couture, R. and J. C. Bourgeois
1977. American woodcock density variations during the breeding season in central Quebec. Proc. Woodcock Symp. 6:93-99.

Crawford, R. D.
1977. Breeding biology of year-old and older female red-winged and yellow-winged blackbirds. Wilson Bull. 89(1):73-80.

Curtis, J. T.
1959. The vegetation of Wisconsin. Univ. Wis. Press, Madison. 657 pp.

Cushwa, C. T., J. E. Barnard, and R. B. Barnes
1977. Trends in woodcock habitat in the United States. Proc. Woodcock Symp. 6:31-38.

Dalrymple, B. W.
1970. Complete guide to hunting across North America. Outdoor Life, Harper and Row, New York. 848 pp.

Dobell, J. V.
1977. Determination of woodcock habitat changes from aerial photography in New Brunswick. Proc. Woodcock Symp. 6:73-81.

Dorney, R. S.
1963. Sex and age structure of Wisconsin ruffed grouse populations. J. Wildl. Manage. 27(4):599-603.

Duffy, M.
1967. Woodcock hunting. La. Conserv. 19(1-2):8-11.

Duke, G. E.
1966. Reliability of censuses of singing male woodcocks. J. Wildl. Manage. 30(4):697-707.

Dumke, R. T. and C. M. Pils
1979. Renesting and dynamics of nest site selection by Wisconsin pheasants. J. Wildl. Manage. 43(3):705-16.

Dunford, R. D. and R. B. Owen, Jr.
1973. Summer behavior of immature radio-tagged woodcock in central Maine. J. Wildl. Manage. 37(4):462-69.

Dunstan, T. C.
1972. Radio tagging Falconiform and Strigiform birds. Raptor Res. 6(3):93-102.

Dwyer, T. J. and J. D. Nichols
1982. Regional population inferences for the American woodcock. Proc. Woodcock Symp. 7:12-21.

Dwyer, T. J., E. L. Derleth, and D. G. McAuley
1982. Woodcock brood ecology in Maine. Proc. Woodcock Symp. 7:63-70.

Einspahr, D. W.
1972. Wood and fiber production from short rotation stands. In Aspen: symposium proceedings. North Cent. For. Exp. Stn., St. Paul, Minn. 154 pp.

Emlen, J. T., Jr.
1956. A method of describing and comparing avian habitats. Ibis 91:565-76.

Faanes, C. A. and S. V. Goddard
1976. The birds of Pierce and St. Croix counties, Wisconsin. Passenger Pigeon 38(1):19-38 and 38(2):57-71.

Forsythe, D. M.
1973. Growth and development of long-billed curlew chicks. Auk 90:435-38.

Gates, J. E. and L. W. Gysel
1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59(5):871-83.

Geis, A. D.
1972. Use of banding data in migratory game bird research and management. U.S. Fish and Wildl. Serv., Spec. Sci. Rep.—Wildl. 154. 47 pp.

Geis, M. B.
1956. Productivity of Canada geese in the Flathead Valley, Montana. J. Wildl. Manage. 20(4):409-19.

Glasgow, L. L.
1958. Contributions to the knowledge of the ecology of the American woodcock, *Philohela minor* (Gmelin), on the wintering range in Louisiana. Texas A. & M. Coll., College Station, PhD Thesis. 158 pp.

Godfrey, G. A.
1970. A transmitter harness for small birds. Inl. Bird-Banding News 42(1):3.
1974. Behavior and ecology of American woodcock on the breeding range in Minnesota. Univ. Minn., Minneap., PhD Thesis. 333 pp.

Godfrey, G. A. and W. H. Marshall
1969. Brood breakup and dispersal of ruffed grouse. J. Wildl. Manage. 33(3):609-20.

Goudy, W. H.
1960. Factors affecting woodcock spring population indexes in southern Michigan. Mich. State. Univ., East Lansing, MS Thesis. 44 pp.

Goudy, W. H., W. K. Igo, and D. R. Beightol
1977. Impact of an urban-industrial environment on woodcock in West Virginia. Proc. Woodcock Symp. 6:119-24.

Grange, W. B.
1948. Wisconsin grouse problems. Wis. Conserv. Dep. Publ. 328. 316 pp.

Graul, W. D.
1974. Vocalizations of the mountain plover. Wilson Bull. 86(3):221-29.
1975. Breeding biology of the mountain plover. Wilson Bull. 87(1):6-31.

Greeley, F.
1953. Sex and age studies in fall-shot woodcock *(Philohela minor)* from southern Wisconsin. J. Wildl. Manage. 17(1):29-32.

Gregg, L. E.
1972. Techniques for banding woodcock in summer habitats in Michigan. Mich. State Univ., East Lansing, MS Thesis. 37 pp.
1982. Woodcock singing ground counts and breeding habitat. Proc. Woodcock Symp. 7:30-33.

Gregg, L. E. and J. B. Hale
1977. Woodcock nesting habitat in northern Wisconsin. Auk 94(3):489-93.

Grinnel, G. B.
1922. Woodcock carrying its young. Auk 39(4):563-64.

Grundtvig, F. L.
1895. On the birds of Shiocton in Bovina, Outagamie County, Wisconsin 1881-1883. Trans. Wis. Acad. Sci., Arts, and Lett. 10:73-158.

Gutzwiller, K. J., C. H. Strauss, K. R. Kinsley, J. S. Wakeley, and G. L. Storm
1982. Relationships between land use and woodcock habitat in Pennsylvania, with guidelines for rangewide use. Proc. Woodcock Symp. 7:86-96.

Haasch, S. J.
1979. Habitat use and ecology of the American woodcock in central Wisconsin. Univ. Wis., Stevens Point, MS Thesis. 76 pp.

Hale, J. B. and L. E. Gregg
1976. Woodcock use of clearcut aspen areas in Wisconsin. Wildl. Soc. Bull. 4(3):111-15.

Horton, G. I. and M. K. Causey
1981. Dispersal of American woodcock in central Alabama after brood breakup. J. Wildl. Manage. 45(4):1058-61.

Hoy, P. R.
1853. Notes on the ornithology of Wisconsin. Trans. Wis. State Agric. Soc. for 1852. 2:341-64.

Hoyt, J. W.
1860. Natural resources of Wisconsin. Trans. Wis. State Agri. Soc. 6:46-49.

Hunt, R. S.
1979. Removal of woody streambank vegetation to improve trout habitat. Wis. Dep. Nat. Resour. Tech. Bull. 115. 36 pp.

Hussell, D. J. T. and G. W. Page
1976. Observations on the breeding biology of black-belled plovers on Devon Island, N.W.T., Canada. Wilson Bull. 88(4):632-53.

Jahn, L. R. and R. A. Hunt
1964. Duck and coot ecology and management in Wisconsin. Wis. Conserv. Tech. Bull. 33. 212 pp.

James, F. C.
1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215-36.

Johnston, C. D.
1976. Wetland use in Wisconsin: Historical perspective and present picture. Wis. Dep. Nat. Resour., Madison. 48 pp.

Keith, L. B.
1964. Territoriality among wintering snowy owls. Can. Field-Nat. 78(1):17-24.

Kemper, C. A.
1958. Destruction at the TV tower. Passenger Pigeon 20:3-9.
1973. Birds of Chippewa, Eau Claire and neighboring counties. Passenger Pigeon 35(2):55-91 and 35(3):107-29.

Kemper, C. A., S. D. Robbins, and A. C. Epple
1963. The ornithological flood of September 18-20, 1963. Passenger Pigeon 26:159-72.

Kendeigh, S. C.
1961. Animal ecology. Prentice-Hall, Inc., Englewood Cliffs, N.J. 468 pp.

Kletzly, R. C.
1976. American woodcock in West Virginia. W. Va. Dep. Nat. Resour. Bull. 8. 46 pp.

Kletzly, R. C. and J. C. Rieffenberger
1969. Local movement of "resident" woodcock in the Canaan Valley of West Virginia. Pp. 22-23 *in* W. H. Goudy, compiler. Woodcock research and management programs, 1967 and 1968. U.S. Bur. Sport Fish. and Wildl., Spec. Sci. Rep.—Wildl. 123. 32 pp.

Klomp, H.
1970. The determination of clutch size in birds — A review. Ardea 58:1-124.

Koenig, W. D.
1982. Ecological and social factors affecting hatchability of eggs. Auk 99(3):526-36.

Kozicky, E. L., T. A. Bancroft, and P. G. Homeyer
1954. An analysis of woodcock singing ground counts, 1948-1952. J. Wildl. Manage. 18(2):259-66.

Kreitzer, J. F.
1973. Thickness of the American woodcock eggshell, 1971. Environ. Contam. Toxicol. 9(5):281-86.

Krohn, W. B.
1971. Some patterns of woodcock activities on Maine summer fields. Wilson Bull. 83(4):396-407.

Krohn, W. B. and E. R. Clark
1977. Band-recovery distribution of eastern Maine woodcock. Wildl. Soc. Bull. 5(3):118-22.

Krohn, W. B., F. W. Martin, and K. P. Burnham
1974. Band-recovery distribution and survival estimates of Maine woodcock. *In* Fifth Am. Woodcock Workshop Proc., Univ. Ga., Athens, December 3-5, 1974. 8 pp., n.p.

Kroll, J. C. and R. M. Whiting
1977. Discriminate function analysis of woodcock winter habitat in east Texas. Proc. Woodcock Symp. 6:63-71.

Kumlien, K. and N. Hollister
1903. The birds of Wisconsin. Wis. Nat. Hist. Soc. Milw. 122 pp.

Lack, D.
1968. Ecological adaptations for breeding in birds. Methuen and Co., London. 409 pp.

Lange, K. I.
1981. Field notes—The winter season. Passenger Pigeon 43(4):146-58.

Lincoln, F. C.
1951. A set of twelve eggs of the woodcock, *Philohela minor*. Auk 68(3):376.

Liscinsky, S. A.
1962. The Pennsylvania woodcock management study. Pa. Game Comm. Final Rep., Pittman-Robertson Proj. W-50-R. 157 pp.
1972. The Pennsylvania woodcock management study. Pa. Game Comm. Res. Bull. 171. 95 pp.

Liscinsky, S. A. and W. J. Bailey, Jr.
1955. A modified shorebird trap for capturing woodcock and grouse. J. Wildl. Manage. 19(3):405-08.

March, J. R. and R. A. Hunt
1978. Mallard population and harvest dynamics in Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 106. 74 pp.

Marshall, W. H.
1982. Minnesota woodcock. The Loon 54(4):203-11.

Martin, E. M.
1979. Hunting and harvest trends for migratory game birds other than waterfowl: 1964-76. U.S. Fish and Wildl. Serv., Spec. Sci. Rep.—Wildl. 218. 37 pp.

Martin, F. W.
1964. Woodcock age and sex determination from wings. J. Wildl. Manage. 28(2):287-93.

Martin, F. W., A. D. Geis, and W. H. Stickel
1965. Results of woodcock wing collections, 1959-1962. J. Wildl. Manage. 29(1):121-31.

Martin, F. W. and E. R. Clark
1964. Summer banding of woodcock, 1962-1963. U.S. Bur. Sport Fish. and Wildl., Mig. Bird Pop. Stn., Laurel, Md., Admin. Rep. 43. 8 pp.

Martin, F. W., S. O. Williams III, J. D. Newsom, and L. L. Glasgow
1969. Analysis of records of Louisiana-banded woodcock. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 23:85-96.

Martinson, R. K.
1966. Proportion of recovered duck bands that are reported. J. Wildl. Manage. 30(2):264-68.

Mayfield, H.
1961. Nesting success calculated from exposure. Wilson Bull. 173:255-61.
1975. Suggestions for calculating nest success. Wilson Bull. 87:456-66.

McCaffery, K. R., J. E. Ashbrenner, and J. C. Moulton
1981. Forest opening construction and impacts in northern Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 120. 40 pp.

Mendall, H. L.
1938. A technique for banding woodcock. Bird-Banding 9(3):153-55.

Mendall, H. L. and C. M. Aldous
1943. The ecology and management of the American woodcock. Maine Coop. Wildl. Res. Unit, Univ. Maine, Orono. 201 pp.

Miller, H. W. and D. H. Johnson
1978. Interpreting the results of nesting studies. J. Wildl. Manage. 42:471-76.

Modafferi, R. D.
1967. A population behavior study of male American woodcock on central Massachusetts singing grounds. Univ. Mass., Amherst, MS Thesis. 57 pp.

Morgenweck, R. O. and W. H. Marshall
1978. Wing marker for American woodcock. Bird-banding 48(3):224-27.

Norris, R. T., J. D. Beule, and A. T. Studholme
1940. Banding woodcocks on Pennsylvania singing grounds. J. Wildl. Manage. 4(1):8-14.

Oberholser, H. C.
1938. The bird life of Louisiana. La. Dep. Conserv. Bull. 28. 834 pp.

Odum, E. P. and E. U. Kuenzler
1955. Measurement of territory and home range size in birds. Auk 72:128-37.

Owen, R. B., Jr., chairman
1977. American woodcock (*Philohela minor-Scolopax minor* of Edwards 1974). Pp. 149-86 *in* G. C. Sanderson, ed. Management of migratory shore and upland game birds in North America. Int. Assoc. Fish and Wildl. Agencies, Wash., D.C. 358 pp.

Owen, R. B., Jr. and W. B. Krohn
1973. Molt patterns and weight changes of the American woodcock. Wilson Bull. 85(1):31-41.

Owen, R. B., Jr. and J. W. Morgan
1975. Summer behavior of adult radio-equipped woodcock in central Maine. J. Wildl. Manage. 39(1):179-82.

Pettingill, O. S., Jr.
1936. The American woodcock *Philohela minor* (Gmelin). Boston Soc. Nat. Hist. Mem. 9(2):169-391.

Pitelka, F. A.
1943. Territoriality, display, and certain ecological relations of the American woodcock. Wilson Bull. 55(3):511-17.

Pursglove, S. R., Jr. and G. L. Doster
1970. Potentialities of the woodcock as a game bird resource in the southeastern United States. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 24:223-30.

Pyrah, D.
1970. Poncho markers for game birds. J. Wildl. Manage. 34(2):466-67.

Rabe, D.
1977. Structural analysis of woodcock diurnal habitat in northern Michigan. Proc. Woodcock Symp. 6:125-34.

1979. Evidence suggesting a second nesting effort by an American woodcock. Jack-Pine Warbler 57(3):166-67.

Ramakka, J. M.
1972. Effects of radio tagging on breeding behavior of male woodcock. J. Wildl. Manage. 36(4):1309-12.

Reynolds, J. W., W. B. Krohn, and G. A. Jordan
1977. Earthworm populations as related to woodcock habitat usage in central Maine. Proc. Woodcock Symp. 6:135-46.

Rieffenberger, J. C.
1969. A nightlighting technique for capturing woodcock and snipe. *In* Third Am. Woodcock Workshop Proc., Univ. Maine, Orono, 30 June-2 July 1969. 8 pp., n.p.

Rieffenberger, J. C. and R. C. Kletzly
1967. Woodcock nightlighting techniques and equipment. Pp. 33-35 *in* W. H. Goudy, compiler. Woodcock research and management, 1966. U.S. Bur. Sport Fish. and Wildl., Spec. Sci. Rep. Wildl. 101. 40 pp.

Robbins, S.
1970. Extreme arrival and departure dates. Passenger Pigeon 32(3):83-137.

Roberts, T. H.
1980. Sexual development during winter in male American woodcock. Auk 97(4):879-81.

Roboski, J. C. and M. K. Causey
1981. Incidence, habitat use, and chronology of woodcock nesting in Alabama. J. Wildl. Manage. 45(3):793-97.

Sanderson, Glen C. (Ed.)
1977. Management of migratory shore and upland game birds in North America. Internat. Assn. Fish and Wildl. Agencies, Washington, D.C. 358 pp.

Schoenebeck, A. J.
1902. The birds of Oconto County. Repr. *in* Passenger Pigeon I(6,7):79-88 and 95-105.

Schorger, A. W.
1929. The birds of Dane County, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Lett. 24:457-99.

Sepik, G. F., R. B. Owen, Jr., and M. W. Coulter
1981. A landowner's guide to woodcock management in the Northeast. Univ. Maine Life Sci. and Agric. Exp. Stn. Misc. Rep. 253. 23 pp.

Sharp, B.
1971. Heavy mortality of migrating birds at Madison's TV towers. Passenger Pigeon 33(4):203-204.

Sheldon, W. G.
1961. Summer crepuscular flights of American woodcocks in central Massachusetts. Wilson Bull. 73(2):126-39.

1967. The book of the American woodcock. Univ. Mass. Press, Amherst. 227 pp.

Shorten, M.
1974. The European woodcock *(Scolopax rusticola).* The Game Conservancy, Engl., Rep. 21. 95 pp.

Spencer, J. S., Jr. and H. W. Thorne
1972. Wisconsin's 1968 timber resource — A perspective. North Cent. For. Exp. Stn., St. Paul, Minn., Resour. bull. NC-15. 80 pp.

Steinfatt, O.
1938. Das brutleban der waldschnepfe. J. fur Ornithol. 86:379-424.

Stone, R. N. and H. W. Thorne
1961. Wisconsin's forest resources. Lake State For. Exp. Stn., Stn. Pap. No. 90, St. Paul, Minn. 52 pp.

Tautin, J.
1977. The current status of woodcock and woodcock surveys in the United States. Proc. Woodcock Symp. 6:17-23.

1982. 1982 status of the American woodcock. U.S. Fish and Wildl. Serv. Admin. Rep. 14 pp.

Temple, S. A.
1972. A portable time-lapse camera for recording wildlife activity. J. Wildl. Manage. 36(3):944-47.

Tuck, L. M.
1972. The snipes: A study of the Genus *Capella*. Can. Wildl. Serv. Monogr. Ser. 5. 428 pp.

U.S. Soil Conservation Service
1966. General soil map—Price County, Wisconsin. 64 pp.

1971. General soil map—Ashland County, Wisconsin. 14 pp.

Vanderschaegen, P. V.
1981. The birds of Forest, Oneida and Vilas counties, Wisconsin. Passenger Pigeon 43(3):69-85.

Weise, C. M.
1971. Relative abundance of small landbirds in southeastern Wisconsin. Passenger Pigeon 33(4):173-88.

Wenstrom, W. P.
1974. Habitat selection by brood rearing woodcock. *In* Fifth Am. Woodcock Workshop Proc., Univ. Ga., Athens, 3-5 Dec. 1974. 19 pp., n.p.

Wetherbee, D. K. and L. M. Bartlett
1962. Egg teeth and shell rupture of the American woodcock. Auk 79(1):117.

Whitcomb, D. A.
1974. Characteristics of an insular woodcock population. Mich. Dep. Nat. Resour. Wildl. Div. Rep. 2720. 78 pp.

Whitmore, R. C.
1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

Wilbur, S. R.
1967. Live-trapping North American upland game birds. U.S. Bur. Sport Fish and Wildl., Spec. Sci. Rep.—Wildl. 106. 37 pp.

Wisconsin Statistical Reporting Service
1967. Wisconsin weather — Causes, variations and effects. Madison. 31 pp.

Wishart, R. A. and J. R. Bider
1976. Habitat preferences of woodcock in southwestern Quebec. J. Wildl. Manage. 40(3):523-31.

Wright, B. S.
1952. Woodcock banding with bird dogs. Pp. 45-46 *in* J. W. Aldrich, compiler. Investigations of woodcock, snipe, and rails in 1951. U.S. Fish and Wildl. Serv. and Can. Wildl. Serv., Spec. Sci. Rep.—Wildl. 14. 58 pp.

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