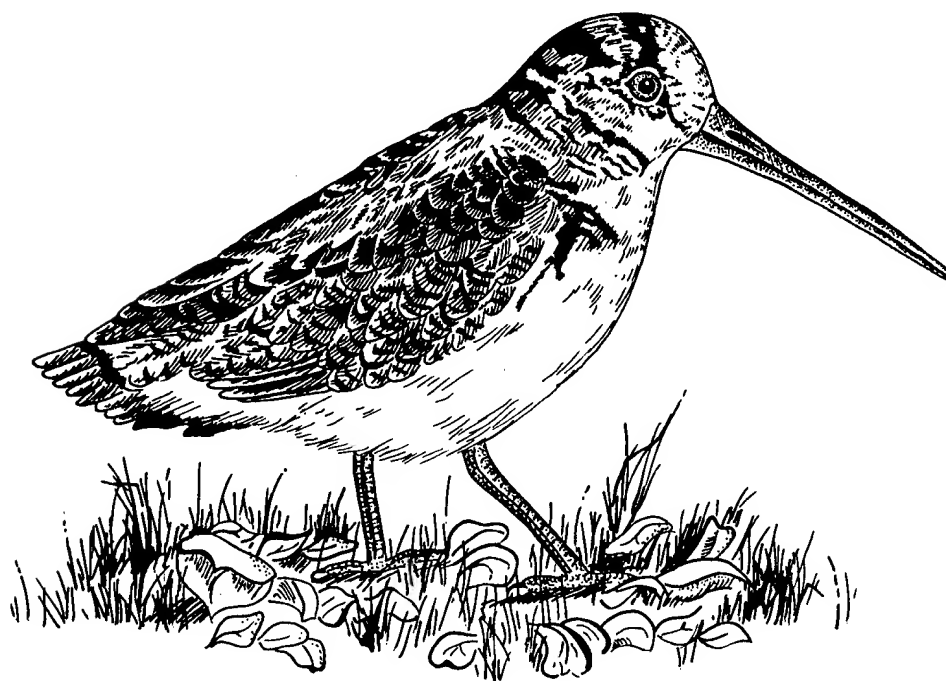# Proceedings of the Eighth American Woodcock Symposium

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Proceedings of the Eighth American Woodcock Symposium

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The Eighth American Woodcock Symposium is dedicated to George A. Ammann, Ph.D., whose contributions to the knowledge of the life history and ecology of the American woodcock are unparalleled.

Foreword

In the 1970's, biologists, managers, and administrators gathered three times at formal symposia or workshops to discuss the management and research findings on the American woodcock. During the 1980's, only one meeting was held despite evidence of declines in numbers of woodcocks in many states and harvest restrictions in the Eastern Management Region. Also in the 1980's, federal funding for research on the woodcock was decreased by the elimination of the Accelerated Research Program for Webless Migratory Game Birds. However, as the decade drew to a close, interest in the woodcock increased and plans were made for a Webless Migratory Bird Hunting Permit, and the *American Woodcock Management Plan* was developed. The permit will provide a better sampling framework for monitoring the harvest of woodcocks, and the plan provides structure and guidance to reverse the decline in the woodcock population.

Like previous symposia, this symposium contained a mix of abstracts, philosophical("give 'em hell Harry!") presentations, technical papers, reviews, and short communications and reports about the European woodcock. The symposium also served as a platform for the implementation of the *American Woodcock Management Plan* through workshops and the formal signing of a cooperative agreement. A workshop on the implementation of the *American Woodcock Management Plan* (facilitator W. Goudy) was held to discuss the development of local and regional management plans. The Ruffed Grouse Society, U.S. Fish and Wildlife Service, and U.S. Forest Servive signed an agreement for a management partnership. A workshop on *Central Hardwoods Woodcock Habitat Management* (facilitator, D. Dessecker) was conducted to present managers with techniques for creating and maintaining habitat for the American woodcock.

Many individuals contributed to the success of this symposium. B. Miller chaired the Symposium Committee. B. Bortner and G. Sepik chaired the National Steering Committee and Program Committee. They were assisted by D. Dessecker, W. Faatz, R. Kirby, J. Longcore, and S. Pursglove. The Staff Conference Committee was chaired by B. Miller who was assisted by W. Bean, W. Faatz, B. Feldt, V. Hesher, T. Hewett, R. Peercy, and R. Stonebraker. The session moderators were C. DuBrock, T. Dwyer, J. Longcore, S. Pursglove, R. Owen, Jr., and W. Robinson. The manuscript reviewers were B. Allen, G. Ammann, M. Haramis, H. Kalchreuter, D. Keppie, F. Knopf, D. Krementz, W. Krohn, D. McAuley, L. Oring, R. Owen, Jr., G. Pendleton, M. Reed, T. Roberts, G. Sepik, R. Sojda, G. Storm, J. Tautin, and M. Whiting. M. Reilly assisted with the preparation of manuscripts for publication. N. Garriott and S. Sorenson were instrumental in the organization and administration of the symposium. V. Hesher was chief cook and organizer of the hog roast, and the Tippecanoe County Conservation Club hosted the fish fry. B. Bean, V. Hesher, and R. Peercy organized and conducted the field trips. B. Bortner and R. Blohm, Office of Migratory Bird Management, U.S. Fish and Wildlife Service, ensured funding for publication of the proceedings.

The symposium was hosted and sponsored by the Cooperative Extension Service and Department of Forestry and Natural Resources of Purdue University. Other sponsors included the Indiana Chapter of the Wildlife Society; the Indiana Department of Natural Resources; Regions 3, 4, and 5 and the Office of Migratory Bird Management, U.S. Fish and Wildlife Service; the Ruffed Grouse Society; the Ruffed Grouse Society Woodcock Fund; and the Washington Office, Eastern, and Southern Regions, U.S. Forest Service. D. Maass, the Ruffed Grouse Society, and Wildwings, Inc., made donations in support of the symposium.

We thank the Krieger Publishing Company, Inc., for permission to cite material from *The Philosophy and Practice of Wildlife Management* (1987) by F. F. Gilbert and D. D. Dodds. We also thank G. Wood for permission to cite from his unpublished work entitled *Conservation of Game for Preservation of Sport*.

To all participants who contributed in so many ways to making the Eighth American Woodcock Symposium a success, we extend our sincere thanks.

Jerry Longcore
Greg Sepik
Editors

Contents

Dr. George A. "Andy" Ammann banding woodcock chicks while his English Setter Katey waits patiently. (Photo: U.S. Fish and Wildlife Service).

Why Bother Worrying About The Woodcock— A Philosophical Essay

by

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When asked to present a philosophical essay on the subject *Why Bother Worrying About the Woodcock?* at this symposium, I was somewhat surprised and disappointed. Surprised because this was the same question I had asked my employer on my first wildlife research assignment 39 years ago. I was expecting an assignment on a more prominent species. Disappointed because we are still asking the same question.

After thinking it over, I realized that I should not be surprised or disappointed. After all, is this not the ultimate question about almost everything to completely satisfy us—why?

Why war and suffering? Why did they not support our plan? Why do I not like mincemeat pie? Why woodcock?

Are the answers always the same? No—not always. Are these questions often repeated? Many are! What was my employer's answer? I have never forgotten. He said, "People, especially hunters, say there are fewer woodcock in the state now than in years past. Your job is to find out if this is true and to determine what can be done about it." A big assignment for a greenhorn biologist who then spent the better part of 7 years in the quest. It was obvious to me, however, that one of the main reasons we should be concerned about the woodcock and all species of wildlife was that it was our profession, our belief, that we were the guardians of the wildlife resource. Did we not dedicate the greater part of our life's work to that cause?

Was my employer's answer to the question applicable today? Yes, it is to a great extent. Certainly we can always use more and better information to direct our management of the species, but do we not already have enough to do a better job on this particular resource? Mendall and Aldous (1943) got us started with their monumental work on the woodcock in their publication *The Ecology and Management of the American Woodcock*. Many years later (Liscinsky 1966) their admonitions were incorporated in the *American Woodcock Research and Management Program* prepared for representatives of the International Association of Game and Fish Commissioners, Bureau of Sports Fisheries and Wildlife, and private wildlife agencies (prepared by committee: L. Glasgow, H. Mendall, W. Goudy, B. Wright, A. Geis, W. Sheldon, G. Ammann, F. Martin, L. Foote, S. Liscinsky [Chairman]). Eleven years later (Sanderson 1977) in a book published by the International Association of Fish and Wildlife Agencies titled *Management of Migratory Shore and Upland Game Birds in North America*, the recommendations section on the woodcock (Owen 1977) read in part: "The objectives listed by Liscinsky (1966) were similar to our objectives. Considerable progress has been made since then, and most general recommendations have been implemented. However, it is appalling that most of the specific recommendations contained in the 1966 report must be reiterated here, now with even greater urgency. To summarize, woodcock management is inadequate."

It is now 12 years later, and we are still struggling to implement those recommendations. And it is my understanding that the *American Woodcock Management Plan* drafted by the U.S. Fish and Wildlife Service in the spring of 1988 is still in draft form.

Perhaps instead of asking "Why bother about the woodcock," we should be asking "Why have we not implemented more of the management recommendations"? Could part of the reason be that there is no consensus among professionals, especially those most responsible, that a problem even

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[1] Retired from the Pennsylvania Game Commission.

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exists. Witness the recent change in bag limits that was prompted from the bottom instead of from the top. Where is the leadership?

Are we afraid to admit there is a problem? Why? Much existing evidence indicates there is; or are we afraid the evidence is not convincing enough? If so, shame on us.

Are we really sincere in accepting our full range of responsibility? If so, why has there been so little improvement in data collecting methods and analysis and in assigning people to the task?

Why are more and more judges and organizations, such as the Audubon Society, the Sierra Club, and the Wilderness Society, questioning our credibility? Do they think we are more concerned about the welfare of the hunters than the welfare of the species?

I could go on and on with this type of soul searching, but these are questions that should be familiar to all of us gathered here. Even though asking questions is an integral part of this symposium, the main thrust, as I understand it, is to find answers. I am certainly pleased with that objective, and I wish you great success.

It must then be my task to stimulate your efforts by reviewing the common and perhaps some less common reasons we should be so concerned about this resource. I chose to quote many authors to show that the question is not new and that their answers are as profound today as they were in the past.

The Woodcock is Unique. Almost every article you read about the woodcock mentions this aspect. Most often this refers to the bird's anatomy and its courtship behavior. For some this is reason enough to preserve the species. Many travel hundreds and sometimes thousands of miles just to observe the male's procedure of attracting a female. Perhaps Leopold (1949) expressed this feature the best. In his book *A Sand County Almanac* we read: "The woodcock is a living refutation of the theory that the utility of a game bird is to serve as a target, or to pose gracefully on a slice of toast. No one would rather hunt woodcock in October than I, but since learning of the sky dance I find myself calling one or two birds enough. I must be sure that, come April, there will be no dearth of dancers in the sunset sky."

Woodcock are Fun to Hunt. Roger Latham, a life-long friend and faithful counselor, taught me about woodcock hunting. He also hired me to study woodcock when he was chief of research for the Pennsylvania Game Commission. And when he was the outdoor writer for the Pittsburgh Press

newspaper he wrote this about woodcock hunting: "Woodcock hunters are extraordinary individuals in many ways. With few exceptions they symbolize the true sportsman—the man who hunts for the recreational benefits involved, not just for meat on the table. He is most often a man who owns one or more bird dogs and does his own training. He is a man who delights in the performance of his dog, in the highly colored foliage, and in the wondrous smells and sights of the autumn woodland.

Yes, woodcock hunting is likely to be a sport appreciated most by the hunter who realizes that killing is not the major object, but that the companionship, the dog on point, the whistle of wings, and a crisp fall day are the real attractions after all."

The Woodcock Holds Well for Pointing Dogs. Gene Wood, in his unpublished presentation titled *Conservation of Game for Preservation of Sport* addressed this point superbly: "I believe that our primary stimulus for hunting woodcock is that it is a bird which holds for the dog. In fact, there probably isn't a species that holds better than woodcock. In my opinion, it is very unfortunate that so many of us have come to measure the quality of our dogs by the number of birds killed over them. The numbers game not only numbs our sensitivity to the ethics of sport, it very importantly dims our awareness of logical principals of conservation.

Finally, I am not against hunting. Furthermore, I don't even recall being happy about missing a woodcock. But, on the other hand, I have always found the kill to be anti-climatic to the thrill of watching my dogs in intensive search and my feeling of swelling pride as I viewed their rigid forms locked on point. To a man that loves bird dogs those experiences just never become common, usual, and old. Woodcock once provided many of those experiences for a lot of men and their dogs. Now it's time for us to take the measures necessary to preserve that tradition for sons and puppies."

The Woodcock is Good to Eat. There are few who will contest this premise, but there are some that do. For example, I have a hunting companion who, jokingly, says he does not eat woodcock because he observed very hungry hounds refusing to eat the offal of woodcock when at the same time they ingested the offal of ruffed grouse and Hungarian partridge. It is true; I was there when this happened. Then there are those who do not like the taste of woodcock because it reminds them of liver, which they seldom, if ever, eat.

On the other hand there are those who cherish the flesh of the woodcock as one of their favorite

foods. And some, like my sister-in-law of French extraction, cook and eat woodcock in a traditional manner that is almost a religious ceremony.

So, to each his own. What more can I say?

These are all valid reasons we should bother about the woodcock, but will they stand the test of time? I submit that we have deeper reasons to conserve this species and other creatures on this planet. They touch our own existence and on how we ourselves are to be conserved.

Have we not been taught that we have dominion over all creatures on this earth? Have we not been taught to live with them and use them wisely? Have we not been taught to cultivate reverence for the land and all the creatures who share it with us?

Down through history, scholars and saints have been prodding us to do a better job of caring for this planet and especially for its creatures. Who has not read the admonition of St. Francis of Assisi, Albert Schweitzer, Feodor Dostoevski, Chief Seattle, Aldo Leopold, and Roger Latham to name a few.

St. Francis recognized that the earth is the Lord's and that we are stewards of the works of his hands. Albert Schweitzer believed that reverence for life is the fundamental principle of morality, namely, that good consists in maintaining, assisting, and enhancing life and that to destroy, to harm, or to hinder life is evil.

Dostoevski (1950) probes even deeper. In his novel *The Brothers Karamazov* he quotes an old monk giving this advice to his followers: "Love all God's creation, the whole and every grain of sand in it. Love every leaf, every ray of God's light. Love the animals, love the plants, love everything. If you love everything, you will perceive the divine mystery of things. Once you perceive it you will begin to comprehend it better every day. And you will come to love at last the whole world with an all-embracing love."

Chief Seattle, at about the same time in history, said these concluding words when deliberating a land treaty with the U.S. Government: "So, if we sell you our land, love it as we've loved it. Care for it as we've cared for it. Hold in your mind the memory of the land as it is when you take it. And with all your strength, with all your mind, with all your heart, preserve it for your children and love it—as God loves us all."

Leopold (1949), the often heralded father of modern wildlife management, was probably highly influenced by the writing of Ouspensky, Thoreau, Muir, and others in preparing his treatise on *The Land Ethic*. One of his most quoted sentences is "that land is a community is the basic concept of ecology, but that land is to be loved and respected is an extension of ethics". And his statement on the basic problem and solution is just as powerful: "We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect".

Roger Latham once wrote: "Perhaps man, like the trees, should raise his arms toward the sky and give thanks for the light of the sun, for the trees and the flowers, for birds and animals, for sparkling streams and clear blue lakes, for mountains and plains, and for all the delights that these blessings bring. And while recognizing their existence, he could resolve to become more intimately acquainted with the beautiful, the delightful, and the inspirational things of nature and to develop an awareness of the true meaning of this life on earth". All of these authors are telling us that we should be worrying about all our resources, which include the woodcock, because it is the right thing to do—for our own welfare and that of the resources. They also infer that we cannot be successful unless we maintain a reverence for the land and the creatures who share it with us. If we who call ourselves a spiritual people have this in our hearts, we can restore this resource and save at least some remnant of a natural heritage. Let us not contribute to that ultimate tragedy of not knowing what we have lost.

One more thought in closing. From time-to-time some adults think the younger generations just do not care. How honest is this appraisal? Would we be here today if that were true? Years ago I was dramatically reminded that many of our youths are as concerned as many adults. One of my sons at about age 18 made a large mosaic kind of poster for me as a Christmas gift. It depicted basic problems people have: pollution, wars, famine, and so on. In among the various pictures was this poem by author Kendrew Lascelles:

When all the laughter dies in sorrow
and the tears have risen to a flood
When all the wars have found a cause
in human wisdom and in blood
Do you think they'll dry in sadness
Do you think the eye will blink
Do you think they'll curse the madness
Do you even think they'll think
When all the great galactic systems
sigh to a frozen halt in space
Do you think there will be some remnant
of beauty of the human race

Do you think there will be a vestige
or a sniffle of a cosmic tear
Do you think a greater thinking thing
will give a damn that man was here

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Techniques for Research into Woodcocks: Experiences and Recommendations

by

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Abstract. We describe methods for the study of the American woodcock (*Scolopax minor*) at the Moosehorn National Wildlife Refuge. Described are techniques for the capture of particular age-sex cohorts during different times of the year, the aging and sexing, the evaluation of habitat components, and the estimation of population size. We describe successful and tried but rejected techniques with radio-telemetry for the study of survival and habitat use.

Key words: Aging, American woodcock, Moosehorn National Wildlife Refuge, research techniques, *Scolopax minor*, sexing, telemetry.

Many techniques were developed to capture American woodcocks (*Scolopax minor*), to study their biology, and to monitor population trends. Although some details about field methods were published, much of the knowledge gained by trial and error has been exchanged only informally among researchers. Since 1975, when we began a long-term study of the management and ecology of the American woodcock at the Moosehorn National Wildlife Refuge (NWR) at Calais, Maine, we developed, evaluated, refined, and sometimes abandoned methods. In this paper, we relate the insights we gained during 15 years of study.

Capture Techniques

Research often necessitates the capture of large numbers of birds of a specific age or sex cohort. Several techniques of capturing woodcocks are described elsewhere (Liscinsky and Bailey 1955; Sheldon 1960; Rieffenberger and Kletzly 1967; Ammann 1974). We describe only techniques used at the Moosehorn NWR.

Adult Males

During courtship, woodcock males may be captured in mist nets around the small area of the singing ground (i.e., display site) where a bird

repeatedly alights after its display flight. We monitor the bird during a courtship period (morning or evening), observe two or more courtship flights, note the direction of take-off and landing, and mark the landing site with a surveyor's flag. If secondary display sites are used, we mark them. On the day of trapping, we place three 3 × 10-m mist nets (61 mm mesh, 4 panels) around both the primary and secondary sites, positioning nets across take-off and approach pathways. This technique usually is effective (Dwyer et al. 1988). However, a bird that bounces from a net that is set too tightly may move to a secondary site.

On large, open sites (e.g., blueberry [*Vaccinium* sp.] fields, pastures) where the birds can avoid the more obvious nets, courting males often are difficult to capture with mist nets. We increase our rate of success at these sites by netting in the morning and either by placing sound recordings of peents near the nets or by having an observer imitate a peenting male. Displaying males are easier to capture during the first half of the breeding season when they are more tenacious to a singing ground and less prone to abandon it when disturbed. Subdominant males and, occasionally, dominant males from adjacent areas can be captured at a singing ground after the dominant male is captured. We hold the captured male in a cotton sack for 5–10 min. Nearby subdominant males usually fly to the singing ground. We have captured as many as four males with this technique at a single site.

Adult Females

In spring, adult females are more difficult to capture than males. Occasionally, females can be caught in mist nets that are set for the capture of displaying males. We have observed that females visit a male's singing ground most frequently during the first 2–3 weeks of the courtship period. To capture females, we erect nets around a male's display site but leave space for the male to fly into and out of the site; we set additional nets around the singing ground, especially along edges of openings and across flight paths (roads, trails). We also capture nesting females by placing mist nets along edges of known nesting areas and feeding sites (e.g., alder [*Alnus* sp.] covers, spring seeps). Females leave nests at predictable intervals to feed and to visit males during the courtship period (McAuley et al. 1993). If a female is nesting within 10 m of the edge of an opening, we erect nets across the flight path after she leaves the nest in the

evening. The female is less likely to see the net when she returns in the waning twilight.

We use pointing dogs to find females on nests. Females on nests can be captured with handheld nets (Ammann 1974). However, we avoid this technique, especially during early incubation when females readily abandon nests. Late in incubation, females may be caught in handheld nets but still not without the risk of causing them to abandon their nests. Some females that we caught on their nests abandoned clutches even though eggs were pipping. Females that abandoned nests usually left the immediate vicinity and traveled as far as 15 km or farther to renest (McAuley et al. 1990).

Females with broods also can be located by pointing dogs and be captured with handheld nets (Ammann 1974). The age of chicks can be determined by measuring the bill length (Ammann 1982). To quantify effort, we record the amount of time a dog searches and the number of dogs we use. Time spent searching is recorded from the minute the dog is released to the minute the dog locates a brood or nest or is removed from the field. We record the number of located broods and nests and whether birds are captured or escape. We then calculate an index of production in that year expressed as broods per dog-hour. Not all dogs have equal ability (Gutzwiller 1990), therefore, only data obtained with the same dog or dogs of similar ability should be compared.

All Sex–Age Cohorts

Capturing Woodcocks in Roost Fields

Woodcocks at the Moosehorn NWR roost at night in fallow fields, clear-cuttings, pastures, hay-fields, and blueberry fields. We have used as many as 25 mist nets/night in these types of habitats to capture woodcocks of all sex-age cohorts as they fly in to roost. We open nets in each area only once per week and change the placement of nets on the day of capture to prevent birds from becoming familiar with net locations. On rainy overcast nights, we employ nightlighting (Rieffenberger and Kletzly 1967) on foot and from a four-wheel drive vehicle to capture woodcocks in these areas and in other areas too large for mist nets. We prepare some larger roost areas (e.g., hayfields) for nightlighting from a vehicle by mowing 2-m-wide strips. Mowing facilitates capture because woodcocks roost in the strips where they are clearly visible. When on foot, crews of only three persons (one person with the light and two with nets) should be used if birds are abundant; otherwise, too many birds are flushed

simultaneously and escape. We use a quartz iodine light powered by a 12-V battery, but any bright light with a focused beam can be used. Handheld nets should have large hoops (≥1 m diameter) and long handles (≥3 m) but should not be too large for accurate and easy maneuvering.

On fields used as night roosts, the age-sex class of hatching-year (HY) males is more predominant than the age-sex classes of HY females, after-hatching-year (AHY) males, and AHY females (Krohn 1971; Gregg 1984; Dwyer et al. 1988; Sepik and Derleth 1993). These age-sex disparities result from the sizes of the available cohorts and from behavioral differences in use of fields among cohorts (Sepik and Derleth 1993). We maximize the capture of adults by trapping in June and July when the use of fields by AHY birds is highest.

Capturing Woodcocks in Daytime Habitats

From 1 June to 31 August, we capture woodcocks of all age-sex cohorts in modified shorebird traps (Liscinsky and Bailey 1955) on traplines in daytime covers (Dwyer et al. 1988). Timing of visits to traps is critical to capture success. Visiting traps once per day during late morning (0800–1200 h) is best because it avoids disturbing birds during crepuscular feeding periods. We place some traps in conifer covers or wet areas. During most years, few birds are caught in traps under conifers, but during droughts, woodcocks use conifer and mixed conifer-hardwood stands almost exclusively (Sepik et al. 1983).

Aging and Sexing Woodcocks

We age and sex woodcocks by examining physical characteristics. We measure culmen length of the bill to determine sex: bill length of less than 64 mm indicates males, and bill length of greater than 72 mm indicates females (Mendall and Aldous 1943). Birds with bill lengths between 64 and 72 mm may be either sex. Measurement (i.e., combined width) of the distal (outer) three primaries of the wing (Martin 1964) determines sex more reliably. With practice, however, birds can be sexed without measurements.

Aging birds reliably by examining plumage characteristics (Martin 1964) is difficult. To achieve about 95% accuracy in differentiating between HY and AHY birds, most technicians without experience need about 20 h of practice with wings of birds of known age and sex. During summer before wing molt is complete, separating HY,

second-year (SY), and after-second-year (ASY) woodcocks can be learned only by practice with live birds in the field. Thus, close supervision of technicians is necessary. Martin (1964) suggested examining primaries and secondaries for feather wear and fading to differentiate between HY and SY birds. We consider tertials (wing feathers closest to the body) more reliable indicators because wear on them is obvious. Martin's (1964:289), depicting differences in feather pattern between ages, is misleading. The figure omits the buffy tip (terminal band) on the edge of the secondaries of adults. However, we observed that the tips of secondaries of all age classes usually have a buffy tip. Also, many adults have secondaries with a dark subterminal bar, but it is always incomplete (personal observation). Most misclassifications are of HY birds identified as AHY birds because observers tend to examine secondaries proximal to the body that have been replaced by adult feathers.

Evaluation of Habitat

Management of the woodcock requires an understanding of habitat use and feasible techniques to improve or create suitable habitat. Sepik et al. (1989) summarized data on habitat requirements and techniques for managing habitats and concluded that, although habitat requirements were studied throughout the breeding range of the woodcock, many researchers failed to consider overall quality of measured habitats. The best available habitats that were measured are not necessarily optimal.

A meaningful assessment of habitat quality should begin with a well-defined hypothesis (Romesburg 1981) and must take into account the population density, productivity, and survival rate of woodcocks over 3 or more years. Habitats should be evaluated for a minimum of 10 years to observe the variable responses of woodcock populations to effects of weather and habitat change. At the Moosehorn NWR, historical data on woodcock density (Mendall and Aldous 1943) show the potential of the area for a larger population of woodcocks. We evaluate responses of woodcocks to current management techniques in relation to these historical population data.

The number of measured habitat variables should be limited according to the objectives of the study (Rexstad et al. 1988; Williams et al. 1990), and most should be applicable to management, except in studies of special aspects of the biology of

the woodcock. We recommend a standardized habitat classification system (Society of American Foresters cover types). Habitat variables that we measure at the Moosehorn NWR include overstory cover type, dominant shrub layer, size class (shrub, pole, mature) of overstory, basal area and height of overstory trees (i.e., stand height), and stems per hectare. Data on most of these variables are usually obtained during routine forest inventories and are available to managers. Limiting the number of variables increases the likelihood that procedures are followed by forest managers who generally manage large areas.

Determination of Earthworm Densities

The measurement of the quality of woodcock habitat should include earthworm abundance, which can vary with soil moisture, vegetation type, and previous land-use practices (Reynolds 1977a). Earthworms can be sampled by several techniques (Reynolds 1973, 1977b:8–10). At the Moosehorn NWR, we use the formalin-extraction method (Reynolds 1972). We recommend that earthworm biomass be reported in grams of dry weight per square meter to be comparable with data from other studies. Comparability of techniques is important for the application of results over a broad area.

Determination of Population Density

The evaluation of responses by woodcocks to management requires measuring population changes. When we began work at the Moosehorn NWR, only 12 fields were available for nighttime roosts, and most of the daytime habitat was composed of alder habitats on abandoned farms and in riparian zones. Each year in 1975–79, we captured 300–475 new birds and 50 birds that we had captured in previous years. The number of recaptures in a banding season were lowest of AHY females, moderate of AHY males, and highest of HY birds of either sex (Dwyer et al. 1988). We estimated population size with the demographically open models of Jolly (1965) and the partially open models of Darroch (1959). We also used the closed-population estimation methods of Otis et al. (1978; also, see Pollock et al. 1990).

Recent singing ground surveys revealed that the woodcock population at the Moosehorn NWR has increased substantially. However, we have been unable to recapture enough birds in the banding season to produce reliable population estimates. Although we now capture more than 500 new birds each year, we recapture only about 150. Evidently, woodcocks have dispersed in response to habitat management at the Moosehorn NWR, and recaptures are too few for reliable population estimates with mark-recapture methods. We now rely on indices of displaying males to judge whether the relative size of the population is changing. Each year, we conduct a singing-ground count (Clark 1970) of dominant breeding males. The surveys are conducted by the same persons each year to minimize observer bias. We also use pointing dogs to locate broods (and nests) to estimate production and relative abundance of females (broods and nests) per hour of search time. With these indices of population size, we determine whether the woodcock population is responding to habitat management.

Telemetry in Studies of Populations and Habitat Use

Telemetry has improved since heavy or bulky transmitters were first used on woodcocks in the 1960's. Transmitters are smaller and lighter, signal strength is greater, and problems from inadequate methods of attachment are largely resolved.

For optimal results, we use a two-stage transmitter, weighing 3.5–4.0 g, with a ground-to-ground range of 0.9 km and a longevity of 3–6 months. We evaluated several harness types (Derleth and Sepik 1990) and determined that most were inadequate. We also tried attachment with only adhesive, but transmitters fell off within 14 days. We now use adhesive (allweather livestock tag cement; Fearing Manufacturing Co., Inc., St. Paul, Minnesota) in combination with a single-loop harness of 45-lb-test, plastic-coated, steel fishing leader (Steelon Leader material, Berkley & Co., Spirit Lake, Iowa) that is embedded in the transmitter during potting and is secured with a size-3 connector sleeve.

A transmitter is attached by separating feather tracts between the wings on the back. The bottom of the transmitter is lightly coated with adhesive and held firmly on the skin. Feathers are pushed against the sides of the transmitter to help hold it in place while the wire is adjusted and secured.

The harness wire, potted into the bottom of the transmitter at a right angle to the antenna, is looped under the wings (in front of the legs), brought across the sternum, and secured by threading each end through a connector sleeve. The connector sleeve is crimped with needle-nose pliers so that the connector lies flat against the body and to the side of the sternum. Excess leader is removed. The wire loop should be tight enough to allow only a pencil to be inserted between the harness and the sternum. We used this method of attachment successfully without apparent adverse effects on birds during a 4-year study of the breeding of the American woodcock (McAuley et al. 1993). Indeed, several male woodcocks that returned to the Moosehorn NWR the year after the transmitters were attached were still carrying the transmitters and were displaying normally when they were recaptured.

This method of attachment allows reuse of transmitters. Transmitters can be refitted by splicing pieces of the wire harness with a connector sleeve to make the harness sufficiently long. We used the same transmitter on four different woodcocks in a single season but had to assign unique codes to each use of the frequency to maintain accurate records.

Monitoring Radio-marked Woodcocks

We use six- or seven-element yagi antennas mounted on trucks and connected to scanning receivers to obtain general locations of birds. Only 12–15 frequencies can be searched for at one time with a scan interval of 2 s. After a signal is detected, the exact location is obtained with either handheld H antennas or three-element yagi antennas. When aerial tracking is necessary, we follow the methods of Gilmer et al. (1981) but use two observers and have each scan for a different group of lost birds. This method is cost-effective when several birds are lost because each observer scans fewer frequencies and the probability of overflying lost birds is reduced.

For studies of habitat use by woodcocks, distinct vegetative types must be identified. Triangulation is unacceptable for determining exact locations of woodcocks. Dense vegetation, large boulders, uneven terrain, and the proximity of the woodcocks to the ground result in large errors (Springer 1979), which can render misleading information about the use of cover types. To identify used cover types, we approach every bird and circle it from a distance of 20 m or less. In this way we can classify the vegetation of the overstory and the understory of the habitat the bird uses. This technique is effective for locating woodcocks and for minimizing disturbance; few birds are flushed.

Good maps and recent aerial photographs are essential for any study of habitat, home range, and movements by woodcocks. We use composite photomaps assembled from aerial photographs (RF = 1:7,920) that are overlaid with a grid system (grid scale 1 in. = 660 ft.).

Monitoring Woodcocks to Determine Survival

For studies of survival, marked birds should be searched for daily and their status determined (i.e., alive, dead, or lost). Time and effort to determine status can be conserved if birds are monitored during the crepuscular periods when they usually move. Occasionally, a bird has to be flushed during the day to determine status; however, signal modulation sometimes is adequate to determine status.

An adequate sample of marked birds is of utmost importance to studies of survival. For most estimates, "... precision is poor unless ≥20 animals are marked ... and for good precision, a minimum of 40–50 birds would need to be tagged" for each cohort (Pollock et al. 1989:13). We found that about 5–10% of radio-marked birds cannot be used for analyses, mainly because transmitters fail or birds emigrate from the study area. Thus, the number of marked birds must be adequate to allow the expected loss.

Monitoring Nesting and Brooding Females

For studies of nest or brood attentiveness, information on how often females leave nest sites or broods and the duration of these recesses is desirable. Rather than having persons continuously monitor birds, we monitor presence, absence, and activity of radio-marked females at and within 10 m of a nest site with a shielded coaxial cable that is suspended above the nest and connected to a receiver and Rustrak recorder (Licht et al. 1989). We also monitor attentiveness and activity of females on nests and with broods with four- or seven-element yagi antennas connected to the recording system and positioned at least 50 m from the bird. Results with the yagi system are sometimes unsatisfactory because extraneous interference and sig-

nal drift produce chart recordings that are difficult to interpret.

Monitoring Woodcocks with Ancillary Markers

We used colored legbands (Richter and Liscinsky 1955; Shissler et al. 1982) on woodcocks with limited success. Usually, the marker is not easily seen unless the bird is standing where its legs are visible (e.g., gravel road) or flies near a person with a spotlight. Because several colors are difficult to distinguish from each other, exact identification is impossible. White, red, and blue are readily distinguished from each other; orange can be substituted for red; green can be substituted for blue; but red and orange or green and blue cannot be used together because they are indistinguishable in the field.

Concluding Remarks

Research techniques are continually changing and being refined. Time, effort, and money may be wasted if mistakes are repeated. Many aspects of research into woodcocks are difficult and often have logistical constraints that adversely affect the quality of research. Research on the habitat requirements and demography of the woodcock is more effective if all of us use the most appropriate methods.

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Breeding Chronology and Habitat of the American Woodcock in Missouri

by

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Abstract.   We report on the chronology of courtship and nesting and on habitat use of breeding American woodcocks (*Scolopax minor*) in central Missouri. We determined the chronology of courtship from a five-stop survey of singing males during 1977–90 and determined habitat use by singing males from complete counts of males in 23 fields and 8 clear-cuttings during some of these years. We observed nesting female woodcocks and broods to determine nesting chronology and habitat use. Males began displaying during the last week of February and the maximum number displayed, on average, during 15–21 March. Females initiated nests between 12 and 31 March, either immediately before or after male courtship waned. The mean maximum number of singing males per hectare on a singing ground during 1979–80 ranged from 0.2 to 8.8 ($\bar{x}$ = 2.5, SE = 0.46). The mean maximum density of singing males per hectare in 0–7-year-old clear-cuttings ranged from 0.0 to 2.3 ($\bar{x}$ = 1.0, SE = 0.19). The density of displaying males increased with densities of all deciduous stems and coniferous stems greater than 2.5 cm dbh and declined with increasing numbers of coniferous stems less than or equal to 2.5 cm dbh and field size (R^2 = 0.83). Habitat parameters more reliably predicted maximum density of singing males than mean density of singing males. Nests usually were in old fields or forest adjacent to old fields, whereas broods tended to be in more mature forest. On average, canopy closure and basal area were greater, litter was deeper, and moisture in the soil was greater at brood sites than at nest sites ($P \leq 0.05$).

Key words: Breeding chronology, broods, habitat, nests, singing grounds, woodcock.

Missouri is on the northwestern edge of the American woodcock's (*Scolopax minor*) winter range and south of areas with high numbers of breeding birds (Owen 1977). Since the 1920's, woodcocks have been considered scarce in Missouri (Bennitt and Nagel 1937). However, surveys of small game harvests suggest an annual harvest of more than 15,000 birds (Sheriff 1982), and field biologists observe displaying males, nests, and

broods each spring in many parts of Missouri. Accurate information on population densities, statewide distribution, chronology of migration, habitat use, limiting factors, and potential for consumptive and non-consumptive use of woodcocks is needed for effective management of this resource in Missouri.

We determined the chronology of courtship and nesting of American woodcocks in Missouri and documented habitat use by displaying males, nesting females, and broods. We compile in this paper results from several unpublished studies, which were conducted at the Thomas S. Baskett Wildlife Research and Education Center (Center) in central Missouri, 1977–90.

Study Area

We conducted studies on the 900-ha Center and adjacent lands in southern Boone County, Missouri. Elevation ranged from 170 m in narrow waterways to 244 m on rolling, narrow ridges with moderate to steep slopes. The area was primarily forested but interspersed with agricultural lands, roads, trails, and powerlines. Agricultural lands were 81 ha (9%) of the area and consisted of row crops, wildlife food plots, pastures, and fields of grasses, forbs, and shrubs. Mixed stands of Eastern redcedar (*Juniperus virginiana*) and pole-sized hardwoods with understories of shrubs and vines were about 144 ha (16%) of the area. Upland oak (*Quercus* spp.)-hickory (*Carya* spp.) forests were about 585 ha (65%) of the area and had sparse to dense understories of shrubs and saplings. Bottomland hardwood stands were about 54 ha (6%) of the area and occurred in narrow valleys along perennial streams. Pine plantations (*Pinus* spp.) were about 36 ha (4%) of the area. Eleven 1–7-year-old regenerating, oak-hickory clear-cuttings, ranging from 1 to 5 ha were scattered throughout the study area. Some clear-cuttings (1–2-years-old) were a mixture of herbaceous plants and deciduous tree seedlings, other clear-cuttings (3–7-years-old) had greater densities of young trees up to 4-m tall and a canopy closure of 50–80%. Mean density of woody stems greater than 1-m tall in 2–4-year-old clear-cuttings was 25,141/hectare (Thompson and Fritzell 1989). Murphy (1983) and Thompson and Fritzell (1989) provide a more detailed description of the habitats.

Methods

From February to March, arrival dates of woodcocks were determined by driving on roads through the study area each night and listening for displaying males. Each week during 1977–90, we determined the number of displaying males by conducting a five-stop roadside survey. We began the survey within 7 days of the arrival of woodcocks and repeated it 1–3 times/week until mid-April. Stops were about 1 km apart, at the same locations each year, and adjacent to fields where woodcocks had been observed previously. We recorded all peenting and displaying males during 2 min at each stop. Counts were begun 2 min after the first woodcock was heard or 15 min after sunset.

We related numbers of displaying males in fields to the amount of woody cover. Every third night from the time birds arrived to mid-April during 1979–80, we counted all displaying males in 23 fields in the study area. The locations of displaying males were marked in each field. We measured the amount of woody cover on 2-m wide transects that ran the length of the field and were every 10 m across the width of the field. We counted by species all woody stems >1-m tall. We measured the size of each field with a planimeter on aerial photographs.

We used multiple regression analysis to relate density of displaying males (males per hectare) in 1979 and 1980 to density of woody stems (stems per hectare) and field size (ha). We compared the results of two regression models with different dependent variables. One model used mean density of displaying males in each field, and the second model used mean maximum density of displaying males in each field during 1979 and 1980. The mean density of displaying woodcocks was calculated as the mean of all censuses during 1979 and 1980. The mean maximum density in each field was calculated as the mean of the greatest density of males in each year. For the independent variables in the analysis, we calculated the density of coniferous stems and density of deciduous stems ≤ 2.5 cm and > 2.5 cm. We transformed values by natural logs of several variables of stem density before analysis (Table 1).

In 1985, 1986, 1989, and 1990, we censused displaying males in clear-cuttings once or twice a week during the 2nd, 3rd, and 4th weeks of March, when courtship activity was greatest (Murphy 1983). In 1985 and 1986, we counted all displaying woodcocks in two stands that were clear-cut in

Table 1. Parameter estimates for a regression model[a] predicting mean maximum density of singing male woodcocks from habitat characteristics of display grounds (n = 23) in central Missouri, 1979–80.

Variable	Regression coefficient	P
Intercept	1.34	0.0001
Deciduous stems ≤2.5 cm/ha	0.001	0.0099
Ln[b] deciduous stems >2.5 cm/ha	0.254	0.0040
Ln coniferous stems ≤2.5 cm/ha	-0.408	0.0023
Ln coniferous stems >2.5 cm/ha	0.235	0.0234
Ln field size (ha)	-0.535	0.0099

[a] Model R^2 = 0.83, F = 16.918, P = 0.0001.

[b] Natural log transformation.

September 1983. In 1989 and 1990, we again counted all singing males in the same two stands as in 1985–86, two other stands clear-cut in January 1983, two stands clear-cut in September 1984, and two stands clear-cut in August 1988. We calculated the mean maximum density of singing males in clear-cuttings at each age during each year. Because these censuses were extended over several years, population differences between years are indistinguishable from effects of clear-cut age on the numbers of displaying males. Therefore, we present these data graphically only for descriptive purposes.

The chronology of nesting was determined by either estimating hatching dates of eggs or by aging chicks (Westerskov 1950; Ammann 1977). From mid-March to mid-May in 1978, we searched for nests with two pointing dogs. Because all nests (n = 6) found in 1978 were destroyed by predators, we delayed searches for nests and broods in 1979 and 1980 until 1 month after the peak display by males to minimize disturbance but enhance the probability of finding flightless broods.

We measured habitat characteristics at each nest and brood location immediately after eggs hatched, after a nest was abandoned, or the day after a brood was found. We recorded the species and diameter of woody plants >1-m tall on a 0.0478-ha circular plot. Basal area was measured with a 10-factor prism. Percent canopy closure was determined with a sighting tube (James and Shugart 1970). Depth of litter was measured at nine points: in the center of the nest or brood location and at points 2- and 4-m north, south, east, and

west. The average height of ground cover and percent of ground cover were ocularly estimated on a 0.0038-ha circular plot centered on the nest or brood location. We removed a core of soil from the center of each plot and determined percent moisture by the gravimetric method (Brady 1974). The distances to the nearest standing water and the nearest field were obtained from topographic maps. The mean differences of woody stems per hectare, basal area, canopy closure, ground cover height, percent ground cover, litter depth, soil moisture, distance to nearest field, and distance to nearest standing water between nest and brood locations were determined with the Mann-Whitney U-test.

Results

Woodcocks usually arrived during the last week of February, and the numbers of displaying males rapidly increased soon thereafter. The number of displaying males remained near its peak for about 2 weeks. The peak mean number of displaying males usually occurred during 15–21 March 1977–90 (Fig. 1).

The 23 fields in our study area were pasture or abandoned fields with varying densities of shrubs and young trees. The most common woody species in the fields were smooth sumac (*Rhus glabra*), Japanese rose (*Rosa multiflora*), Eastern redcedar (*Juniperus virginiana*), wild plum (*Prunus* spp.), persimmon (*Diospyros virginiana*), slippery elm (*Ulmus rubra*), and coral berry (*Symphoricarpos orbiculatus*).

Densities of singing males and woody stems varied greatly among fields. On average, the highest densities of singing males occurred in the oldest fields with the highest densities of woody stems (Table 2). Mean maximum density of displaying males was more reliably predicted by field characteristics (R^2 = 0.83, F = 16.9, P < 0.0001) than was mean density (R^2 = 0.75, F = 10.2, P < 0.0001). The density of displaying males increased with densities of all deciduous stems and coniferous stems >2.5 cm dbh and decreased with increasing density of coniferous stem ≤2.5 cm dbh and field size (Table 1).

The mean maximum density of singing males in 0–7-year-old clear-cuttings ranged from 0 to 2.3 males/hectare ($\bar{X}$ = 1.0, SE = 0.19; Fig. 2).

Thirty nests and 10 broods were found during 1978–80. We estimated that all clutches were initiated between 12 March and 31 March (Fig. 3).
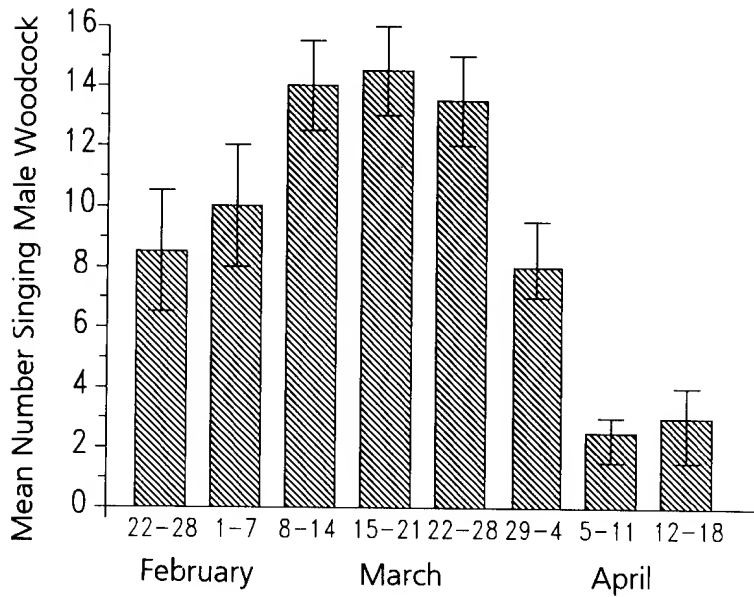
Fig. 1. Mean (SE) number of displaying male woodcocks detected by roadside survey at the Thomas S. Baskett Research and Education Center in central Missouri, 1977–90.

Table 2. Density of displaying male woodcocks and habitat characteristics of fields ($n = 23$) at the Thomas S. Baskett Wildlife Research and Education Center in central Missouri, 1979–80.

Variable	$\overline{X}$	SD	Min	Max
Mean maximum density of displaying males (males per ha)	2.5	2.2	0.2	8.8
Number of:				
deciduous stems ≤2.5 cm/ha	429.6	620.4	0.0	2,331.6
deciduous stems >2.5 cm/ha	46.3	70.8	0.0	254.6
coniferous stems ≤2.5 cm/ha	66.7	141.8	0.0	569.5
coniferous stems >2.5 cm/ha	32.6	61.1	0.0	217.8
Field size (ha)	2.4	2.1	0.4	8.0
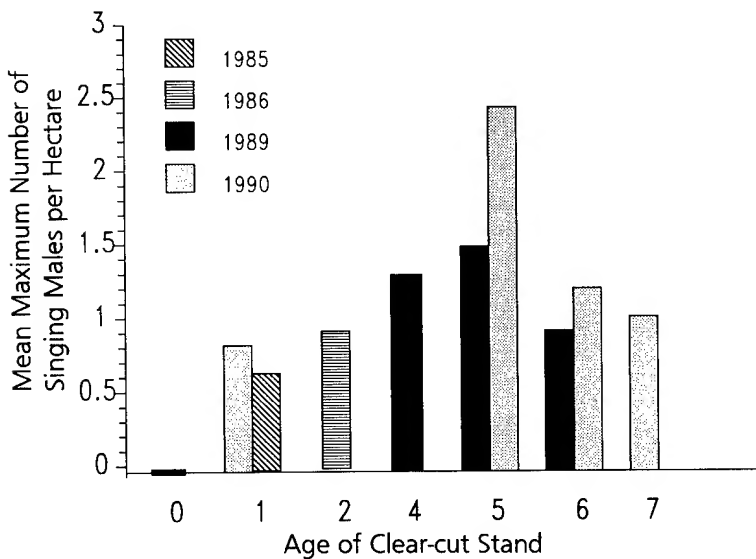
Fig. 2. Mean maximum number of displaying male woodcocks observed in 0-7-year-old clear-cuttings at the Thomas S. Baskett Wildlife Research and Education Center in central Missouri, 1985–90.
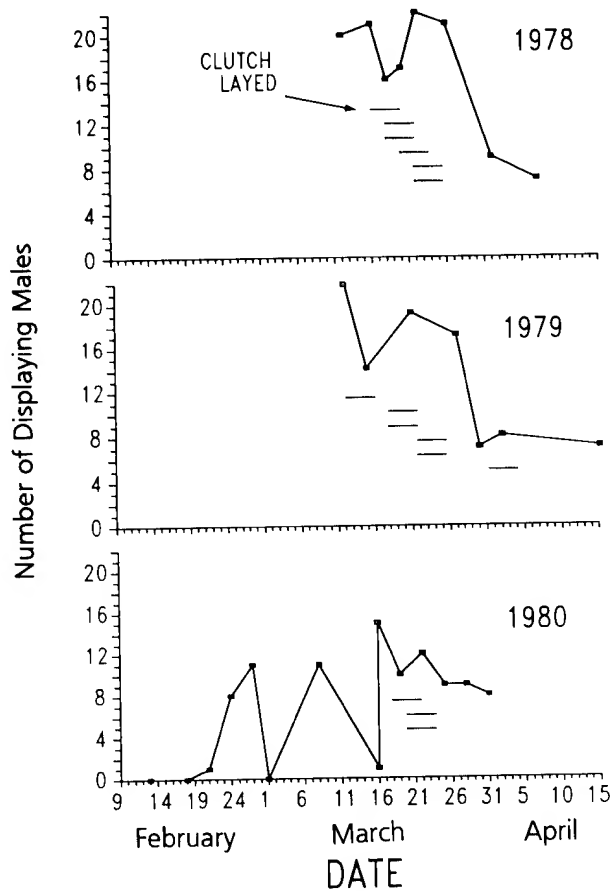
Fig. 3. Nesting dates of woodcocks at the Thomas S. Baskett Research and Education Center in central Missouri in relation to displays by males, 1978-80.

they initiated nests after the decline began (Fig. 3).

Nests were in old fields (n = 17), at the interface of forests and old fields (n = 11), and in forests (n = 2). Both nests in the mature forest were <20 m from an opening. Broods were in old fields (n = 3), at the interface of forest and old fields (n = 7), and in forests (n = 4) habitats. Basal area, canopy closure, litter depth, and soil moisture were substantially greater in sites where broods were found than at nest sites (P < 0.05; Table 3). Broods in openings were younger ($\overline{X}$ = 3.6 days, SE = 3.5) than broods along edges ($\overline{X}$ = 7.9 days, SE = 2.2), which also were younger than broods in the forest ($\overline{X}$ = 12.9, SE = 3.0).

Discussion

Woodcocks arrived when the daily minimum temperature was greater than 0° C and the wind was from the southeast (Murphy 1983). Numbers of displaying males on singing grounds in east Tennessee peaked between 7 March and 12 March 1978 (Roberts and Dimmick 1978), about 1 week earlier than in our study area. In east Texas (Tappe et al. 1989), the peak of courtship display during 1978-86 was on 17 February, 1 month earlier than in our study. These peak display dates show an orderly progression from the southern to central United States.

Many authors suggested that some woody cover is desirable on display grounds (Mendall and Aldous 1943; Sheldon 1967; Wishart and Bider 1977). Gutzwiller and Wakeley (1982) also observed in-

Whereas in 1978 females initiated nests before displaying by males declined, in 1979 and 1980

Table 3. Habitat characteristics at woodcock nest and brood locations at the Thomas S. Baskett Wildlife Research and Education Center in central Missouri, 1978-80.

Variable	Nest sites (n = 30)		Brood sites (n = 14)	
	$\overline{X}$	SD	$\overline{X}$	SD
Woody stem per hectare	3,133	987	3,767	1,650
Basal area (m^2 ha)	6.0	2.2	11.7[a]	3.3
Canopy closure (%)	36	19	86[a]	11
Ground cover height (cm)	29.6	14.6	26.2	21.9
Ground cover (%)	23.5	10.3	48.3	35.4
Litter depth (cm)	2.5	1.2	4.8[b]	0.7
Distance from field (m)	2.5	2.9	12.3	11.5
Distance from water (m)	35.3	18.3	14.5	13.5
Soil moisture (%)	15.6	4.5	54.5[b]	9.3

[a] Means different between nest and brood site, P < 0.05, Mann-Whitney U-test.
[b] Means different between nest and brood site, P < 0.01, Mann-Whitney U-test.

creased use of display grounds with greater shrub density. Owls may be important predators of male woodcocks on singing grounds (Sheldon 1967), and on several occasions we observed great horned owls (*Bubo virginianus*) on display grounds. We concur with Wishart and Bider (1977) that dense shrubs may help deter avian predators. Dense woody cover also may provide barriers that isolate males and thereby allow greater densities of displaying males. None of the singing grounds we censused, including dense, 7-year-old clear-cuttings, contained cover that was uniformly too dense for use by displaying woodcocks. All clear-cut stands were used by singing males within 2 years after timber harvest. Displaying males also used clear-cuttings in aspen stands in Wisconsin soon after clear-cutting (Hale and Greg 1978).

Although woodcocks preferred fields and used clear-cuttings with high densities of woody stems, they selected landing sites with sparse or low vegetative cover. In fields with woody cover, woodcocks used open areas, trails, or old roads with few, if any, woody stems. In clear-cuttings, displaying males landed on old skid trails, on log landings, or in other open areas. Woodcocks often sing in only a small portion of a field (Mendall and Aldous 1943). Dense woody cover on several of the display grounds also was used as diurnal cover.

The quality of surrounding nesting and brood-rearing cover also may be an important factor of the suitability of a field as a display ground (Dwyer et al. 1988). In our study area, woodcocks used singing grounds and surrounding cover for nesting and brood-rearing habitat.

Maximum density of displaying males may be more closely related to habitat structure than mean density because it represents the number of simultaneously displaying woodcocks in a field. A high mean density, which might not be as dependent on habitat structure as maximum density, could result from repeated use by one or few individuals.

The observed difference in nest initiation dates in relation to the date male display activity peaked between 1978 and 1979-80 could be an artifact of our use of different methods. Our estimated date of nest initiation in 1978 was based on estimated hatch dates of clutches, whereas dates of nest initiation in 1979-80 were determined to be the estimated age of flightless broods.

Nests were initiated during the peak of the males' displays (7-15 March) in Tennessee (Roberts and Dimmick 1978) but about 1 week earlier than in our study area. In Alabama, hatching peaked between 28 February and 28 March

1974-78 (Roboski and Causey 1981), more than 1 month earlier than in our study area. Likewise, most clutches in east Texas were layed during February (Whiting and Boggus 1982). Conversely, successful clutches were not initiated until April in Michigan (Ammann 1980). Similar to the patterns of the display of males, dates of nesting are progressively later in northern than in southern breeding areas.

Most nests were in old fields. Unlike in Missouri, nests in Alabama usually were in mid-successional to mature forest (Roboski and Causey 1981). Whereas nests in Missouri and in more northern states (Liscinsky 1972; Bourgeois 1978) usually were in dry upland sites, nests in Alabama usually were in flat bottomlands near water (Roboski and Causey 1981). Broods were mostly in forest edges or in forests where tree basal area and canopy closure were greater than at nest sites. Similarly, Bourgeois (1978) reported that basal area was greater and trees in the intermediate size classes were more numerous at brood sites than at nest sites. Dwyer et al. (1982) reported that, as the brood matures, the habitat preferences of the chicks change toward more open, mature forest stands. Because most broods hatched in old fields, we believe most broods gradually move from old fields to forest habitats during the 2 weeks after hatching.

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A Census Method for Roding Eurasian Woodcocks
in France

by

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Abstract.   The number of roding Eurasian woodcocks (*Scolopax rusticola*; i.e., seen and heard birds and only heard birds) was recorded at 42 sites in France. One hundred and forty calls recorded at the same station during 25 evenings from March to July were analyzed from sonograms. The number of calls increased with the number of males (r^2 = 0.74). Woodcocks were most active from late-May to early-June. At this time, the number of observations is relatively stable from one evening to the next, and a minimum of five observations is registered at sites with a large abundance of woodcocks. A census method for monitoring the breeding population of the Eurasian woodcock at a national level is proposed and is based on the record of roding males during a single visit at fixed but randomly chosen listening stations in May–June.

Key words: Census method, France, index of abundance, roding, *Scolopax rusticola*, woodcock.

The Eurasian woodcock (*Scolopax rusticola*) is a common bird in France (Ferrand 1985a), and an annual survey of the breeding population is needed for monitoring this species. As Hirons and Owen (1982a) emphasized, "estimating the number of courting males in the breeding season will always be far easier for *Philohela*, which display on small, discrete singing grounds, than for *Scolopax* where several males perform songflights over the same extensive areas." Indeed, the specific behavior of this species (Ferrand 1979; Hirons 1980) eliminates the direct use of classic census methods reviewed by Mannan and Meslow (1981) for nongame birds and by Martinka and Swenson (1981) for game birds.

In forested areas, observations of roding males during May and June identify potential favorable areas for breeding (Ferrand and Landry 1986; Hirons 1988). However, it is impossible to relate the number of observations to the number of clutches or broods or to an annual index of fledged young. The objective for conducting this study was to formulate from previous and new work a survey method to monitor nationwide populations of male Eurasian woodcocks in France.

Methods

Study Areas

The two principal study areas were in the forests of Rambouillet (13,000 ha) and Compiègne (14,500 ha). These forests are in the Paris Basin, respectively 50 km southwest and 60 km north of Paris. In the study areas, the dominant species are oak (*Quercus pedunculata, Q. sessiliflora*) and beech (*Fagus sylvatica*) in well-drained areas and European alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and hornbeam (*Carpinus betulus*) in marshy areas. The main herbaceous species are *Mercurialis perrennis, Polystichum filixmas,* and *Carex pendula* in Compiègne and *Deschampsia aquilinum* and *Festuca tenuifolia* in Rambouillet.

Observations also were made in forested, mountainous areas (9 sites in the Massif Central, 10 sites in the Alps and Jura, and 2 sites in the

Pyrenees) and on the plains in the southwest (5 sites) and north (16 sites) of France. These study areas are deciduous forests with the same species of trees as the Compiègne and Rambouillet forests and coniferous forests of mainly spruces (*Picea* spp.) and firs (*Abies* spp.).

Field Techniques

The counting of roding males is the basis of my proposed method for surveying woodcocks. Roding, a display flight by males at twilight, is performed above about a 60-ha area every morning and evening (Ferrand 1979). Roding males are seldom in the air continuously for more than 20 min, and a bird's usual evening display consists of two to four flights. Most birds display for about twice as long in the evening as in the morning. When a male finds a receptive female, he remains with her for 3–5 days before resuming display flights (Hirons and Owens 1982b). Because of the male's mobility, observers must use fixed listening stations and record the number of roding males (i.e., seen and heard birds and only heard birds) during a specific period. This period lasts from 1800 h (UT) to 1830 h (UT) in March but from 1910 h (UT) to 2040 h (UT) in June.

Analysis of Calls

To determine the number of males that the recorded calls represent, we used a proposed method by Beightol and Samuel (1973) and Bourgeois and Couture (1977) for American woodcock males that are identified by sonographs of the peent call. For identifying Eurasian woodcocks in our study, we selected three variables from a graphic illustration of the pattern of sonograms to identify the individual males (Ferrand 1987). Ten birds were identified from their sonograms, and the relation between the number of contacts and the number of individual males was evaluated. Every evening, the number of different tape-recorded males and the number of analyzed calls were compared. After a log transformation of the data, a coefficient of determination for analyzed calls and number of roding males was calculated. We applied this acoustic-recognition method to 140 woodcock calls recorded at the same listening station in the forest of Rambouillet during 25 evenings from 24 March to 22 June 1982.

Timing of Counts of Roding Males

Observations should be made when the number of observations is greatest. Observations during 6 years (1977–82) at the same listening station in the forest of Compiègne indicated that Eurasian woodcocks display between March and July and that roding peaks from late-May to early-June (Ferrand 1985b; Nemetschek 1977). To verify the peak of the roding period, we collected data during 1985–87 on 42 sites in France. On most sites, observations were conducted twice a week during March–July. The mean difference in number of observations in April–June above and below 500 m altitude was tested by one-way ANOVA. To minimize variation, I sought an observation period that was relatively stable (Table 1). A Kruskall-Wallis test was applied to the means of the coefficients of variation (C.V.) of each period to test for heterogeneity. Concentrating on the long-period roding sites, I analyzed 36 series of observations from 20 sites that included at least 5 observations/month in April–June. I examined data on a monthly basis (Table 2).

Table 1. Mean (SD) of the coefficient of variation for the number of observed roding Eurasian woodcocks by altitude and abundance in April, May, and June in France, 1985–87. Thirty-six data sets were recorded annually at 20 sites.

Features of sites	Mean coefficient of variation of the number of roding contacts		
	April	May	June
Low abundance[a] (n = 19)	72.1 (39.9)	63.5 (43.2)	104.7 (93.9)
High abundance[a] (n = 17)	52.4 (34.1)	31.5 (12.6)	33.6 (13.5)
Total (n = 36)	62.8 (38.1)	48.4 (36.0)	71.1 (76.9)

[a] Sites of low abundance are considered those with a mean of <10 contacts from April–June and sites of high abundance are those with a mean of ≥10.

Table 2. Mean (SD) number of observed roding Eurasian woodcocks by altitude and abundance in April, May, and June in France, 1985–87. Thirty-six data sets were recorded annually at 20 sites.

Features of sites	Mean number of roding contacts		
	April	May	June
Altitude <500m (n = 17)	8.9 (6.5)	11.3 (5.9)	12.7 (8.6)
Altitude >500m (n = 19)	5.6 (4.1)	8.8 (6.1)	7.9 (6.7)
Low abundance[a] (n = 19)	4.1 (2.5)	5.2 (3.1)	3.9 (3.3)
High abundance[a] (n = 17)	10.5 (6.0)	15.3 (3.5)	17.2 (5.0)
Total (n = 36)	7.2 (5.5)	9.9 (6.1)	10.2 (7.9)

[a] Sites of low abundance are considered those with a mean of <10 contacts from April–June and sites of high abundance are those with a mean of ≥10.

Results

Relation of Calls to Number of Males

Of the total roding observations, 38.6% could be assigned to an individual. The coefficient of determination (r^2) between analyzed calls and number of different males was 0.74 ($F = 65.4$, $P < 0.01$) (Fig. 1).

Period of Maximum Contacts

Two periods of roding were observed: a short period in March–April at listening stations below the altitude of 500 m and a long period during March–July at listening stations at the altitude above 500 m and in the large forests of Rambouillet and Compiègne. Migrating woodcocks performed roding where they happened to be, one evening here and the next evening somewhere else. After April, all woodcocks had reached their breeding sites and performed only in these sites.

No differences were detected among means of the number of observations during April–June ($F = 2.4$, $P = 0.08$) and among sites below an altitude of 500 m ($F = 1.3$, $P = 0.27$) and above an altitude of 500 m ($F = 1.5$, $P = 0.22$). No difference existed between sites of low abundance, that is, where the mean of the number of observations was <10 during April–June ($F = 1.0$, $P = 0.35$). Nevertheless, a highly significant difference was detected in the sites where the mean of the number of contacts was >10 during April–June ($F = 8.61$, $P < 0.001$). Values were greater in May and June than in April.

Stability of the Number of Contacts

Heterogeneity of means of the coefficients of variation (C.V.) was $H = 6.9$ ($P = 0.03$). The lowest coefficient of variation was in May. No difference was detected among the three periods ($H = 3.9$,
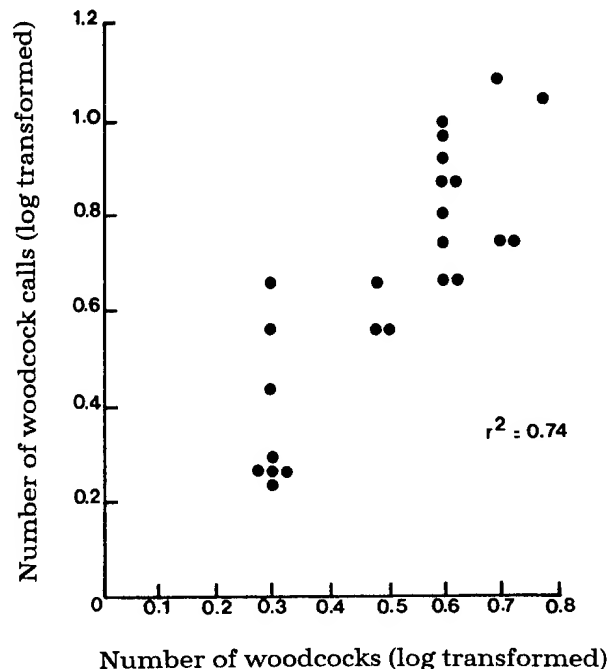
Fig. 1. The number of calls increased (logarithmic transformed data) with the number of male woodcocks during 25 evenings at the same listening station in the forest of Rambouillet from March to June 1982.

$P = 0.14$) in sites ($n = 19$) with relatively low abundance. However, the mean coefficients of variation from the sites of relative high abundance ($n = 17$) were different ($H = 9.1$, $P = 0.01$). The greatest stability of observation is in May and June.

Discussion

Minimum Number of Observations

The presence of roding birds can be detected reliably when the probability to observe a single woodcock is greatest. The greatest probability of detecting roding, even in sites where the abundance of woodcocks is low, is from mid-May to mid-June. At this time, at least one woodcock was seen at the sites where from April to June the mean number of observations was greater than five (Fig. 2). Moreover, at least five woodcocks were seen each evening at sites where the mean number of observations was 10 or greater. A single visit to the listening point from mid-May to mid-June provides the best chance for measuring relative abundance.

Number of Observations as an Index of Abundance

The number of analyzed calls is equal to the number of calls that could be detected with the tape-recorder and, thus, is restricted to a limited area. From one evening to another, the number of contacts at the same site can vary greatly and make interpretation of results difficult. The increase in the number of identified individuals is principally from an increase in different roding woodcocks during each evening of observation. However, the proportion of calls that could be assigned to an individual fluctuated from 12.5% to 83.3%, indicating the difficulty of tape-recording. Data for the analysis were obtained by a method that is similar to the fixed-distance point count method (DRL., i.e., dénombrement à rayon limité; Fowler and McGinnes 1973; Scherrer 1982). Scherrer (1987) compared results of a DRL with a radius of 30 m (DRL30) to a DRL with a radius of 75 m (DRL75) and concluded that "the DRL75 is the more accurate and the DRL30 is neither accurate nor precise." An increase in the length of the radius increases reliability of the index of abundance. Because an observer has a greater radius of detection than a tape-recorder, the former is more reliable. In this way, the highly significant coefficient of determination obtained by a less efficient method suggests that the positive relation between the number of contacts and the number of different woodcocks at the observation site is correct.

National Census Method

To monitor populations of male woodcocks at a national scale in France, the number of observed roding males in May–June seems to be at this time the only index of abundance. Because France is divided into *departements*, I propose a stratified sampling design with each *department*, a stratum in which samples are randomly obtained. Optimization of the size of sampling units by the distribution of organisms was discussed by Scherrer (1987). In May–June when the distribution of rod-

Fig. 2. Relation between the mean number of male woodcocks in April–June and the minimum number of woodcocks from mid-May to mid-June. Thirty-six data sets were collected annually in 20 sites in France during 1985–87.

ing males is clumped (Ferrand and Landry 1986), many small sampling units are recommended. However, the costs of organizing and conducting the census limit the number of sampling units and require a more prudent sampling design. In a previous study, Ferrand (1979) estimated an annual roding area of about 300 ha. I used this value to fix the sampling unit size 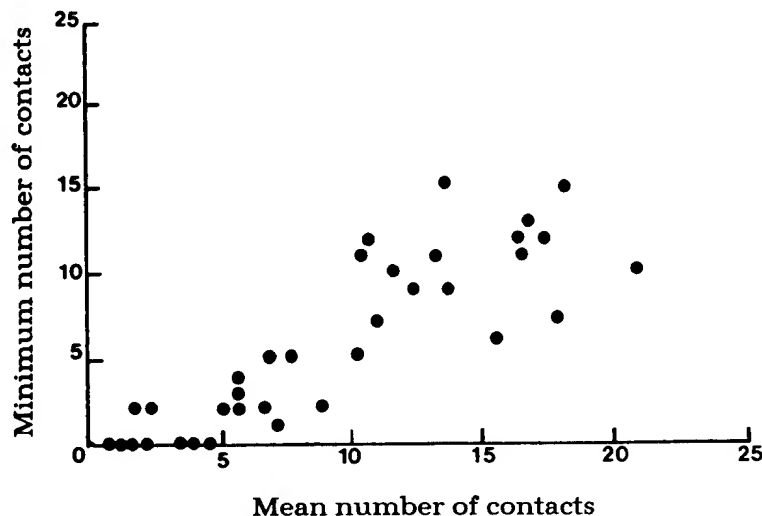at 2 × 2 centigrades (mapping system of coordinates: a grade is equal to 1/400 of the earth circumference) or about 280 ha. Only units with predominant forest (greater than 90%) should serve for sampling. Small forests (less than 300 ha) and sites at perimeters of forests, which are less favorable for roding (Ferrand and Landry 1986), should not be used for sampling.

The listening point should be in the center of the sampling unit or at least remain as close as possible to the center of the unit. Listening stations may have to be shifted toward an open area (e.g., a clearing or a crossing of forest roads) to facilitate acoustic and visual observations because woodcocks prefer to fly over open areas (Ferrand and Landry 1986). Sampling should be conducted during good weather, notably in the absence of rain and wind that impede visual and acoustic observations.

Because of difficulties in reaching listening stations, particularly in mountainous areas, I propose a single visit to as many listening points as possible. This seems appropriate for the greatest probability of detecting roding woodcocks in May and June because the greatest number of different woodcocks are roding then. A single visit is recommended also by Jarvinen and Vaisanen (1981) for censuses in large geographical areas.

Because the highest cost is the observer's travel and because the total contacts during one evening are a relative index of abundance, the census should not be limited in duration but continue for the entire roding period, that is, for about 90 min (Ferrand 1985b).

Trends in populations are often determined from random sampling in the year n and from subsequent sampling in years $n + 1$, $n + 2$,...in sampling units defined in year n (e.g., the Breeding Bird Survey [BBS]; Bystrak 1981). Geissler and Noon (1981) discussed the BBS results as trend estimates and proposed a model. They concluded that external variables and particularly the habitat changes on each sampling-line largely influence the results and therefore dictate a survey of habitat. This constraint increases cost of sampling (Bystrak 1981) and cost of analysis of data. Therefore, I propose a random sampling method with replacement, that is, the sample is renewed each year and all members of the sampling population are given an equal chance of being drawn (Cochran 1977). Application of this method is easy and reduces bias from habitat changes.

For each listening station, the observer records the seen and heard woodcocks. The annual results are expressed as a frequency of occurrence. The estimator and its variance are calculated by the method of Cochran (1977). A criticism of the frequency index is that a listening station with one observation has the same weight as a listening station with more than one observation. A minimum number of five observations seems to separate high and low abundance (Fig. 2). Three indices can be calculated each year: W, the total relative frequency index; W1, the relative frequency index at the low-abundance sites (1–4 observations); and W2, the relative frequency index at the high-abundance sites (greater than 4 observations).

The W index indicates a spatial occupation rate for the species. The interpretation of the demographic trend is based on the extension and not on the distribution area of the population. Exceptional weather, for instance, may produce a local concentration or dilution of the population, even if its size remains stable; but this census method accounts for variations in abundance. The definition of two abundance classes and the survey of their relative frequencies allow a more reliable interpretation of a demographic trend. To determine the statistical significance of the variations, we can compute a Z-statistic for each of these indices ($Z = [N_i(Fc_i - Fc)^2 / Fc(100 - Fc)]$, where $Fc = Fc_i/K$ with K, the number of frequencies to compare, N_i is the size of each year sample, Fc_i is the frequency of occurrence obtained each year).

Application of the Census Method

To evaluate the census method, I randomly selected and visited 52 of 518 potential sampling sites in the Paris Basin in 1987. The total relative frequency index was $W = 0.44$ ($s^2 = 0.004$). The W value close to 0.5 indicated the ability to detect within-year variations of this variable. Indeed, under these conditions the confidence limit is narrow and easy to compute because W is different from 0 and 1. The relative frequencies of each of the abundance classes were $W1 = 0.367$ ($s^2 = 0.004$) and $W2 = 0.078$ ($s^2 = 0.0011$).

Summary and Conclusions

Single-observation sessions at fixed, randomly selected listening stations in the forest are the basis of the proposed census method. This technique does not lead to a precise monitoring of the population but permits detection of strong numerical variations in the population of breeding woodcocks.

An interpretation of demographic variations, however, should be compared with a survey of habitat as Gregg (1982) and Dwyer et al. (1983) emphasized for monitoring populations of the American woodcock. An extensive application of census data based on singing males already was attempted for mourning doves (*Zenaida macroura*) in North America (Grue et al. 1978) and for several species (Farina and Meschini 1987) in Italy. In the first instance the census data were obtained by selection of sites of high, medium, and low abundance. Such a use is applicable to our study. With a LANDSAT image, Babin and Couture (1987) proposed a method to inventory the breeding habitat of the American woodcock. A similar application of remote sensing could be planned for the habitat of the Eurasian woodcock.

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Effects of Weather on Earthworm Abundance and Foods of the American Woodcock in Spring

by

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Abstract.   Earthworms composed greater than 90% (dry weight and volume) of food consumed by 48 American woodcocks (*Scolopax minor*) collected during the springs of 1987–89 on the Moosehorn National Wildlife Refuge, Maine. The availability of earthworms seemed related to amount of snow in winter and persistence of frost in the soil in spring. When earthworms were less available, the intake of food by woodcocks declined and the relative importance of litter-inhabiting prey (Coleoptera and Araneae) increased. Reduced intake of food lowered the the body mass of female woodcocks in 1989 and evidently caused a 3–4 week delay in nesting. Results suggest that conditions in winter and spring affect availability of food and subsequently influence body mass, time of nesting, and reproductive success of the woodcock.

Key words: American woodcock, earthworms, foods, Maine, reproduction, sampling, *Scolopax minor*, weather.

The American woodcock (*Scolopax minor*) is one of the migratory birds that arrives earliest on breeding grounds in the northeast. Environmental conditions can be severe and may affect food availability and the bird's diet, body condition, and reproduction. The importance of food supply in determining timing and extent of reproduction in birds is documented (Drent and Daan 1980; Martin 1987). There is evidence of atypical feeding behavior and even starvation of wood-cocks after snowstorms or unusually persistent frost (Mendall and Aldous 1943). Although foods of the American woodcock during the non-breeding season have been studied (Pettingill 1936; Sperry 1940; Krohn 1970; Miller and Causey 1985), quantitative data on foods eaten by woodcocks during spring are lacking. The effects of weather during winter and spring on the availability of earthworms and the composition of the woodcock's diet are not documented.

We collected data on foods of the woodcock, availability of earthworms, and depth of frost in the soil on the Moosehorn National Wildlife Refuge (NWR). Our objective was to assess the effects of

weather on earthworm availability and its relation to woodcock diets and body mass of females.

Study Area and Methods

Woodcocks were collected on the Baring and Edmunds units of the Moosehorn NWR, Washington County, Maine. The refuge is in spruce-fir (*Picea-Abies*) forest. Farm abandonment, wildfire, and clear-cutting during the early 1900's produced stands of birch (*Betula* spp.), red maple (*Acer rubrum*), and aspen (*Populus* spp.); speckled alder (*Alnus rugosa*) is on the wetter sites (Dwyer et al. 1988). Clear-cutting for management of woodcock habitat has been extensive on the Baring Unit since 1978 (Sepik and Dwyer 1982).

Woodcocks were acquired from late-March to late-May 1987-89 by shooting them over a pointing dog, by collecting nesting females when they returned from an incubation recess, and by collecting incidental mortalities. Immediately after collection, 70% ethanol was forced down the esophagus to retard digestion of soft-bodied invertebrates. At the lab, birds were weighed on a top-loading balance to the nearest 0.1 g after the contents of the esophagus and stomach (proventriculus and ventriculus) were removed and preserved in 70% ethanol. The contents were later submerged in a shallow dish and examined with a stereomicroscope. All identifiable animal parts, vegetative matter, and grit were removed and separated. The volume was determined to the nearest 0.05 mL by water displacement in a graduated cylinder. The samples were dried to constant weight in a convection oven at 50° C and weighed to the nearest 0.1 mg. Volumes less than 0.05 mL and dry weights less than 0.1 mg were recorded as trace and later assigned the respective values of 0.03 mL or 0.05 mg for calculations of aggregate amounts. Unless otherwise stated, food percentage is presented as aggregate percent volume. Stomachs of woodcocks collected before 15 April (an approximate date for initiation of egg-laying in Maine; Mendall and Aldous 1943) that did not contain earthworms were examined for the presence of earthworm sitae.

We sampled earthworms on 50-m long transects in three known spring covers of woodcocks (one alder site and two aspen-maple sites). We collected samples from the 2nd week in April through the 3rd week in June (10 sampling periods). We sampled along each transect once in each sampling period in 1988 and twice in 1989. The earthworms were sampled with a 10-cm diameter soil corer that was plunged into the soil to a depth of 10 cm. Each sample consisted of 10 cores taken in five pairs, 1 m apart and perpendicular to a randomly selected point on the transect. We hand-sorted each core at the site and removed all earthworms. Earthworms were later dried to constant weight in a convection oven at 50° C. The average depth of frost below the litter-soil interface was determined from cores at each site. We used identical methods to sample earthworms at sites where we collected birds and centered pairs of cores on the approximate flush site. We sampled in flush sites within 24 h after a bird was collected.

Results

We collected 51 adult woodcocks; 5 males and 4 females in 1987, 8 males and 11 females in 1988, and 13 males and 10 females in 1989. Forty-three birds were shot over a pointing dog, five were collected when they returned to a nest after an incubation recess, and three were incidental mortalities. Forty-eight woodcocks contained identifiable animal remains in their upper digestive tract. Esophagi of 14 birds contained 56.7 mL (9.0 g dry weight) animal matter. Esophageal contents were mostly earthworms, although two esophagi contained Coleoptera larvae (Table 1). The stomachs of 46 birds contained 36.7 mL (4.5 g) of animal matter representing several taxonomic orders (Table 1). Earthworms occurred in 70% of the stomachs and composed >90% of the animal matter by weight and volume. Earthworms composed 97% of the combined animal matter in esophagi and stomachs. Spiders, adult beetles, beetle larvae, and dipterid larvae occurred in ≤46% of the stomachs but combined accounted for only 8% of the volume. Centipedes occurred in only 4% of the stomachs and composed a trace in the aggregate totals. The frequency of food items in the diet did not differ (X^2 = 10.65, df = 6, P = 0.10) between male and female woodcocks.

Grit and vegetative matter in stomachs totaled 2.2 mL (11.5 g dry weight) and were 6% of the total stomach contents. Vegetation was in about 50% of the stomachs and comprised small rootlets, seeds, and unidentified fragments.

During the pre-nesting period (before 15 April), foods were more diverse in woodcocks collected in 1989 than in woodcocks collected during the previous 2 years (Table 2). The mean volume of animal material in the digestive tracts was lower in 1989 (0.2 mL) than in 1987 and 1988 (1.1 mL; Mann-

Table 1. Percent volume (vol), dry weight (dwt), and frequency of occurrence (freq) of animal matter in the upper digestive tracts of woodcocks collected on the Moosehorn National Wildlife Refuge, Maine, from late-March through late-May 1987–89.

Taxa	Esophagus (n = 14)			Proventriculus and ventriculus (n = 46)		
	Vol	Dwt	Freq	Vol	Dwt	Freq
Oligochaeta	100	100	100	93	93	70
Chilopoda	0	0	0	tr[a]	tr[a]	4
Araneae	0	0	0	2	1	28
Coleoptera						
Larva	tr[a]	tr[a]	14	2	2	33
Adult	0	0	0	2	3	46
Diptera	0	0	0	2	2	33

[a]Trace, <0.5%.

Whitney U, df = 1, P = 0.001), and fewer woodcocks contained earthworms (X^2 = 10.22, df = 1, P = 0.001; Table 2). Similarly, the percent volume of earthworms was lower in 1989 (Mann-Whitney U, df = 1, P < 0.001) than in previous years (Table 2). Earthworm setae did not occur in 2 of 7 woodcocks collected before 15 April 1989. In contrast, all birds collected before 15 April 1987 and 1988 contained earthworms or their setae. The occurrence of spiders in woodcocks had a converse trend because it was greater (X^2 = 7.25, df = 1, P = 0.007) in 1989 than in previous years (Table 2). Ten of the 13 woodcocks with spiders were collected in March or April of 1989 and only 1 in 1987 and 2 in 1988. Similarly, percent volume of spiders (Mann-Whitney U, df = 1, P = 0.002) and beetle larvae and adults (Mann-Whitney U, df = 1, P < 0.001) were higher in 1989 than in previous years.

The masses of female woodcocks (without ovaries and oviducts) collected during March and April were lower in 1989 ($\overline{X}$ = 188.2, SE = 11.4 g, n = 5) than in the previous 2 years ($\overline{X}$ = 223.0, SE = 19.8 g, n = 8; t = 3.547, df = 11.0, P = 0.005). This difference was related to variable amounts of body fat (W. M. Vander Haegen, USDA Forest Service, Orono, Maine, unpublished data).

The biomass of earthworms was lower in 1989 than in 1988 (Mann-Whitney U, df = 1, P = 0.049). Earthworm abundance in 1989 remained low through April and did not reach 1988 levels until mid-May (Figure). Similarly, sampling at flush sites of birds collected before 15 April revealed no earthworms in 1989 (n = 5), whereas earthworms were collected at all examined flush sites in 1987 (n = 4; biomass data not available) and 1988 (n = 8; mean biomass = 8.3 g/m^2 dry weight). The depth

Table 2. Percent volume (vol) and frequency of occurrence (freq) of animal matter in the upper digestive tracts of woodcocks collected on the Moosehorn National Wildlife Refuge, Maine, before 15 April 1987–89.

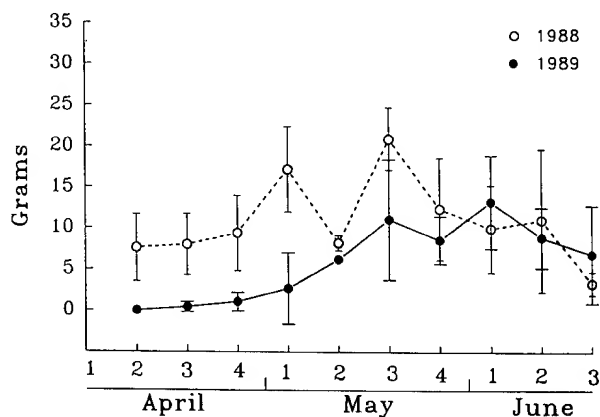| Taxa	1987 (n = 6)		1988 (n = 13)		1989 (n = 9)	
	Vol	Freq	Vol	Freq	Vol	Freq
Oligochaeta	94	83	98	85	42	22
Chilopoda	0	0	0	0	2	11
Araneae	2	17	tr[a]	15	16	67
Coleoptera						
Larva	1	33	1	23	14	33
Adult	2	83	tr[a]	15	18	78
Diptera	1	67	1	23	8	22

[a]Trace, < 0.5%.

Figure. Biomass (dry weight) of earthworms sampled at reference transects in three covers of woodcock habitat in spring, Moosehorn National Wildlife Refuge, Washington County, Maine. Numbers above months indicate sampling periods in weeks. Sampling along transects was conducted once each week in 1988 and twice each week in 1989. *Symbols* and *error bars* indicate mean ± 1 SE.

of frost below the litter-soil interface on examined transects in 1989 averaged 5 cm in the 2nd and 3rd week of April and 10 cm in the 4th week of April and was recorded at 10 cm on only one transect in the 1st week of May. All transects were devoid of frost to a depth of 10 cm by the 2nd week in May. In contrast, all transects were clear of frost to a depth of >10 cm by 13 April in 1988.

Discussion

Earthworms comprised over 90% of the total animal foods consumed by woodcocks in this study and in 20 woodcocks collected during April–July in an earlier study in Maine (Mendall and Aldous 1943). In contrast, earthworms comprised 64–88% of animal foods in woodcocks collected at other locations and times of the year (Pettingill 1936; Sperry 1940; Miller 1957; Krohn 1970; Pace and Wood 1979; Miller and Causey 1985). Beetles (larvae and adults) comprised less than 10% of the animal foods of woodcocks in our study and in most other studies (Pettingill 1939; Sperry 1940; Mendall and Aldous 1943; Miller and Causey 1985) but were of greater importance in birds collected on or entering summer roosting fields (Sheldon 1961; Krohn 1970). Mendall and Aldous (1943) found no adult beetles in woodcocks in Maine, whereas Krohn (1970) reported 1% by volume. Spiders occurred in 25% of the woodcocks

collected during 10 months from a large geographic area (Sperry 1940) but not in woodcocks collected on the wintering grounds (Pace and Wood 1979; Miller and Causey 1985). Percent volume of spiders reported by Mendall and Aldous (1943), Sperry (1940), and Krohn (1970) were similar to the overall value we report. Although ingestion of different invertebrates by woodcocks varied with location and season, the importance of earthworms in the diet of woodcocks during spring on northern breeding grounds is clear.

Low availability of earthworms in April and early May on our transects in 1989 was attributed to persistent frost in the soil. Precipitation in Washington County during winter 1989 (December–March) was 47% below the 29-year mean (U.S. Department of Commerce 1988, 1989) from reduced snowpack and frost in the soil that persisted longer than usual. Many earthworm species overwinter by migrating below the depth of frost (Edwards and Lofty 1977) and are not available to woodcocks until the frost dissipates. The availability of earthworms in 1989 did not match that of 1988 until frost dissipated to a depth of 10 cm. The reduced availability of earthworms in 1989 was further noted by the lack of earthworms at flush sites of collected woodcocks. Birds collected in feeding covers in 1987 and 1988 typically contained earthworms, indicating they had recently fed. Flush sites of five birds collected in 1989 were devoid of earthworms; and frost occurred in the upper 10 cm of soil at two of the five sites.

Low availability of earthworms in 1989 was reflected in the foods of woodcocks collected before 15 April. Overall, birds consumed less food in 1989. Although earthworms were still the most important item in the diet (42% by volume), the percent volume of beetle larvae and adults (32%) and spiders (16%) increased significantly from the previous 2 years. Several woodcocks contained earthworms or setae, suggesting that earthworms were available at some sites. Although seeps and stream margins were probably free of frost and may have provided suitable feeding sites, they probably did not provide sufficient numbers of earthworms. Snowstorms on 30 March and 8 April each deposited 20 cm of snow on the refuge and probably limited access to these sites for several days. Snow melted quickly, however, and a considerable amount of ground was bare within 2–3 days after each storm.

The high frequency of occurrence of beetles and spiders in woodcocks collected early in 1989 may have been the result of low availability of earth-

worms. Most consumed spiders were wolf spiders (Lycosidae; Vander Haegen and Jennings 1990) that live in leaf litter. Spiders and beetles living in leaf litter are probably less affected by soil frost and thus are available to woodcocks when the ground is frozen. Low volume of food in the upper digestive tracts and low masses of females in 1989, however, suggest that these foods were not available to foraging woodcocks in sufficient quantities to replace nutrients usually derived from earthworms.

Availability of food in breeding areas is important to female woodcocks preparing to nest. Fat and protein, whether of endogenous or exogenous origin, must be available in sufficient amounts to develop follicles. Furthermore, stored fats are used as energy by incubating females (Vander Haegen 1992). Masses of pre-nesting females were lower in 1989 than in the other years of the study, suggesting reduced availability of nutrients that year. As a result, initiation of nesting on the refuge in 1989 was 3–4 weeks later than usual (U.S. Fish and Wildlife Service, Orono, Maine, unpublished data) and suggested delayed follicle development. Delayed nesting can be detrimental to productivity by reducing time available to renest, an important component of reproduction in woodcocks (McAuley et al. 1990). Time available for renesting may be limited by low availability of earthworms in summer and energy requirements during molting before fall migration (Rabe et al. 1983).

Weather extremes can harm woodcocks. Low body mass associated with reduced availability of earthworms was reported of woodcocks during a drought in August 1978 (Sepik et al. 1983). During the drought, the biomass of earthworms in feeding covers averaged about 4 g/m^2 and effected a shift in habitat use, cessation of roosting flights, and delayed molt. The mean biomass of earthworms on our transects in spring 1989 remained well below this level through the 1st week in May. Deep snow cover in spring can delay nesting and limit available nesting cover, and snowstorms during the nesting period can cause abandonment or increased predation of clutches (Mendall and Aldous 1943; Gregg 1984). Our data suggest that winters with limited snowfall also can be detrimental because frost penetrates deep into the soil and limits availability of earthworms during the critical pre-nesting period. Reduced availability of food in early spring may explain low productivity observed on the refuge in 1989 when annual production indices, based on summer ratios of immature to mature females, were substantially below the mean of the previous 12 years (G. F. Sepik, Moosehorn NWR, unpublished data).

Acknowledgments

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Discrimination Between Constant-Zero and Non-Zero Survey Routes on Singing Grounds of the American Woodcock in Eastern Texas

by

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Abstract.   We used discriminant function analysis to characterize habitat and soil types of constant-zero and non-zero survey routes on singing grounds of the American woodcock (*Scolopax minor*) in eastern Texas. Woodcocks were surveyed twice on each of 60 routes. A discriminant function was derived based on occurrence of habitat and soil types along each route. Woodcocks were along routes with moderately drained fine sandy loam soils and unoccupied homesites but not along routes with poorly drained fine sandy loam, moderately drained fine loamy sand, excessively drained loam, and pastures. These results indicate that management of the woodcock in eastern Texas should focus on maintaining early- to mid-successional stage habitats on moderately drained fine sandy loam soils. In addition, discriminant function analysis may be helpful for making decisions about the selection or deletion of routes from a survey.

Key words: American woodcock, eastern Texas, discriminant function analysis, *Scolopax minor*, Singing-Ground Survey.

The North American Woodcock Singing-Ground Survey for monitoring population trends of the American woodcock (*Scolopax minor*) is based on counts of courting males heard at randomly located routes in the breeding range. Because routes are located randomly, many are in marginal habitat where few or no woodcocks are heard (Tautin et al. 1983). When no woodcocks are heard on a route for 2 consecutive years, surveys are not conducted along the route for the next 5 years; for analytical purposes, the constant count of zero woodcocks along this route is assumed (Tautin et al. 1983). In the sixth year, surveys along the route are resumed. If no woodcocks are heard in the 6th year, the count along the route continues to be considered a constant zero.

A long-term decline in the singing-ground survey index in the eastern region is attributed to a decline in suitable habitat (Dobell 1977; Owen 1977; Dwyer et al. 1983). Dobell (1977) developed a woodcock singing-ground habitat index based on crown cover classes of habitat, determined from aerial photographs, at each stop (listening point) along 54 routes in New Brunswick. The number of courting males and the habitat index significantly correlated ($r = 0.15$). Also with aerial photographs and multiple regression analysis, Dwyer et al. (1983) investigated relations between habitat types and counts of courting males at survey stops along 78 routes in nine northeastern states. Their model identified habitat types that were significantly related to the number of heard males ($R = 0.47$). However, these studies were conducted in the northern portions of the woodcock's range.

The singing-ground survey was adapted for use in eastern Texas (Tappe 1987; Tappe et al. 1989), and the Texas Parks and Wildlife Department began an operational survey in 1988. A technique for quantifying singing-ground habitat along survey routes in eastern Texas was described by Tappe and Whiting (1989). Each stop along a route was divided into four quadrats. The predominate habitat type in each quadrat was recorded according to categories outlined by Tappe (1987). The amount (percent) of a route consisting of a specific habitat type was then calculated by summing the number of quadrats for which that type was recorded and dividing the sum by the total number of quadrats on the route. Tappe and Whiting (1989) also used this method and correlation analyses to investigate the relations between habitat types and numbers of courting males in eastern Texas. However, no studies have been conducted of habitat or soil types by constant-zero (no woodcock recorded for 2 consecutive years) and non-zero singing-ground routes. We used discriminant function analysis (DFA) as an exploratory, descriptive model to characterize differences in variables between constant-zero and non-zero singing-ground routes in eastern Texas.

Methods

This study was conducted in the counties of Angelina, Cherokee, Nacogdoches, Rusk, San Augustine, and Shelby in eastern Texas. Thirty singing-ground routes (five in each county) were randomly located, and surveys were conducted along them in February 1986 and January–February 1987. During January–February 1988 and 1989, 30 routes in these counties were added. Thus, 60 surveys were conducted, two along each route. Ten stops were 0.6 km apart on each route. Surveys began 22 min after sunset. The number of courting male woodcocks heard during a 2-min interval at each stop was recorded at each route.

Habitat types at each route were quantified with the method of Tappe and Whiting (1989). Each quadrat was classified as being in a specific class, category, and sub-category as outlined by Tappe (1987). For example, a quadrat could be in the subcategory "seedling," category "pine monoculture," class "forested land." The percentage of each specific habitat type along each route was then determined. The designated habitat types in the analysis were pasture, brush, occupied homesite, unoccupied homesite, pine seedling, pine sapling, pine pole, pine-hardwood sapling, and pine-hardwood pole.

We used unpublished U.S. Soil Conservation Service soil maps to measure the length of each route in specific soil types and to determine the percent of each soil type along each route. Soils were classified by general soil types defined on the soil maps. Soil types in the analysis were poorly drained fine sandy loams, moderately drained fine sandy loams, moderately drained fine loamy sands, and excessively drained loams.

Because habitat and soil types were expressed as percentages, they were transformed to stabilize variances with the arcsine (arcsine square-root [relative frequency]) transformation. Habitat and soil types at constant-zero and non-zero routes were compared by analyzing data with stepwise DFA in the *Statistical Package for the Social Sciences* (SPSS; Norusis 1985). Variables were selected for inclusion in the discriminant function by maximizing Mahalanobis's distance between the two group centroids based on an F-to-enter ≥ 1.0. The jackknife procedure (Lachenbruch 1967) was used to reclassify observations for estimating the true classification rate of the derived model. Because DFA can produce spurious relations under certain conditions (Rexstad et al. 1988), only variables occurring on $\geq 25\%$ of the routes were selected for analysis (i.e., variables with a poor range of values over all observations were not selected). The relative importance of each variable for discriminating between routes with and without woodcocks was determined by the relative magnitude of the standardized discriminant function coefficients and by the correlations between values of the function and values of the variables. Fur-

thermore, only variables that were expected to affect the number of heard woodcocks were selected to facilitate interpretation of results (e.g., "open water" was excluded).

Results and Discussion

The mean number of heard woodcocks per route was 2.6 in 1986, 3.6 in 1987, 1.4 in 1988, and 1.5 in 1989. Woodcocks were heard in at least 1 of 2 years on 68.3% (41) of the routes but in neither of the 2 years on 31.7% (19) of the routes.

Analysis by stepwise DFA resulted in a six-variable function (Table). The two group means (constant-zero vs. non-zero) were different (Wilk's λ = 0.73, P = 0.007) and the canonical correlation between discriminant scores and groups indicated a moderate relation (r = 0.52). The covariance matrices were not significantly different (Box's M = 30.19, P = 0.21). The overall estimated classification success of the derived model was 71.7%; 80.5% (33) of the non-zero routes were correctly classified, and 52.6% (10) of the constant-zero routes were correctly classified. Because prior probabilities (based on sample sizes) of correct classification were 0.317 of constant-zero and 0.683 of non-zero routes (56.7% overall estimated classification success expected by chance), the derived discriminant function correctly classified group membership at a greater than the expected rate (χ^2 = 3.56, 1 df, P = 0.059). The correlation coefficients indicated that the percent of moderately drained fine sandy loam soils was the most important discriminating variable along a route (Table 1). However, the standardized function coefficients indicated that the percent of moderately drained fine loamy sand soils was the most important variable. The remaining variables were ranked similarly between the correlation coefficients and function coefficients. Moderately drained fine sandy loam soils and unoccupied homesites were on routes on which woodcocks were heard. Thus, negative correlation coefficients correspond with variables that characterize non-zero routes. The standardized function coefficient of the unoccupied homesite variable also is negative; however, the function coefficient of the fine sandy loam variable is positive. This indicates that the contribution of fine sandy loams and unoccupied homesites to the discriminant function is shared. Thus, because percent of fine sandy loams was the variable added to the function in the first step and its contribution to the function is shared

Table. Standardized coefficients and correlation coefficients of stepwise discriminant function analysis of habitat and soil types of constant-zero and non-zero survey routes on singing-grounds of the American woodcock in eastern Texas, 1986–89.

Habitat variable	Standardized coefficient	Correlation
Pasture	0.477	0.19
Unoccupied homesite	−0.838	−0.47
Poorly drained fine sandy loam	0.762	0.34
Moderately drained fine sandy loam	0.367	−0.52
Moderately drained fine loamy sand	1.129	0.36
Excessively drained loam	0.379	0.11

by the unoccupied homesite variable, the relative importance of the variables is probably more reliably reflected by the correlation coefficients than by the standardized function coefficients.

The habitat and soil types identified as important discriminant function variables agree with previously published descriptions of habitat and soil associations with woodcocks. Owen and Galbraith (1989) reported that earthworm biomass was greatest in moderately drained fine sandy loams. Boggus and Whiting (1982) suggested that percent of sand that exceeds certain limits restricts the probing of woodcocks. Our findings that routes with woodcocks have a higher percentage of fine sandy loam soils and a lower percentage of fine loamy sand soils than routes without woodcocks seem to agree with results of these studies. Sandy loam soils with a higher clay and silt content have a better water-holding capacity than loamy sand soils and probably support earthworms better. In addition, our finding that constant-zero routes have a higher percentage of poorly drained fine sandy loams and excessively drained loamy soils than non-zero routes agrees with the findings of Miller (1957) and is similar to Owen and Galbraith's (1989) results about the abundance of earthworms. Many studies revealed that most singing-grounds consist of early- to mid-successional stage habitats (Sheldon 1956; Marshall 1958; Maxfield 1961; Nicholson et al. 1977; Dwyer et al. 1983). Unoccupied homesites along routes in eastern Texas were related to high numbers of woodcocks, probably because the older homesites

are on fertile soils and the abandoned surrounding area is in an early- to mid-stage ecological succession that is typical of unoccupied homesites in eastern Texas. Although pasture, the result of grazing by cattle, may be considered an early successional stage, it was on routes without woodcocks.

Our findings suggest that management of habitat for the woodcock in eastern Texas should emphasize the maintenance of early- to mid-successional stage habitats on moderately drained fine sandy loam soils. In addition, discriminant function analysis may be helpful for making decisions about the selection or deletion of routes from a survey.

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Premigratory Dispersal and Fall Migration of American Woodcocks in Maine

by

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Abstract.   During 1982–84, 108 American woodcocks (*Scolopax minor*) were radiomarked in northeastern Maine to monitor premigratory dispersal. Dispersal did not differ by age or sex. Moves of greater than 10 km from centers of traditional activity were suspected of 5 juvenile males, 4 juvenile females, 3 adult males, and 1 adult female. In 1984, 12 woodcocks were monitored until migration. Migration peaked during the 1st week of November, and timing of migration did not differ by age or sex classes. Woodcocks that remain in Maine through early November are exposed to hunters throughout most of the hunting season.

Key words: American woodcock, dispersal, fall migration, hunting, *Scolopax minor*.

In general, dispersal is greater by young than by adult birds and greater by females than by males (Gauthreaux 1982). Dispersal of post-fledging American woodcocks (*Scolopax minor*) has been documented through banding (Mendall and Aldous 1943; Gregg 1984) and radio telemetry (Gregg 1984), but the magnitude and chronology of dispersal are unknown.

Before use of radio telemetry, the study of the chronology of the fall migration of American woodcocks was limited to the recovery of banded birds (Mendall and Aldous 1943; Sheldon 1967; Krohn et al. 1977). Nothing is known about age- and sex-specific timing of fall migration by woodcocks, but in shorebirds, females usually leave before males and adults leave before young (Gauthreaux 1982). The monitoring of radio-marked woodcocks provided information about the onset of fall migration but has been limited to studies in Pennsylvania (Coon et al. 1976) and Wisconsin (Gregg 1984). Our purpose was to determine the extent and timing of dispersal by woodcocks during summer and to determine when the age and sex cohorts of woodcocks migrated in the fall.

Study Area

We conducted our study at the Moosehorn National Wildlife Refuge (NWR) on the border of New

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Brunswick in northeastern Maine. The refuge is typical of much of the Northeast where forestry, farm abandonment, and wildfire created a diverse, second-growth forest. The refuge is composed of pure stands of spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) and hardwood stands of birch (*Betula* spp.), red maple (*Acer rubrum*), and aspen (*Populus* spp.), which are gradually being replaced by conifers. Management of the forest was initiated in 1976 to improve habitat for woodcocks by increasing age and species diversity of the forest. A detailed description of the area and the management is provided in Sepik et al. (1986) and Dwyer et al. (1988).

Methods

Woodcocks were captured with mist nets (Sheldon 1967), nightlighting (Rieffenberger and Kletzly 1967), and ground traps (Liscinsky and Bailey 1955) during 25 May–23 September 1982–84. All woodcocks were banded and their age and sex determined by plumage characteristics (Martin 1964). In 1982, four methods of radio attachment were used, and a system with a single-loop wire harness (Cochran 1972) and animal tag cement applied to the base of the transmitter was the most reliable (Derleth and Sepik 1990) and was used exclusively in 1983–84. Only woodcocks that were monitored >9 days were included in an analysis of dispersal.

Monitoring began at the end of May and ended on 1 September in 1982–83 and on 15 November in 1984. Woodcocks were located once during the day (1 h after sunrise to 1 h before sunset) and again at night (1 h after sunset to 1 h before sunrise). Having obtained a general direction of their location with a four- or seven-element Yagi antenna mounted on a vehicle, we located woodcocks by walking in the direction of their radio signals that we received with a three-element Yagi antenna (Derleth and Sepik 1990). Woodcocks were not flushed except by accident, unless they became inactive for >48 h. Individuals that could not be located from the ground were searched for with aerial techniques (Gilmer et al. 1981) except during September–November 1984 when only ground searches were made. Ground searches covered an area with a radius of about 10 km from the usual activity center of a lost individual, whereas aerial searches encompassed an area with a radius of 40 km. Woodcocks that were >10 km from their traditional activity sites or could not be located

were considered to have dispersed (move before 15 October) or migrated (move after 15 October).

Temperatures were obtained from a hygrothermograph at a weather station at the refuge. Age- and sex-specific dispersals were examined with Chi-square analysis. Dates of migration were ranked and analyzed with the Mann-Whitney U-Test. The accepted level of significance was 0.05.

Results

One hundred and forty-two woodcocks were radiomarked (35 adults and 107 juveniles), however, only 32 adults (16 males and 16 females) and 76 juveniles (40 males and 36 females) were used in the analysis of dispersal. The average (SD) observation period was 70.6 (45.6) days of adults and 38.8 (25.3) days of juveniles.

We detected no age-specific ($X^2 = 0.01$, 1 df, $P > 0.05$) or sex-specific ($X^2 = 0.56$, 1 df, $P > 0.05$) differences in premigratory dispersal. The number of radio-marked woodcocks that dispersed was small (Figs. 1 and 2). During 1 June–15 October 1982–84, contact was lost with 9 juveniles (5 males and 4 females) and 4 adults (3 males and 1 female). Two juvenile females and 1 juvenile male were relocated by aerial searches 22.1, 13.6, and 10.6 km, respectively, from their centers of traditional activity. Contact was not re-established with the other individuals. All juveniles moved during August and the 3 adult males moved in July. No moves of juveniles were recorded during 1983 or of adult males in 1984. No adult females dispersed during the summer of any year. In 1984, 1 juvenile male dispersed during early October and 1 adult female, in September.

Twelve woodcocks were monitored until migration in 1984 (3 juvenile males, 4 juvenile females, 2 adult males, 3 adult females). Migration proceeded in the following order: 1 juvenile female departed on 26 October; 1 juvenile male on 29 October; 1 adult female on 30 October; 1 juvenile female on 31 October; 1 adult female and 1 juvenile male on 2 November; 2 juvenile males, 2 adult males, and 1 juvenile female on 7 November; and 1 adult female on 14 November (Figs. 1 and 2). We noted no differences by age ($U = 11.5$, $P = 0.31$) or sex ($U = 22.5$, $P = 0.45$) class in the timing of migration.

The mean temperature in October 1984 was equal to the 31-year average (8° C). During the first 25 days of the month, only 1 radio-marked woodcock was suspected to have left the study area
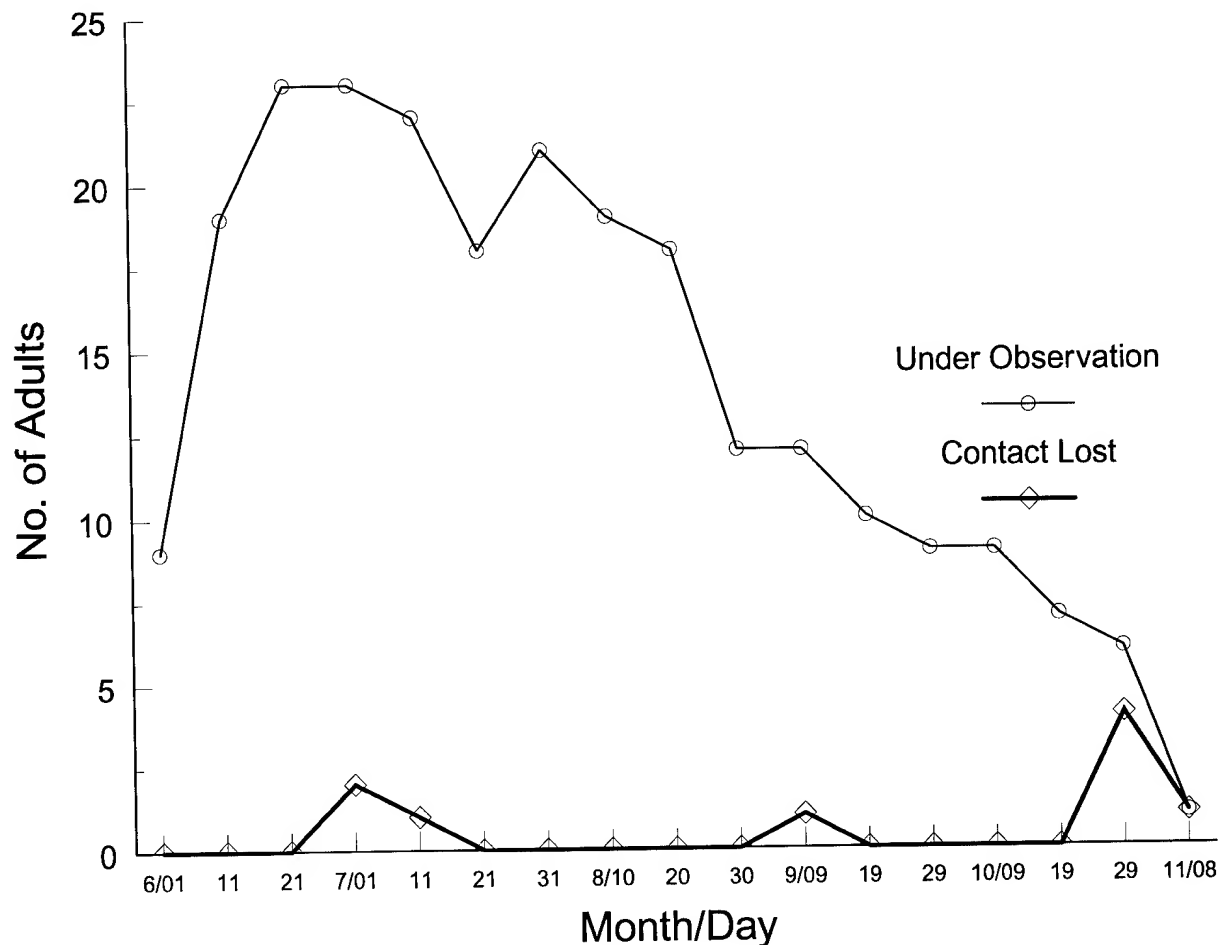
Fig. 1. Numbers of radio-marked adult woodcocks that were monitored and numbers of radio-marked adult woodcocks with which radio contact was lost, Moosehorn National Wildlife Refuge, 1982–84.

although temperatures at night were below freezing in 12 nights. However, 75% (n = 9) of the radio-marked individuals migrated during a 9-day period (30 October–7 November) when temperatures at night were consistently below freezing ($\bar{x}$ = –4° C).

No woodcocks were relocated after the start of migration. However, on the morning of 9 November, a juvenile female that was last located during the day on 7 November was shot near Hyde Park, New York, a linear distance of 680 km from its last known location.

Discussion

Woodcocks banded in the spring and summer were relocated during the same year at substantial distances from their capture sites (Mendall and Aldous 1943; Krohn and Clark 1977; Gregg 1984). The timing of these dispersals was unknown because most recoveries were during the hunting season; moves could have occurred during the summer or during migration. Likewise, the portion of the population that made premigratory moves was unknown. Gregg (1984) attributed the loss of signals from 6 of 17 radio-marked juveniles in Wisconsin to premigratory dispersal. Three of these birds were relocated after dispersal at distances of less than 10 km. The other three birds were not relocated. Gregg (1984) did not record any dispersal by seven radio-marked adults.

We found that premigratory dispersal of woodcocks was limited to only a small portion of the population. We assumed that the loss of a signal that could not be attributed to any specific cause meant a bird had moved. Some signal loss may
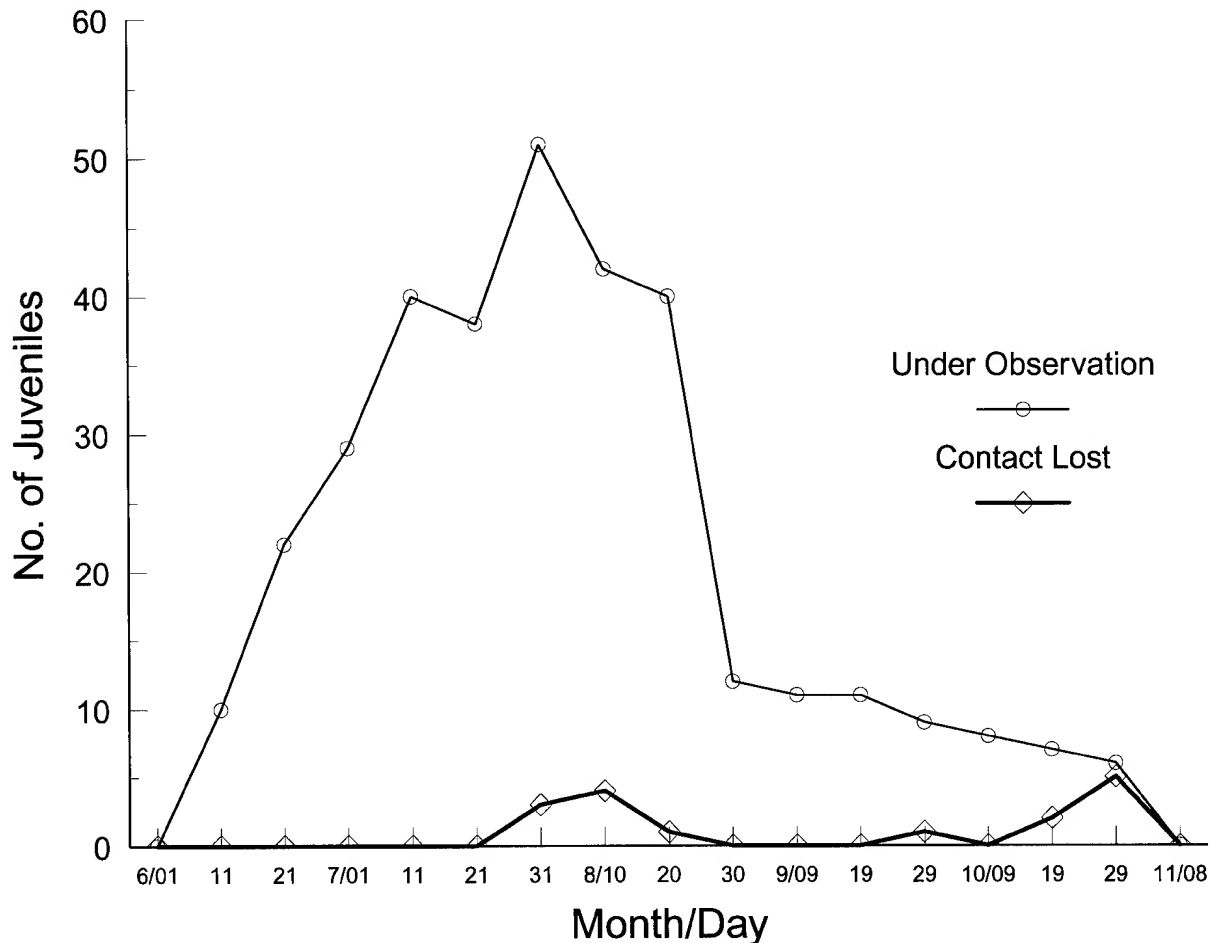
Fig. 2. Numbers of radio-marked juvenile woodcocks that were monitored and numbers of radio-marked juvenile woodcocks with which radio contact was lost, Moosehorn National Wildlife Refuge, 1982-84.

have been from radio failure or from damage to the radio by predators, therefore, our estimates of dispersal are liberal.

Dwyer et al. (1988) believed that juvenile male woodcocks dispersed widely during their 1st year. This conclusion was based on a lower than expected number of recaptures of 2nd-year birds that had been banded the previous year on singing grounds. During the summer, Gregg (1984) recaptured fewer than expected woodcocks that had been banded the previous year as juveniles. He also noted a lack of direct recoveries of juveniles north of his banding sites and concluded that dispersal took place in the spring. Our data support dispersal of young woodcocks in the year after they hatched.

The peak of migration by female woodcocks in Pennsylvania varied between 30 November-8 December 1973 and 18-29 November 1974 (Coon et al. 1976). Gregg (1984) monitored five radio-marked woodcocks until the onset of migration and found that migration in Wisconsin varied from 10 October to 9 November. We found that most woodcocks migrated during a 9-day period, which coincided with consistent temperatures below freezing at night. Coon et al. (1976) and Gregg (1984) also reported that cold weather preceded migration.

Coon et al. (1976) recorded flight speeds of 36 and 45 km/h during the migration of two radio-marked woodcocks. If the woodcock that was recovered near Hyde Park, New York, had flown at these speeds, the total flight time would have been 15-19 h during 2 days. Assuming that migration occurred only at night (Coon et al. 1976), the minimum average flight speed by this individual was 26 km/h (13 h of darkness/night for two nights).

Based on the number of direct recoveries of woodcocks banded in Wisconsin, Gregg (1984) be-

lieved that juveniles migrated before adults because more juveniles than adults were recovered during October. However, Gregg (1984) did not consider the fact that he banded more juveniles than adults, thus, his conclusions are questionable. We found no difference in departure dates by age- or sex-class. Body mass and deposition of fat of adults and juveniles peak by the end of October (Owen and Krohn 1973), therefore, there is no physiological need for staggered departures.

Current (1992) regulations limit the length of the hunting season for woodcocks to 45 days in the eastern management region. Traditionally, the season in Maine extends from about 1 October to 15 November, and most hunting occurs in October. Liscinsky (1972) believed that hunting of woodcocks before the influx of northern migrants limited populations of resident woodcocks in Pennsylvania. The validity of this is unverified, but, because of minimal dispersal in summer and migration in November, resident woodcocks are vulnerable to hunters during most of the season in Maine.

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Habitat Use, Home Range Size, and Patterns of Moves of the American Woodcock in Maine

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Abstract.   We determined the distances of daily moves, sizes of home ranges, and use of habitats of 88 radio-marked American woodcocks (*Scolopax minor*) at the Moosehorn National Wildlife Refuge during the summer and early fall of 1982–84. Age- and sex-specific sizes of total, nighttime, and daytime home ranges and mean distances between consecutive daytime, nighttime, nighttime and daytime, and daytime and nighttime locations of the woodcocks were calculated monthly. The sizes of the daytime home ranges were similar between the age and sex classes. However, in July the mean distances were greater between the daytime locations of adult males ($\overline{X}$ = 513 m) than between the daytime locations of juvenile males ($\overline{X}$ = 245 m) and greater between the daytime locations of adult females ($\overline{X}$ = 331 m) than between the daytime locations of juvenile females ($\overline{X}$ = 188 m). The sizes of nighttime and total home ranges and the mean distances between nighttime locations were not different among age and sex classes.

Crepuscular moves did not differ by age, but the mean crepuscular moves were longer by males of both age classes than by females. Irrespective of age or sex, the sizes of daytime home ranges and the distances between daytime locations were smallest by birds using balsam fir (*Abies balsamea*) and speckled alder (*Alnus rugosa*) cover and largest by birds using aspen (*Populus* spp.) cover. The mean sizes of the daytime home ranges ($\overline{X}$ = 14.6 ha) were smaller and the distances between daytime locations (179 m) were shorter by woodcocks using sapling stage stands than by woodcocks using pole ($\overline{X}$ = 18.2 ha and 231 m) and mature ($\overline{X}$ = 29.6 ha and 258 m) stands. Earthworm biomass and the woodcocks' use of habitats, sizes of daytime home ranges, and distances between daytime locations did not correlate. Openings for nighttime roosting were used less by females than by males. Differences in mobility and use of nighttime habitat were related more to sex than to age.

Key words: American woodcock, daytime habitat, home range, nighttime habitat, *Scolopax minor*.

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Habitat use by the American woodcock (*Scolopax minor*) during the summer and early fall was summarized by Owen (1977) and Sepik et al. (1989). Woodcocks spend the day feeding in dense stands of shrubby early-growth hardwoods that grow on moist soils with an abundance of earthworms. At dusk, woodcocks move to clearings or other forested cover to roost and, at sunrise, return to a feeding cover. Relations between nighttime roosting sites and daytime feeding covers and the variables that influence changes in habitat use by woodcocks are poorly documented. In this study, we monitored the activity of radio-marked woodcocks from late spring to mid-fall of 1982–84 to determine whether seasonal changes in sizes of home-ranges and patterns of moves were related to age and sex. We also measured habitat variables and earthworm biomass at sites that radio-marked woodcocks used to determine whether these parameters influenced the sizes of home ranges and patterns of moves.

Study Area and Methods

We conducted this study at the Moosehorn National Wildlife Refuge, which is in northeastern Maine near the border with New Brunswick. This area is typical of much of New England where farms abandoned during the early part of this century reverted to mature forest. During our study, management that improved habitat for woodcocks was initiated by increasing age and species diversity of the forest. Details of this program and the response of woodcocks to this management were documented by Sepik et al. (1977), Sepik and Dwyer (1982), Sepik et al. (1986), and Dwyer et al. (1988).

Radio-marked woodcocks were monitored from 1 June to 20 October 1982–83 and from 1 June to 15 November 1984. Capture techniques, radio-marking techniques, and monitoring procedures were described by Derleth and Sepik (1990).

The sizes of the total, daytime, and nighttime home ranges of each woodcock were calculated each month during June–October with the minimum-area method (Mohr 1947). Distances between consecutive (moves between locations on successive days or time periods) daytime, daytime and nighttime, nighttime and daytime, and nighttime locations of each bird also were determined by month. The sizes of nighttime and daytime locations and the mean distances of moves were calculated only for woodcocks that were located more than five times during 1 month. The sizes of the total home ranges were calculated only for birds for which more than five nighttime and five daytime locations were calculated. Data collection on home range size and daily moves of birds ceased when the individuals moved >10 km from their center of activity.

During June–August 1982–84, we used the formalin-extraction method (Raw 1959) to sample the abundance of earthworms at two 0.25-m^2 sites in daytime locations of randomly selected radio-marked woodcocks. The biomass (dry weight) of earthworms was estimated with the technique of Reynolds et al. (1977). The cover type at each site was defined by the Society of American Foresters classification system (Anonymous 1975). We added speckled alder (*Alnus rugosa*) as a forest type. The size class based on the diameter at breast height (dbh) of the forest stand (shrub, dbh <10 cm; pole, dbh >10 and <30 cm; mature, dbh >30 cm) was determined with a plotless sampling method (Dilworth and Bell 1977). Major understory species and the density of understory shrubs within a 4-m radius of each location were also recorded .

During June–October 1984, the type of habitat the radio-marked woodcocks used at nighttime was recorded by type of opening (blueberry [*Vaccinium* sp.] field, clear-cutting, marsh, natural opening, other opening) or as forested habitat.

We used the analysis of variance (ANOVA) to examine home range sizes, distances between locations, use of cover type, use of understory type, use of forest stand by size class, and use of nighttime habitat by age and sex of the woodcocks. Means were tested among months. We used the Tukey HSD test as a post-hoc test when ANOVA revealed differences among groups and t-tests to compare the mean difference between two groups. If variables among years or among months were not different, data were pooled for age-specific and sex-specific comparisons. When home-range sizes and mean distances of moves were not different among years, we pooled data of all 3 years. Between-month comparisons were made when seasonal differences were detected. The Pearson correlation matrix was used to examine relations among earthworm biomass, home-range sizes, and distances between locations. Regression analysis was used to detect changes in earthworm biomass over time. We used a logarithmic transformation of all measurements of home range size, distances between ranges, and earthworm biomass because data were not normally distrib-

uted. The accepted level of significance for all analyses was $P = 0.05$.

Results and Discussion

Home Range and Movement

We calculated the sizes of home ranges and distances between locations of 88 American woodcocks (32 juvenile males, 30 juvenile females, 12 adult males, 14 adult females; Table 1). The average (SD) observation period of juvenile males was 45.6 (25.2) days; of juvenile females, 48.5 (28.6) days; of adult males, 99.8 (39.0) days; and of adult females, 76.8 (42.9) days. The monthly mean home range sizes and mean distances between locations did not differ among years (ANOVA, $P > 0.05$) by age class and by sex class.

Sizes of Daytime Home Ranges and Distances between Daytime Locations

We expected the sizes of the daytime home ranges and the distances between consecutive daytime locations to increase through the season because of seasonal declines in the abundance of earthworms (Reynolds et al. 1977). However, the sizes of the daytime home ranges of juvenile males ($F = 0.762$, $P = 0.554$), adult males ($F = 0.841$, $P = 0.508$) and adult females ($F = 1.455$, $P = 0.236$) did not differ between months (Table 1). The sizes of the daytime home ranges of juvenile females differed among months ($F = 6.267$, $P < 0.001$), and differences were related to the small home ranges in June and October (Table 1).

The mean distances between the daytime locations of juvenile males ($F = 0.823$, $P = 0.516$), juvenile females ($F = 2.351$, $P = 0.066$), and adult females ($F = 2.181$, $P = 0.091$) did not differ among months. The distances between the consecutive daytime locations of adult males differed by month ($F = 2.891$, $P = 0.035$) as a result of substantially longer moves in July (Table 1).

We expected the daytime home ranges and the distances between the daytime locations to be larger by juveniles than by adults because Owen and Morgan (1975) reported that radio-marked adult woodcocks were more sedentary than juveniles. We detected no differences between the monthly mean sizes of the daytime home ranges (Table 1) of adult and juvenile males ($t = -0.912$, $P = 0.364$). Adult females had smaller daytime home ranges than juvenile females only in June ($t = -2.773$, $P = 0.018$).

The monthly mean distances between consecutive daytime locations of females did not differ ($t = -0.203$, $P = 0.839$). In July, the mean distances were larger between consecutive daytime locations of adult than of juvenile males ($t = 2.670$, $P = 0.014$).

Gregg (1984) measured the sizes of daytime home ranges of 16 radio-marked woodcocks in Wisconsin from late spring to mid-fall and reported the mean sizes of daytime home ranges of all age and sex classes combined was 13 ha, which is similar to our findings (Table 1).

Evidently, all age and sex classes of woodcocks were able to find adequate food throughout the summer and fall within a relatively small area. However, in July the distances were larger between consecutive daytime locations of adult males ($\overline{X} = 513$ m) than of juveniles males ($\overline{X} = 245$ m; Table 1). In July adult females moved farther ($\overline{X} = 331$ m) than juvenile females ($\overline{X} = 188$ m), but high variability precluded statistical significance. During this period when postnuptial molt begins (Owen and Krohn 1973) and availability of earthworms is limited, adults are at their minimum mass. Therefore, the increased distances between daytime locations of adults may be related to the need to forage more widely to find sufficient food. Although this search does not encompass a larger area than that of juveniles, it is more intensive.

Sizes of Nighttime Home Ranges and Distances Between Nighttime Locations

Gregg (1984) captured few adult woodcocks in mist nets at nighttime roost sites during the summer. He attributed the low capture rate to decreased mobility caused by postnuptial molt. Therefore, we expected differences in the sizes of nighttime home ranges by age and by month. When we found none (Table 1), we concluded that the postnuptial molt does not influence the nighttime mobility of adults and, thus, does not explain the different rates of capture by Gregg (1984).

Sizes of Total Home Ranges and Distances of Crepuscular Moves

If seasonal age-specific or sex-specific variations in mobility and energetic requirements exist, they should be reflected in changes in the sizes of total home ranges and in crepuscular moves. However, we detected no differences in the sizes of the total home ranges of adult and juvenile males and of adult females (Table 1). The sizes of the total home ranges of juvenile females changed monthly ($F = 8.668$, $P < 0.001$); home ranges were smaller in June

Table 1. Distances between locations, mean sizes of home ranges (minimum convex polygon), and number of observations (n) of radio-marked American woodcocks, Moosehorn National Wildlife Refuge, 1982–84.

Age–Sex class month	Distances (m) between locations				Size (ha) of home range		
	Daytime and daytime	Nighttime and nighttime	Daytime and nighttime	Nighttime and daytime	Nighttime home range	Daytime home range	Total ha
Juvenile male							
June	147	166	398[c]	395[h]	7	7	27
July	245[o]	374	645	619	41	17	74
August	180	365	546	516	38	18	72
September	146	719	593	620	41	7	91
October	153	548[b]	819[d]	843[i]	68[m]	19	120[l]
Mean	180	342[a]	560	544	32	13	67
n	992	528	713	690	820	1,141	1,859
Juvenile female							
June	59	135	137[c]	154[h]	3	0.4[n]	5
July	185	320	450	510	43	14	76
August	168	731	436	452	26	18	64
September	178	355	249	494	16	14	81
October	94	135[b]	214[d]	203[i]	7[m]	1	14[l]
Mean	157	266	359[a]	417[a]	17[a]	8[a]	40[a]
n	913	603	794	665	802	1,024	1,897
Adult male							
June	252	228	450[e]	436	28	35	81
July	513[o]	491	987[f]	1,020[j]	29	22	103
August	187	391	505	504	81	16	102
September	202	398	473[g]	465[k]	51	12	69
October	184	500	198	217	9	7	17
Mean	265[a]	351	387[a]	510[a]	34	19	74
n	761	454	590	564	622	857	1,529
Adult female							
June	153	175	159[e]	204	18	14[n]	34
July	331	396	594[f]	606[j]	39	39	108
August	132	369	280	325	30	11	41
September	134	202	170[g]	201[k]	14	7	38
October	120	192	189	208	8	7	17
Mean	162	264	254	293	21	13	42
n	727	532	625	588	659	838	1,472

[a] Among month differences ($P < 0.05$).

[b–o] Values with the same letters are significantly different ($P < 0.05$).

and October (Table 1). The sizes of the total home ranges did not differ by age or by sex.

Distances between daytime and nighttime locations and between nighttime and daytime locations of juvenile males ($F = 1.101$, $P = 0.369$ and $F = 1.254$, $P = 0.303$, respectively) and adult females ($F = 2.642$, $P = 0.054$ and $F = 2.116$, $P = 0.104$, respectively) did not differ among months. However, monthly differences in the distances between day-

time and nighttime ($F = 4.825$, $P = 0.004$) and nighttime and daytime ($F = 4.415$, $P = 0.006$) locations of adult males were caused primarily by longer distances in July (Table 1). Monthly differences in the distances between daytime and nighttime ($F = 3.740$, $P = 0.010$) and nighttime and daytime ($F = 4.740$, $P = 0.003$) locations of juvenile females were caused by shorter distances in June and October. Distances between locations were sex-

specific (ANOVA, P < 0.05) and were reflected in longer crepuscular moves by males than by females (Table 1).

Direct comparisons of our data with data of previous studies are not possible because of different methodologies. However, Owen and Morgan (1975) reported a difference between the sizes of the total home ranges of adult and juvenile woodcocks during the summer in Maine. These researchers' measurement of total home range, however, was a composite of the locations of all radio-marked birds. Furthermore, they did not test for differences between sexes within each age class. Dunford and Owen (1973) reported no differences in crepuscular moves between juvenile males and females, but data were not analyzed statistically. Owen and Morgan (1975) reported that adult woodcocks moved an average of 170 m from daytime to nighttime sites. However, they did not examine differences in crepuscular moves by month or by sex. Without this analysis, their conclusion that juveniles are more mobile than adults is questionable. Our data suggest that differences in mobility are sex-specific but not age-specific and are reflected in crepuscular moves (Table 1).

Daytime Habitat Use and Earthworm Biomass

We expected that woodcocks that used high quality habitat would move less between daytime locations and have smaller daytime home ranges than woodcocks that used habitat of lower quality. The sizes of the daytime home ranges ($F = 2.675$, $P = 0.016$) and the distances between the consecutive daytime locations ($F = 3.344$, $P = 0.004$) varied among cover types (Table 2). Daytime home ranges were smaller and distances between them were shorter in alder and in balsam fir (*Abies balsamea*), which is a low-value cover type for woodcocks, than in aspen (*Populus* spp.), which is a high-value cover type (Table 2).

Size class of trees within the various cover types may have affected the home range sizes and moves of woodcocks. Woodcocks moved shorter mean distances ($F = 4.169$, $P = 0.011$) and had smaller home ranges ($F = 3.032$, $P = 0.050$) on sites of sapling-stage trees (dbh < 10 cm) than on sites with larger trees (Table 3). Only 8% of the aspen sites used by radio-marked woodcocks were in the sapling stage, whereas 42% of the balsam-fir stands were in the sapling stage. The sizes of the daytime home ranges ($F = 1.707$, $P = 0.098$) and distances between daytime locations ($F = 1.848$, $P = 0.070$) of woodcocks

using different types of understories did not differ. We did not find meaningful correlations between the density of the understory shrubs and the sizes of the daytime home ranges ($r = 0.149$) or the distances between daytime locations ($r = 0.101$).

We expected that the daytime home ranges and the distances between daytime locations would increase as earthworm biomass decreased, that earthworm biomass at sites the radio-marked woodcocks used would decrease through the season, and that earthworm biomass would differ among cover types, size classes of forests, and understory shrub densities. The daytime home ranges ($r = -0.089$, $P = 0.203$) and the distances between the daytime locations ($r = -0.094$, $P = 0.177$) did not correlate with earthworm biomass. Earthworm biomass ($\overline{X} = 8.9$ g/m^2, dry weight) at flush sites did not vary during the season ($r = 0.028$, $P = 0.069$). Earthworm biomass did not differ among cover types ($F = 0.342$, $P = 0.960$), forest size classes ($F = 0.993$, $P = 0.372$), or understory shrub classes ($F = 1.599$, $P = 0.101$). Likewise, density of understory shrubs and earthworm biomass did not correlate ($r = 0.036$, $P = 0.599$).

Earthworm biomass ($\overline{X} = 8.9$ g/m^2) that we measured at sites used by radio-marked woodcocks was similar to earthworm biomass measured at

Table 2. Mean distances between daytime locations and mean sizes of daytime home ranges (minimum convex polygon) of radio-marked American woodcocks (all age–sex groups combined) by type of cover, Moosehorn National Wildlife Refuge, June–August 1982-84.

Society of American Foresters[a] forest cover types	Mean distance (m) between daytime locations (n)	Mean size (ha) of daytime home range (n)
Balsam fir	179[b] (24)	10.8[c] (23)
Aspen	267 (50)	36.3 (53)
Grey birch–red maple	232 (30)	16.0 (32)
White pine	259 (21)	29.1 (21)
Red spruce	203 (9)	14.1 (9)
Red spruce–balsam fir	216 (25)	14.8 (25)
Alder	162 (46)	11.8 (46)

[a] Anonymous 1975.
[b] Among cover type differences ($F = 2.675$, $P = 0.016$).
[c] Among cover type differences ($F = 3.344$, $P = 0.004$).
[n] Sample size.

Table 3. Mean distances between consecutive daytime locations and mean sizes of daytime home ranges (minimum convex polygon) of American woodcocks by size class of forest, Moosehorn National Wildlife Refuge, June–August 1982–84.

Size class (dbh in cm)	Mean distance (m) between daytime locations (n)		Mean size (ha) of daytime home range (n)	
<10	179[a]	(83)	14.6[b]	(86)
10–30	231	(93)	18.2	(94)
>30	258	(46)	29.6	(47)

[a] Differences among all size classes ($F = 4.169$, $P = 0.011$).
[b] Differences among all size classes ($F = 3.032$, $P = 0.050$).
[n] Sample size.

flush sites in New York ($\overline{X} = 8.23$ g/m^2, dry weight; Parris 1986) and in northern Maine ($\overline{X} = 8.4$ g/m^2, dry weight; Nicholson et al. 1977). Reynolds et al. (1977), also working in Maine, reported that sites rarely used by radio-marked woodcocks had an average earthworm biomass of 7.8 g/m^2, commonly used sites had an average biomass of 15.4 g/m^2, and heavily used areas had a biomass of 18.2 g/m^2. However, because these researchers randomly sampled the sites used by radio-marked woodcocks more than 1 year after the sites were used, these data are not comparable to ours.

Our data suggest that during periods of average precipitation, adequate numbers of earthworms are available to support woodcocks in a variety of habitat types. In certain cover types (i.e., aspen >10 cm dbh) woodcocks must move extensively to find adequate foods, but the high survival rates of woodcocks during our study (Derleth and Sepik 1990) suggest that survival and mobility may be unrelated during normal weather.

Nighttime Behavior and Habitat Use

Studies revealed that banded juvenile males were most numerous and banded juvenile and adult females were more numerous than banded adult males in nighttime roosting fields (Krohn 1971; Gregg 1984; Dwyer et al. 1988). This disparity in capture rates was attributed to either greater susceptibility of juvenile males to capture (Krohn 1971; Dunford and Owen 1973) or to decreased mobility of adults during the postnuptial molt (Gregg 1984).

We believe that differences in the sex ratio of juvenile woodcocks captured in nighttime roosting fields result from sex-specific differences in habitat use. We found that the frequency of use of openings by juvenile males and females did not differ by month ($F = 1.381, P = 0.279$ and $F = 1.171, P = 0.171$, respectively). However, juvenile males used openings more often ($\overline{X} = 70\%$) than juvenile females ($\overline{X} = 50\%, F = 2.428, P = 0.033$; Table 4). This difference (20%) is similar to the difference in the number of juvenile males and females captured with mist nets (22%) and by nightlighting (28%) in the same study area by Dwyer et al. (1988). Thus, juvenile males and females were caught in nighttime roost sites at about the same frequency as the birds used the openings.

Although the capture of adult males in roosting fields is the lowest of any age–sex class, the frequency of use of openings by adult males did not differ from that of juvenile males ($F = 2.271, P = 0.051$; Table 4). Adult and juvenile males did not differ in the distances they traveled from daytime to nighttime or from nighttime to daytime locations. Dwyer et al. (1988) reported that the sex ratio of adult woodcocks caught in ground traps in feeding covers, which probably provides an unbiased sex and age ratio of the population, did not differ from ratios of adults caught with mist nets and by nightlighting. Thus, we conclude that few adult males are caught in roosting fields because they are the smallest cohort in the population and not because they are more difficult to capture or less mobile during molt.

Use of forest openings by adult females varied by month ($F = 8.731, P < 0.001$) and was less than that of adult males in June ($t = 3.638, P = 0.005$), August ($t = 4.94, P < 0.000$), and September ($t = 2.411, P = 0.042$; Table 4). Adult females also used openings less frequently than juvenile females in August ($t = 2.445, P = 0.031$). Because of this difference in use of openings by adult females, we expected the sex ratio of adults caught in roosting fields to differ from the sex ratio of adults caught in feeding covers. However, Dwyer et al. (1988) reported that sex ratios of adults did not differ by capture technique. This inconsistency may be explained by the capture technique used in roosting fields. The rates of capture with mist nets are greater in July when use of openings by adult males and females was similar, but the rates of capture with mist nets are lower in June and August.

The difference in the use of openings in August between adult ($\overline{X} = 26\%$) and juvenile females ($\overline{X} = 54\%, t = 2.445, P = 0.031$; Table 4) may be a result

Table 4. Frequency (%) of use of openings at nighttime by radio-marked American woodcocks, Moosehorn National Wildlife Refuge, 1982–84.

Age–Sex	June	July	August	September	October	Mean
			Month			
Juvenile male	100	81	58	76	53	70[e]
Juvenile female	55	61	54[b]	47	28	50 [e]
Adult male	76[a]	83	64[c]	51[d]	30	60[f]
Adult female	36[a]	87	26[c,b]	20[d]	39	42[g]

[a–e] Values with the same letters are significantly different (*P* <0.05).

[f] Between month difference (*P* = 0.009).

[g] Between month difference (*P* < 0.001).

of increased demands for energy by molting adult females. Although adult females still make crepuscular moves, these moves are to forested sites where feeding may occur. Feeding at night by adult females may be necessary to gain the fat reserves for migration. Adult males may not be affected similarly because males do not have the energy demands of laying eggs and rearing broods. Additional research into female behavior and use of nighttime habitat is needed.

The greater use of forest openings at night by male woodcocks suggests that these sites provide some benefit for males. Wishart and Bider (1977) reported courtship in roosting fields throughout summer and into fall, thus, males may try to maintain or establish courting areas after the breeding period. Dwyer et al. (1988) believed that females played an important role in determining whether a male used an opening for courtship during the breeding season. Females, therefore, also may play a role during the post-breeding season by briefly interacting with males during crepuscular flights in summer and fall. Both the distances between the nighttime locations and the sizes of nighttime home ranges were larger by all age and sex groups than the sizes of daytime home ranges and distances between daytime locations, suggesting some type of habitat exploration or social interactions. Conversely, not all roosting sites are used as singing grounds in the spring, and not all singing grounds are used as summer roosting sites.

Conclusions and Recommendations

Monthly, age-specific, and sex-specific differences in the lengths of moves and sizes of home ranges were minimal. Significant differences were predominantly related to sex. Failure to detect differences may have been related to weather because rainfall was near normal during the study and woodcocks were not stressed by a drought. Furthermore, differences may not have been detected because the number of radio-marked woodcocks was small. Variability in the patterns of moves among individuals was large, and some individuals changed their patterns of moves periodically. For instance, it was not unusual for a woodcock to use the same daytime cover for 2–3 weeks and then use several different covers during the next week. Some individuals rarely used the same roosting field or daytime cover. These patterns of behavior are probably common and thus greatly increase variances in the sizes of home ranges and moved distances, resulting in the lack of statistical differences.

Woodcocks used a variety of cover types, but the abundance of earthworms among sites did not differ. The only habitat variables associated with differences in the sizes of daytime home ranges and distances between them were the size classes of the overstory and cover type. These two variables may be good indicators of the quality of woodcock habitat, but our study site was in an area that was predominantly mature woodlands. After critically reviewing research into habitat use in the Northeast, Sepik et al. (1989) emphasized that woodcocks use the best available habitat, which may not be the best habitat. Woodcocks also may be able to survive in several different types of habitat when weather is average but may require some specific habitat component during adverse weather. For instance, Sepik et al. (1983) reported that woodcocks used conifer cover extensively during a summer drought but did not use conifers during years of average precipitation.

During two periods, moves and behavior seemed to be affected by energy requirements of adults. In July, adult males and females traveled farther between consecutive daytime locations than juveniles of the same sex. This indicates that adults may need to forage more then because of their low body mass. Adult females used forest openings less in August than either adult males or juvenile females; this corresponds to the period of postnuptial molt of adult females. However, adult females still made crepuscular flights, suggesting they moved to different sites to feed.

Differential capture rates of age and sex classes in roosting fields are the result of sex-specific differences in use of openings and of the sizes of the different cohorts in the population. Females are less prone to capture during most months because they use forest openings less than males. Both adult and juvenile males use openings at the same frequency, but adult males are far less numerous in the population than other age-sex classes and, thus, fewer are captured.

Studies similar to this study should be repeated in habitats of different types and qualities. Survival rates should be measured at the same time to assess habitat quality and the effects of weather on the population. Studies of this type during periods when woodcocks are stressed can help define limiting factors and critical habitats.

Acknowledgments

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Survey of Woodcock Habitat with Landsat: Possibilities and Limitations of Remote Sensing

by

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Abstract. We describe a general procedure for surveying American woodcock (*Scolopax minor*) habitat with Landsat satellite imagery. The procedure is supervised, digital classification of six steps that alternated from field classification of habitats to analysis of remote sensing imagery and extented from qualitative to quantitative evaluation. Five land-cover categories were selected: woodcock habitat (early successional forest), forest, agriculture, urban and bare ground, and water. Because numerical data were specific to each image, the entire procedure was repeated each time we used a different image. Remote sensing is a suitable and economical technique for surveying potential woodcock habitat on a large scale. The results of two inventories revealed that potential woodcock habitat constituted only 3% and 4% of the total areas. At least 80% of those habitats were occupied by woodcocks, as evidenced by splashings, probe holes, and flushed birds.

Key words: American woodcock, habitat survey, Landsat imagery, remote sensing.

The management of the American woodcock (*Scolopax minor*) requires knowledge of the status of populations and the amount of available habitat. The annual singing-ground survey provides a reliable index of the size of the displaying male woodcock population in spring (Tautin et al. 1983; Shissler and Samuel 1985). Habitat requirements of the woodcock are generally known, but our knowledge has gaps (Cade 1985; Sepik et al. 1989). Information on amount of available habitat, however, is limited. Data on habitat abundance are needed because the decline in numbers of woodcocks in the eastern management region during the last 20 years is attributed largely to losses in amount of habitat (Dwyer et al. 1983).

Thus, a cost-effective technique that biologists can apply to observe and to quantify changes in woodcock habitat is necessary. Dobell (1977) used aerial photography to measure habitat along singing-ground survey routes in New Brunswick. Satellite imagery, however, was suggested to yield adequate and rapid results over a large area at a

lower cost (Laperriere 1976). Remote sensing with satellite imagery was first used to study caribou (*Rangifer tarandus*) habitat (Lent and Laperriere 1974). Research into habitats of the wood stork (*Mycteria americana*; Jensen et al. 1986), ruffed grouse (*Bonasa umbellus*; Palmeirin 1985), and wild turkey (*Meleagris gallopavo*; Katibah and Graves 1978) are recent examples of efficient use of remote sensing for surveying wildlife habitats.

Our objective was to describe a procedure with remote-sensing imagery from a satellite for surveying woodcock habitat. The possibilities and the limits of this technique also were appraised. Our report addresses the user of remote sensing and not the designer. Therefore, most of the technical aspects of imagery analyses are omitted.

Material and Methods

Landsat is an unmanned satellite system that operates in the international public domain. Users anywhere in the world may purchase imagery at uniform prices and priorities. The thematic mapper (TM) systems of the satellite platform of Landsats 4 and 5 record images of 185 km (north–south) by 185 km (east–west). Each image consists of pixels (picture elements), arranged in regular rows and columns. Each pixel is a 30 × 30 m square. For each pixel, the scanner measures the intensity of reflectance for six channels, each of which corresponds to a different band of the electromagnetic spectrum, including the visible near and mean infrared regions and the thermal infrared. Each channel provides particular information on the features of the surface of the land. The images are recorded in digital form and then processed by computers to produce a film image.

Initially, we used a Landsat-4 TM image (4 August 1984) of a study area (3,807 km^2) in the Saint Lawrence lowlands northwest of Montreal (Quebec) that included urban areas, farm-forests, and forests. This first study enabled us to examine the applicability of remote sensing for the study of woodcock habitat (Babin and Couture 1987; Perras et al. 1988). A confirmation of those possibilities was obtained during a second experiment with a Landsat-5 TM image (25 August 1984) of only farm-forest area (2,676 km^2) southeast of Trois-Rivieres (Quebec). In both experiments, only a small portion of the images was used because of a limited budget. Images were recorded when vegetation had fully developed. Field work was started in 1985 for the first experiment and in 1988 for the

second experiment. We believe that the delay between the year the images were taken and the year field work was done did not influence the technical aspects of this research. We used the results of these two experiments in desiging a general procedure that could be used by anyone who wanted to use remote sensing imagery to survey woodcock habitat. Digital image processing was conducted at the Centre d'applications et de recherches en Télédétection of the Sherbrooke University (Quebec). The ARIES-III (Dipix Co.) software image-processing program was used.

We used a six-step process (Fig. 1) for evaluating habitat in the field (odd numbers) and for analyzing remote-sensing imagery (even numbers) in the laboratory. We explain each of the different steps.

Training Site Selection (Step 1)

We used supervised digital classification. The first step in a supervised classification is to select a representative site, called training site, of each land-cover category. The analyst then enters training site information in the computer to define the image. The categories of land cover we chose were woodcock habitat (early successional forest), forest (>25 years), agriculture, water, and urban and bare ground. This last land-cover category included cities, roads, and other hard surfaces. Forest and agriculture classes were used to distinguish woodcock habitat. The remaining classes were more general and offered reference marks that facilitated the interpretation of thematic maps.

All training sites of the different land-cover categories were determined from available ground information, except woodcock habitat, which was selected and measured according to a precise procedure. Woodcock habitat was defined as sites where we found nests and broods or where we flushed woodcocks during spring–fall. Variables at each training site (Table 1) were measured according to Bourgeois (1977), Coon et al. (1982), Kinsley et al. (1982), and Gutzwiller et al. (1983). Habitat measurement was according to Kinsley et al. (1982). A square 0.04-ha plot with the principal contact point at the center was established at each nesting, brooding, and flush site. The plot was divided into 100-m^2 quarters that were subdivided into 25-m^2 and 6.25-m^2 subplots. Large trees, medium and small trees, and shrubs in the plot were sampled on four random 25-m^2 and 6.25-m^2 subplots in each quarter. Data on cover and herbaceous height in four random 6.25-m^2 subplots also were collected. Cover was estimated; height and

Fig. 1. Flow diagram of the general procedure for a survey of woodcock habitat with remote sensing.

Table 1. Variables measured on woodcock habitat training sites and on validation sites selected as potential woodcock habitat from remote-sensing imagery in the Saint Lawrence lowlands northwest of Montreal, 1987.

Cover (percentage of total of four 6.25-m^2 plots)
    bare ground
    herbaceous vegetation
    small woody stem (<0.3 m)
Height
    herbaceous vegetation (average, cm)
    of nearest edge (m)
Density (expressed as number of stems per 25 m^2)
    small shrubs (≥0.3 m but <1.25 m)
    small trees (≥2.5 m and <7.6 cm DBH)
    medium trees (≥7.6 cm DBH and ≤15.2 cm DBH)
    large trees (≥15.2 cm DBH)
    total number of trees
DBH (cm), mean of all trees
Basal area, total (m^2/ha)
Number of tree species
Distance
    to nearest edge (m)
    to water (m)

Each land-cover category was represented by more than one training site to cover the full range of reflectance characteristics. Geographic positions and sizes of training sites were determined from aerial photographs.

Preliminary Classification (Step 2)

The training sites of each land-cover category were localized on a composite color projection of the image on a video screen (Fig. 2a). Spectral values for each pixel in each spectral band at a training site were used to define the decision space (range of values) for that category. After the clusters for each training site were defined, the computer assigned the remaining pixels in the scene to a land-cover category. Next, a thematic map that depicted each land-cover category as a different color was produced (Fig. 2b).

Qualitative Verification (Step 3)

The objective of the third step of the procedure was to refine the preliminary classification. We verified all areas of the different land-cover categories to ensure they were correctly classified. To do so, 100 sites were randomly located in woodcock

distances were measured with a tape. Twenty-six nesting, 17 brooding, and 22 flush sites were measured. That sample represented the description of an area of 315 pixels of woodcock habitat training sites.
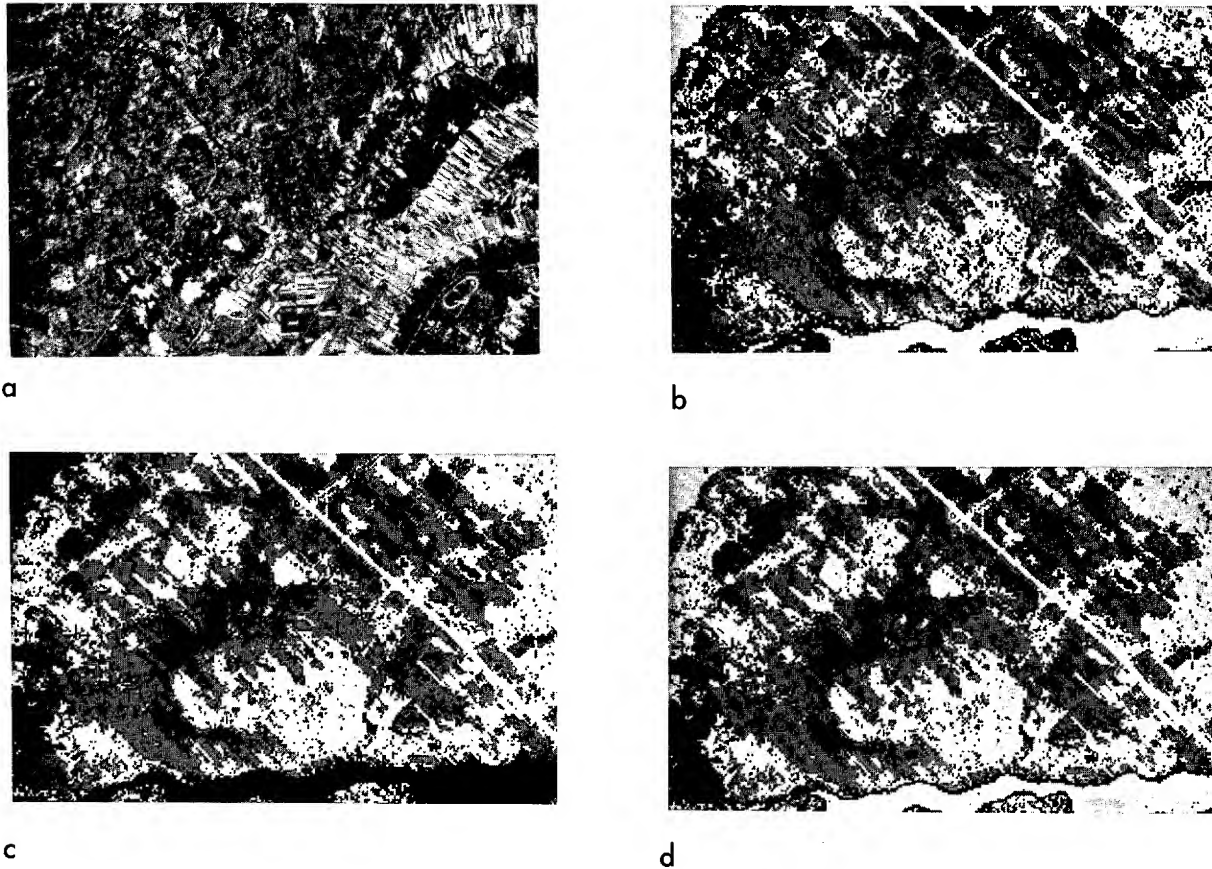
Fig. 2a. Composite color projection on a video screen. **Fig. 2b.** Thematic map with each land-cover category as different color. **Fig. 2c.** Corrected thematic map after integration of qualitative verification. **Fig. 2d.** Final, corrected thematic map after quantitative validation.

habitat, forest, and agriculture categories. These sites were visited and reclassified if necessary. Field observations at this stage of the procedure were qualitative. Habitats that were too old were reclassified as forest, and habitats that were too young were reclassified as agriculture. Sites that were reclassified were used to create new training sites and were assigned to their new land-cover category.

First Classification (Step 4)

A corrected thematic map, the first classification, was produced to integrate the observations of the qualitative verification (Fig. 2c). After the distribution of forest, woodcock habitat, and agricultural areas was known, these categories were retained as the only three target land-cover categories of the survey because the immediate

objective was to delineate woodcock habitat in forest and agriculture areas. Moreover, the classes of water, urban, and bare ground were well identified at this time of the analysis.

Quantitative Verification (Step 5)

To validate the results of the first classification, 40 validation sites, evenly distributed in the woodcock habitat category, were selected. To avoid geographic localization errors, each validation site was centered on a square of at least nine pixels ($8,100 \ m^2$) of woodcock habitat. At each validation site, a minimum of three sampling stations was randomly selected, and the variables (Table 1) were measured at each station. These were minimum requirements. Validation sites of more than nine pixels, so that more than three stations could be measured, were more reliable. The values of

each variable at each station were pooled to obtain average values for a validation site. Field work for selecting training sites and for quantitative verification were made at a comparable time of the year.

The next task was to compare (*t*-test) the mean values of habitat variables measured on a validation site to the mean values of the same variables on all the training sites (Step 1). To be retained as potential woodcock habitat, a validation site had to have mean values that were equal to or within 1 SD of the values of the training sites. We believe, however, that with our current knowledge about woodcock habitat, a validation site that has at least 12 of 15 variables (80%) in the range of variations of the training sites should be considered potential woodcock habitat. Pixels that did not belong to the woodcock habitat category were reclassified as forest or agriculture.

Final Classification (Step 6)

A final thematic map (Fig. 2d) with the corrections from the quantitative validation procedure was drawn.

Results and Discussion

Possibilities

With this remote-sensing technique, we determined the amount of available woodcock habitat in a region. The results from a relatively populated region (first experiment) showed that woodcock habitat decreased from the preliminary to the final classification as the precision of information increased. We also found that the amount of available woodcock habitat was relatively small (Table 2). Another inventory southeast of Trois-Rivières where farmland and forest were predominant revealed that the amount of potential woodcock habitat was only 4% of the total area. The thematic map made with remote sensing also provided information about the geographical distribution of woodcock habitat. Additional relations could be obtained by superimposing this thematic map on a topographic map to combine other cultural and topographics features.

The locations in our studies (3,807 and 2,676 km^2) were sufficiently large to provide areas adequate for monitoring, although we used only a portion of the entire image (34,225 km^2). The large total dimension of an image, however, allows the choice of several monitoring areas.

A network to monitor available woodcock habitat can be established with several thematic maps, such as the one described and produced for a given area. Some years later, updated thematic maps can be produced for these same areas and differences in imagery, analyzed for changes in available woodcock habitats. Because Landsat-5 will be in service for several more years and Landsat-6 was launched in 1991, images will continue to be available. Furthermore, remote-sensing imagery avoids the lack of access to some areas, which often hampers ground surveys.

The cost of surveying woodcock habitat with remote sensing was $2.75/km^2 (Babin and Couture 1987). This amount included the purchase of a quarter section of an image and the cost of image processing (e.g., computer time, image analyst) but excluded the costs of field work. Estimation of the cost of field work was more difficult because cost

Table 2. Example of each land-cover category determined by remote sensing for a region in the Saint Lawrence Lowlands northwest of Montreal, 1987.

	Classification type[a]					
	Preliminary		Initial		Final	
Class	Km^2	%	Km^2	%	Km^2	%
Woodcock habitat	290	8	182	5	106	3
Agriculture	765	20	853	22	1,051	28
Forest	883	23	861	23	816	21
Water	338	9	338	9	323	8
Urban, and bare-ground	1,530	40	1,572	41	1,510	40

[a] Preliminary classification determines the area of land-cover categories on thematic maps produced by the training sites. The initial classification determines the areas of land-cover categories after qualitative verification. The final classification indicates the area of potential woodcock habitat determined by remote sensing.

depends on both salaries and distance to field sites. Yet, for an area of about 3,000 km², two skilled people (technician and biologist) can complete the evaluation in 2 months. The low cost of image processing is explained by the small number (five) of land-cover categories that we used. Generally, land-use and land-cover analysis often include more than 10 land-cover or land-use categories and are more costly. The specificity of woodcock habitat structure makes the evaluation easier.

Limitations

The technical aspects of image processing, as used in woodcock habitat survey, can be learned with appropriate training, but it takes at least 6 months. Image-processing systems vary in price and capability. The less expensive systems ($50,000) are hosted on mini computers (IBM 386). Because memory is limited, most of these systems can process only small subscenes of Landsat images. The more expensive systems ($150,000–250,000) are supported only on large computers and can process entire Landsat images. Some users may require processed images but do not wish to invest in a processing system. Several commercial and educational facilities can, for a fee, process images to the user's specifications.

The data that describe the elements (e.g., spectral signatures, band ratios, biomass index) to classify habitats on one TM image cannot be used to classify habitats on another TM image. All the different phases (Fig. 1) must be repeated each time a different TM image is used. Image processing is more complex if two images are needed to cover a study area because radiometric corrections must be made to compare reflectance values of both images.

Landsat satellites are sun-synchronous and take images of the same area every 16th day. Obtaining an image for a specific day may be impossible because of climatic conditions (i.e., presence of clouds), which often affect the quality of the images. Cloud cover, relatively unknown over arid regions, is an important limitation over humid regions such as the northeastern North America, a major breeding area of the woodcock. We evaluated the availability of an image for the months of June, July, and August for the area southeast of Trois-Rivières and determined that only a mean of three images a year with less than 30% cloud cover is available for 1984–89. When satellite remote sensing images are not available, however, images taken from an airplane can be used.

Areas designated as woodcock habitat with remote sensing can be considered only potential habitat, (i.e., these habitats have a vegetative structure that is favorable for woodcocks). Although Babin and Couture (1987) reported that at least 80% of those habitats were occupied by woodcocks, we still must define the quality of the sites. The amount of available woodcock habitat may well be overestimated because all pixels of that category, even those that were alone in a field, contributed to the total area. Moreover, the method for measurement of training sites and validation sites is time-consuming and must be simplified.

Summary and Conclusion

Satellite imagery is effective for habitat and land-use mapping because of its comprehensive coverage, reasonable cost, and availability (Best 1982). The use and development of computer methods increased the ease of interpreting data, and quality and utility of image data have steadily improved. Remote sensing provides an alternative to aerial photographs for habitat mapping over large areas.

The habitat type favored by woodcocks is generally the early successional stages, which are subjected to rapid change. This change causes habitat distribution maps to become obsolete in a few years, but remote sensing can be used to create new maps rapidly. Furthermore, if we consider that the size of the woodcock population may be proportional to the amount of available habitat, it should be possible to derive an index of the total population for different parts of its range by measuring the amount of available habitat.

Acknowledgments

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Care, Behavior, and Growth of Captive-reared American Woodcocks

by

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Abstract. We raised 14 American woodcocks (*Scolopax minor*) from 23 eggs for experimental work and maintained 6 birds for 13 months. Two of seven eggs taken early in incubation from the nests of wild hens and all ($n = 16$) eggs taken late in incubation hatched in a commercial incubator. Communal and individual cages with wire-mesh bottoms and padded tops maintained clean and healthy birds. The night crawler (*Lumbricus terrestris*) was the most convenient food for maintaining the captive woodcocks. Smaller species of worms (probably *Aporrectodea* spp.) were fed to chicks for the first 2 weeks. Captive, full-grown woodcocks held at thermoneutral temperatures ingested about 50% of their body weight in night crawlers daily. The captive chicks grew at lower rates than chicks of birds in the wild but eventually attained masses comparable to wild birds. The chicks probably required feeding at intervals of ≤30 min during the day to maintain growth rates comparable to those of birds in the wild, and vitamin supplements or exposure to sunlight prevented calcium deficiency in the captive chicks. The young, hand-reared woodcocks were useful experimental animals. They tolerated a variety of laboratory conditions; however, fractious behavior of birds older than 60 days precluded their use in foraging trials.

Wild birds have been reared in captivity for studies of metabolism (Gray and Prince 1988; Thompson and Fritzell 1988), growth (Beintema and Visser 1989), and other physiological measurements in the laboratory. Captive-reared birds also have been used for studies of foraging behavior and habitat-specific rates of food intake in the field (Kimmel and Samuel 1978; Healy 1985).

Most research on captive American woodcocks (*Scolopax minor*) involved adults caught in the

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wild (Stickel et al. 1965a; Liscinsky 1972; Rabe et al. 1983). Stickel et al. (1965b) maintained wild-caught adult woodcocks in captivity for studies of pesticide poisoning and presented information on maintaining captive birds. Gregg (1984) maintained young woodcocks in captivity, and Brown and Chase (1954) briefly described their success in raising four chicks to fledging. As part of a study of woodcock energetics (Vander Haegen 1992), we raised birds from eggs and maintained them for experimental use during 1988–89. In addition to our techniques for rearing and maintaining captive woodcocks, we describe feeding and other behaviors and rates of food ingestion and growth of the birds.

Incubation and Brooding

Twenty-three eggs were obtained from six nests at the Moosehorn National Wildlife Refuge (NWR), Washington County, Maine. Most eggs (16) were removed from nests within 1–2 days of hatching; seven eggs were taken from nests abandoned early in incubation. The eggs from the abandoned nests were left unattended for 24–36 h before being moved to an incubator (Model 802, G. Q. F. Manufacturing Co., Savannah, Georgia). The eggs were incubated at 37.5° C and 68% relative humidity. All 16 eggs obtained late in incubation and two of the seven eggs from abandoned nests hatched.

When a chick's feathers had dried (usually 6–12 h), it was color-banded and moved to a cardboard box. A 250-watt heat lamp suspended over the box served as the brooder. The temperature at the bottom of the box was maintained at 32° C by varying the height of the heat lamp, which was constantly turned on. The bottom of the box was lined with absorbent paper towels, which were changed daily. Water was available ad libitum in a shallow dish, but the chicks were observed drinking only once. The brooder box was in a heated basement without windows.

Cages

Beginning at the age of 14 days, the birds were housed in wire cages constructed from 1.2 × 1.2-cm wire-mesh that was stapled to a wooden frame and maintained in an unheated building at the Moosehorn NWR. The cages were 1 m long, 1 m wide, and 0.5 m high and had a 30-cm wide hinged door bisecting the top. The size and location of the door enabled us to easily remove food and water trays and to quickly reach a bird anywhere in the cage. The cages were elevated 7 cm above the floor on wooden blocks and the removable, wire-mesh bottom allowed feces to drop through to newspapers. The newspapers were replaced every morning, and the cages were thoroughly scrubbed every week. Fourteen birds were maintained in these cages for >1,300 bird-days with no foot infections and only one injury attributable to the wire-mesh floor. We stapled 1-cm thick foam sheeting across the inside top of the cage to prevent head injuries. A heating pad in each cage was used by the birds during cool periods (<18° C). During particularly cold nights (<5° C), a blanket was placed over the cage to retain heat.

Although predators could not enter cages, the proclivity of the birds to poke their bills through the wire-mesh walls allowed a raccoon (*Procyon lotor*) to injure two birds by grasping their bills. Further injuries of this type were prevented by installing a 15-cm high cardboard guard along the bottom of each cage wall.

Beginning at the age of 130 days, the woodcocks were housed individually in 46 × 36 × 33-cm wire cages made of 1.2 × 1.2-cm wire-mesh with removable bottoms of 1.7 × 1.7-cm wire-mesh. The lower 15 cm of each side were constructed of stainless-steel sheeting and each cage was placed in a stainless-steel tray. The bottom of the cage was elevated 5 cm above the steel tray, allowing feces to drop through to newspapers. Each cage had a hinged, wire-mesh access door on the front. We installed 0.5-cm thick foam sheeting on the inside top of each cage to prevent head injuries. The newspapers were replaced daily, and the cages were scrubbed weekly. The combination of wire-mesh floor and weekly scrubbing prevented diseases reported by Stickel et al. (1965b) and allowed the birds to maintain plumage without access to bathing water.

When the woodcocks were 130-days old, the cages were placed in either a walk-in or cabinet-model environmental chamber at the University of Maine, Orono, and maintained at 20–23° C (at the lower end of the woodcock's thermoneutral zone; Vander Haegen 1992). Light was provided by fluorescent tubes. Photoperiod was maintained at 13L:11D (typical of early September in Maine) through day 275 and was advanced to the current outside photoperiod over several weeks. The cages were removed from the chambers each morning for replacement of food, water, and newspaper.

The birds were transported in 52 × 36 × 35-cm cardboard boxes with ventilation slits, and not more than three birds were placed in one box. When startled, the birds occasionally flew into the top of the box, but the cardboard top prevented injuries. Wrapping birds in muslin bags for transportation, as suggested by Stickel et al. (1965b), was not necessary. We clipped flight feathers from one wing of all the captive birds as soon as they were capable of flying to keep the birds from injuring themselves or escaping.

Foods

We fed the captive woodcocks several species of oligocheates, which are commercially available and can maintain captive woodcocks (Stickel et al. 1965b). For the first 3 weeks, we fed the chicks a diet of locally obtained earthworms from a wholesale distributor. These worms were readily eaten by the young chicks and are probably among the species eaten by woodcocks in the wild (Reynolds 1977). Because these worms did not survive well in storage, even when refrigerated, and are available only seasonally, we do not recommend them as a long-term source of food.

The staple food for our captive woodcocks was the night crawler, a species not normally eaten by woodcocks in the wild (Reynolds 1977) but readily eaten by captive birds (Stickel et al. 1965b). We began feeding night crawlers to the woodcocks as soon as the birds were large enough at about 12 days to ingest them. Night crawlers were available from a commercial distributor throughout most of the year.

The large size of the night crawlers (2–4 g), simplified the tasks of feeding and maintaining records of amounts eaten by each bird. Night crawlers survived well in feeding trays, especially when the trays were equipped with guards to prevent birds from walking in them and when the cages were maintained at moderate (18–21° C) temperatures. The night crawlers also survived well in damp peatmoss at 7° C and became nearly inactive and easy to contain during storage. Night crawlers are expensive, however, and their availability may be limited during drought. When a drought limited the availability during August 1988, we obtained African night crawlers (probably *Eudrilus eugeniae*; Stickel et al. 1965b) from a commercial grower (May's Happy Chick Farm, Gulfport, Mississippi). The woodcocks readily ate these worms and maintained their weight on them during a 3-week period. However, African night crawlers are difficult to store because they cannot tolerate temperatures below 7° C and are small (about 0.5 g) and highly mobile.

Feeding

The chicks were offered earthworms within a few hours of being moved to the brooder box. One to three worms were usually accepted by the chicks at the initial feeding. Chicks were fed until satiated 8–9 times/day (ca. every 1.5–2.0 h) from 0630 h–2030 h. Chicks that were 1–4 days old could seize worms suspended above their bills but were incapable of grasping worms on the cage floor. We fed 3–4-cm pieces of night crawlers to 12-day-old chicks.

Twelve-day-old chicks were allowed to forage for earthworms in shallow pans with damp peatmoss and 16-day-old chicks were no longer hand-fed. Pans were placed in cages at 0630 h and removed at 2030 h. Worms were replenished in the pans every 2 h. Twenty-day-old birds were shifted to a diet of night crawlers, and the frequency of replenishment was reduced until by day 30 food was replenished only in the early morning and again at ca. 1200 h. In communal cages, night crawlers were provided in 39 × 28 × 7-cm plastic trays with tight-fitting lids. The center of each lid was removed, leaving a 4-cm lip around the top edge of the tray. A 2–3-cm space between the surface of the peat and the lid of the tray prevented most night crawlers from escaping. In cages with one individual, night crawlers were provided in a 35 × 7 × 6-cm plastic tray.

The captive woodcocks often removed but did not eat night crawlers from trays. The removal of night crawlers from trays and the compaction and soiling of peat by probing birds resulted in substantial mortality of night crawlers, but loss was reduced by modifications to the feeding trays. As part of an experiment to determine the efficiency of food assimilation by woodcocks, we outfitted the smaller food trays in the cages for one bird with wire-mesh guards to prevent the birds from defecating on the peat. Guards were constructed of 0.6 × 0.6-cm wire-mesh and covered the entire food tray. The top of the guard extended 7 cm above the back of the tray and sloped to meet the tray's front edge, preventing the birds from walking on top and defecating onto the peat. A 3 × 35-cm opening along the front edge of the tray allowed the birds to probe and remove night crawlers without entering the

tray. The birds adjusted quickly to the guards, and intake rates remained stable. With the guards in place, the peat remained loose and clean, and removal of night crawlers by the birds without eating them declined, thereby increasing survival of the night crawlers.

Water was provided in circular (11 cm) glass bowls with straight 6-cm deep walls, but we rarely observed birds drinking. Evidently, the night crawlers provided sufficient moisture except during winter when birds were housed in the environmental chambers. The chambers circulated dry indoor air of low relative humidity, and the birds evidently were dehydrated. We increased relative humidity in the chambers, and the amount of drinking by the captive birds declined. Bathing water was used on exceptionally hot days by birds housed outside in communal cages.

Prepared Diets

Several species of shorebirds have been raised or maintained in captivity on prepared diets. Kersten and Piersma (1987) maintained live-trapped adult ruddy turnstones (*Arenaria interpes*), black-bellied plovers (*Pluvialis squatarola*), and Eurasian oystercatchers (*Haematopus ostralegus*) on a diet of commercial pellets formulated for the mink. Beintema and Visser (1989) reared northern lapwing (*Vanellus vanellus*), black-tailed godwit (*Limosa limosa*), and redshank (*Tringa totanus*) chicks on a diet of commercial chicken food, supplemented with dried shrimp and, on occasion, live insects. To facilitate keeping woodcocks in captivity, we attempted to develop a suitable prepared diet for them.

The specialized bill of the woodcock requires food that is easy to grasp and to handle. First, we tried a semi-moist, high protein mash that was successfully used in raising insectivorous songbirds (D. E. Kroodsma, University of Massachusetts, Amherst, personal communication). This food was unacceptable because the woodcocks were unable to grasp and swallow the mash. Similarly, commercial pellets (5 mm length, 3 mm diameter) for salmonids were too rigid for grasping by the woodcocks. To simulate the shape and consistency of natural earthworms, we developed a process of extruding mash in semi-soft, spaghetti-like strands. We mixed the mash with a small amount of unflavored gelatin, heated the mixture as directed on the gelatin package, and forced the mixture through two holes (3 mm diameter) in the end

cap of a length of plastic pipe (2 cm inside diameter) using a wooden dowel as a plunger. When the strands cooled, we cut them into 2–3-cm lengths and kept them refrigerated. The woodcocks manipulated and swallowed these semi-soft pellets with little effort.

Pellets were offered to three 21-day-old woodcocks and were eaten along with the usual diet of night crawlers. To determine whether woodcocks can be maintained on pellets alone, we fed only pellets ad libitum to three birds. Although the birds ate 10–20 pellets daily, they were not eating a sufficient quantity to maintain weight; each bird lost about 10 g during 5 days. Because we were raising these birds for other experimental work, we resumed their usual diet. It is possible that the birds would have eventually increased intake to maintenance levels, thus future experimentation with artificial diets may be warranted.

Behavior

Although our goals did not specifically include imprinting birds on humans, the chicks imprinted on us in varying degrees. We held each bird for several minutes numerous times each day during their first 2 weeks and thereafter at least once each day during weighing. Most birds showed little fear of us, but some were more wary than others. The wary chicks paced rapidly along the back wall of the brood box when we were near, whereas the calmer birds approached us for food.

Chicks, beginning at the age of 8 days, were brought outside for one feeding each day. The chicks were allowed to walk freely, but they generally stayed within several meters of us. After 15–20 min, the chicks frequently attempted to brood under the seated handler. Loud noises or the approach of another human elicited a fright response, and the chicks either froze or ran to the seated handler and hid.

The behavior of the birds changed distinctly at about the age of 60 days when they became more intolerant to humans. Specifically, the birds were inclined to become motionless when approached either in a cage or outside, and they sometimes attempted to fly when approached outside. The timing of this change corresponded with the age at which broods break up (ca. 64–72 days; Horton and Causey 1982). Even birds that seemed the most imprinted and had submitted readily to handling became wary and more intolerant. This behavior

negated our attempts to use birds beyond the age of 60 days for foraging trials.

Growth Rates

We weighed (nearest 0.1 g) each bird daily on a top-loading balance before the first morning feeding or before food was replenished in the trays. After day 60, the trays were left in the cages overnight and, hence, birds may have fed before being weighed. We measured bill length (nearest millimeter) daily until the birds were 30-days-old.

During the first 15 days, rates of growth were lower of the captive woodcocks than of the wild birds (Fig. 1). Dwyer et al. (1982) used linear regression to estimate rates of growth of wild male (5.1 g/day) and female (6.2 g/day) chicks during the first 15 days of life. We used a similar analysis for data on captive-reared birds (Fig. 1) and obtained values of 2.8 g/day for males and 4.2 g/day for females. The lower rates of growth of captive birds suggest that our feeding schedule was insufficient to support maximum growth. Differences in mean mass between captive male and female woodcocks became significant at day 10 ($t = 3.63$, $n = 12$, $P = 0.007$). Bill growth during the first 15 days was slightly lower than in wild birds (Fig. 2); however, by the age of 120 days, the captive birds attained bill lengths within the ranges of those
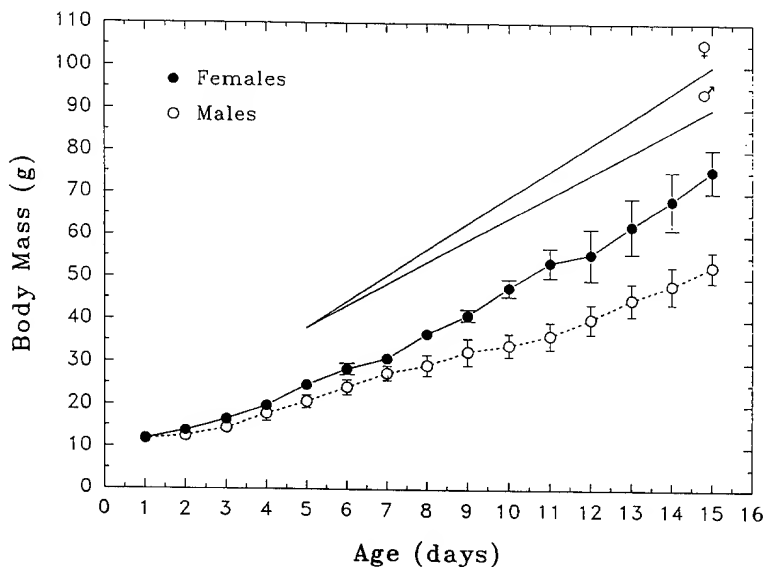
Fig. 1. Mean mass of captive-reared male ($n = 7$) and female ($n = 5$) woodcocks. The *vertical lines* indicate ± 1 SE. The *regression lines* represent growth rates of wild woodcocks (Dwyer et al. 1982).

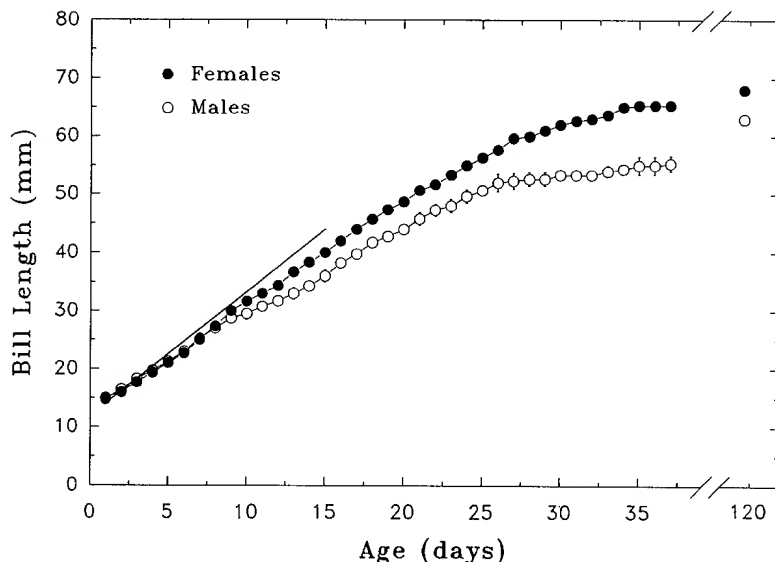**Fig. 2.** Mean bill lengths of male ($n = 7$) and female ($n = 5$) captive-reared woodcocks. The *vertical lines* indicate ± 1 SE. The *regression line* represents growth rates of wild ≤15-day-old birds (sexes combined; Ammann [1982]).
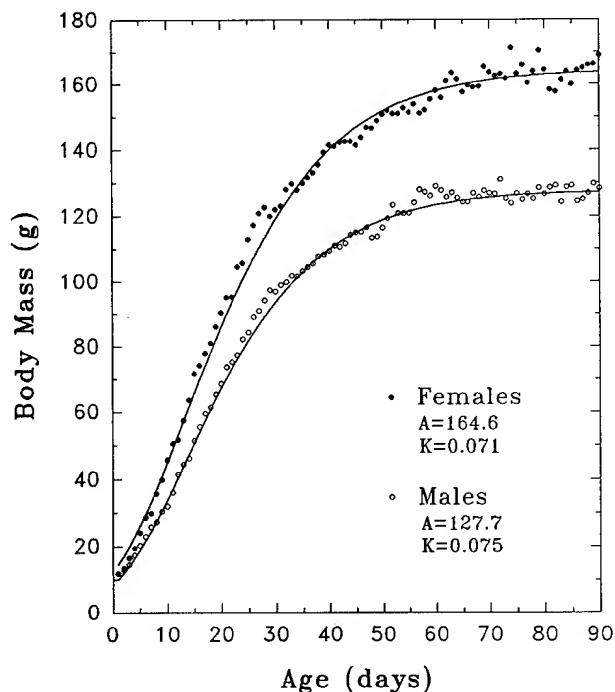
Fig. 3. Mean mass of male (n = 3) and female (n = 3) captive-reared woodcocks. Growth curves fit by the Gompertz growth equation (Ricklefs 1967) where A = asymptotic value and K = Gompertz growth coefficient.

reported by Mendall and Aldous (1943) for adult woodcocks.

Growth curves for the first 90 days were fitted by the Gompertz equation (Ricklefs 1967) and reached asymptotes of 128 g for males and 165 g for females (Fig. 3). These values were 7–10% below the means reported for fledged juvenile woodcocks in late July in Maine; males equalled 142 g and females 177 g (values represent weighted means derived from Owen and Krohn [1973]). Subsequently, captive males attained a mass (SE) of 152.7 (3.9) g (age ca. 170 days) and captive females, 180.9 (1.9) g (age ca. 110 days), comparable to the mass of juvenile wild woodcocks in early September (premigratory) in Maine (males 154 g and females 187 g; values from Owen and Krohn [1973]). Captive birds were maintained at a constant photoperiod through day 275 and thus did not undergo premigratory hyperphagia.

Our determination that hand-fed captive birds did not grow as fast as birds in the wild is not surprising; we probably did not feed the captive birds as often as a wild female would have. Diurnal brooding periods of radio-tagged female woodcocks

with less than 10-day-old chicks rarely exceeded 30 min (W. M. Vander Haegen, USDA Forest Service, Orono, Maine, unpublished data). We suggest that captive chicks be fed every 30 min during the day for the first 12–14 days after hatching.

Ingestion Rates

We measured the rates of food ingestion of individual birds during the first 15 days when the chicks were fed by hand or were observed while foraging in shallow trays. From day 16 to day 130, the birds were in communal cages and individual rates could not be determined. Later, when the birds were housed in individual cages (after day 130), the numbers of night crawlers placed in individual feeding trays and the numbers left uneaten from the previous day were recorded each morning. Earthworms and night crawlers were obtained in batches of 1,000, and we weighed a representative sample of 20 worms from each batch. To calculate a wet weight of food ingested by each bird, the mean weight of each batch was multiplied by the number of eaten worms.

The rates of ingestion increased steadily from day 2 to day 15, and the chicks generally ate their weight or more in earthworms each day (Fig. 4). The rates of ingestion were generally greater by females than by males, but analysis of variance revealed variability among individuals that precluded meaningful tests between sexes.

The rates of ingestion by full-grown birds varied daily. To obtain a representative value for full-grown birds, we averaged the daily amount ingested by 201–250-day-old males and females when body masses remained relatively unchanged. The mean (SE) daily ingestion rate of males was 69.7 (4.2) g (range = 62.2–76.9, n = 3) and of females, 93.8 (7.6) g (range = 82.1–108.0, n = 3). These values represent about 50% of their body weight. Values of 68–77% were obtained for captive, full-grown woodcocks in studies of wild-caught birds presumably held in an uncontrolled environment (Stickel et al. 1965a).

Health

Most hatchling woodcocks appeared vigorous and strong, although three died during the 1st week. A calcium deficiency was suspected when the early-hatching chicks were 8-days-old and began convulsing after eating. An examination of the
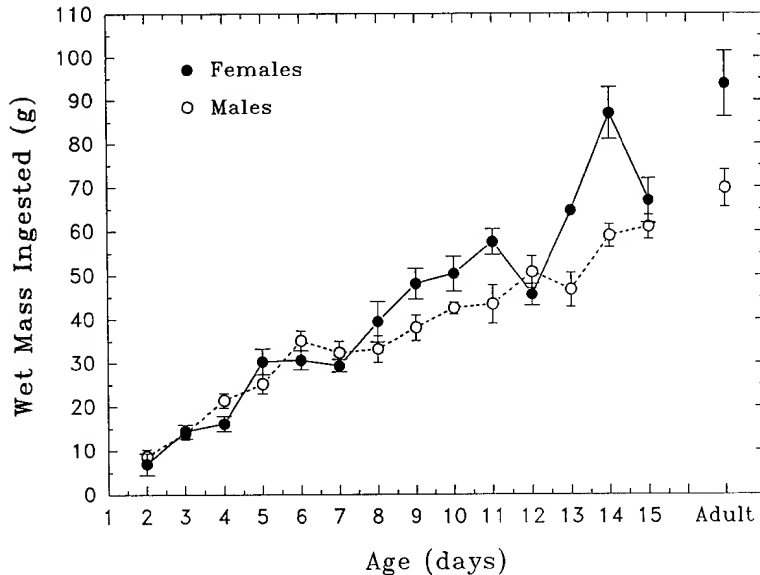
Fig. 4. Mean daily ingestion by male (n = 7) and female (n = 4) captive-reared woodcocks during ages 1–15 days and as adults (mean ingestion by three males and three females during a 50-day period beginning at age 201 days). The *vertical lines* indicate ±1 SE.

chicks revealed soft leg bones; a femur of one chick fractured while the bird was being handled. During the first 8 days, the birds received no sunlight, and we believe the calcium deficiency resulted from insufficient vitamin D rather than from low dietary calcium. Beginning with day 9, we fed the birds outside once each day for vitamin D synthesis from exposure to sunlight. We also began providing multivitamins (Avitron Multivitamin, Carter-Wallace, Inc., Cranbury, New Jersey) to all birds to avoid future deficiencies. We administered a 0.5-cc dose to each bird 2–3 times/week by injecting it into earthworms. All birds received vitamins until 4-months old. Within 2 days of exposing the birds to sunlight and beginning the vitamin treatment, the convulsions abated and soft bones were not observed again. Seven late-hatching chicks that were exposed to sunlight and received vitamin treatment beginning at the age of 2 days did not develop these signs. Growth rates of these birds were similar to those of birds hatched earlier, indicating that calcium deficiency did not cause a reduced rate of growth.

Adult woodcocks were mostly injury-free. Although the birds were handled every day during weighing, outdoor foraging trials, and laboratory experiments, only two minor injuries occurred.

On several occasions, a bird substantially reduced its food intake for several days. In three such instances, we submitted fecal samples for analysis to the University of Maine Animal Health Lab. No pathogenic bacteria or parasites were detected in the feces. In each instance, the bird resumed normal feeding without ill effects. Although temporarily eating less in response to disturbance (e.g., moving cages to a new location or power outages in the environmental chamber) was normal for birds; the response was generally similar among birds. The cause of individual cessation of feeding remains unknown.

Cost

The major expense for maintaining woodcocks in captivity was food. The cost per 1,000 night crawlers varied from $36.00 in early 1988 to $65.00 in late 1988 when severe drought reduced the supply. During the drought, African night crawlers were purchased for $21.00 per 1,000, including shipping. Our total cost for food to raise 12 birds to fledging and to maintain 6 for an additional 13 months was about $7,000.

Raising hatchling woodcocks was labor-intensive, primarily, because of the required high frequency of feeding. Maintaining six adult birds in individual cages, however, required only 1 h/day. Washing six individual cages required an additional 2 h/week.

Use of Woodcocks for Experiments

Captive-reared woodcocks were excellent experimental subjects, tolerating a variety of experi-

mental conditions. Our experiments required that birds be conditioned to a laboratory environment so that metabolic rates would not be elevated by unusual stress. During experiments, the woodcocks were confined to small plexiglass chambers (22 × 21 × 10 cm) for periods of ≤14 h. While in the chambers, the birds behaved as they did in their cages; probing the floor, preening, sleeping, and rarely displaying signs of discomfort. Our experiments involved holding birds at temperatures below 0° C, which caused them no apparent harm. When forced to walk on a motorized treadmill for analysis of energy expenditure, three of four birds also behaved normally. We attribute this tolerance to their early and continued exposure to humans while being raised in captivity. Although wild-caught woodcocks adapt fairly well to captivity (Stickel et al. 1965b), their behavior, as described by these authors, was less placid than that of our captive-reared birds.

We used captive-reared woodcocks in foraging trials in feeding covers, observing their food intake for 10-min periods. Young birds allowed observers to remain within a few feet of them at all times. Initially, the birds stayed in a small area, perhaps a result of feeding in small trays, but after several trials, the birds extended their foraging to a larger area. Although we did not begin the trials until the birds were 30-days-old, the chicks may have performed suitably at a younger age. The behavioral changes after 60 days of age precluded further use of the birds in foraging trials because the birds ran or flushed when approached.

When deciding between using wild-caught or captive-reared woodcocks for experiments, researchers should consider the importance of the psychological state of the birds. When the outcome of experiments may be altered by stress, captive-reared birds are a better choice. Raising woodcocks from eggs, however, is labor-intensive, expensive, and may be unnecessary for some experiments. Imprinted birds are probably the best choice for studies of foraging for which birds must be followed closely in the field. The behavioral changes that precluded our continuing forage trials with birds older than 60 days may be avoided by imprinting the birds more strongly during their first few days of life. Healy and Goetz (1974) provide details for imprinting precocial chicks for experimental use. However, the behavioral changes we observed may occur despite rigorous attempts to imprint chicks, and these changes may be inherently associated with normal dissolution of the brood bond.

Acknowledgments

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Use of Daytime Microhabitat by Wintering Woodcocks in Coastal South Carolina

by

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Abstract. During the winters of 1977–78 and 1978–79, we located and flushed American woodcocks (*Scolopax minor*) from 12 bottomland hardwood stands in the Francis Marion National Forest with the aid of pointing dogs. We flagged locations from which woodcocks flushed and later returned to measure characteristics of vegetation surrounding the sites. Also, we obtained identical measurements from random sites in three stands. Results indicated that woodcocks flushed from sites with higher than average overstory densities, overstory basal areas, sapling densities, and midstory densities but lower than average understory densities. However, differences in midstory density and sapling density were inconsistent across study stands. Our study and those of others revealed that during daylight hours the American woodcock is a bird of coverts. That is, woodcocks select specific areas in a stand that offer more overhead cover than an average point in a stand. This finding may be unimportant for understanding the selection of habitat by woodcocks except that biologists must understand how specific methods to describe a habitat may influence the description.

Key words: American woodcock, daytime habitat, *Scolopax minor*, winter habitat.

The 1990 American Woodcock Management Plan (U.S. Fish and Wildlife Service 1990) highlights the lack of investigations of habitat requirements of woodcocks (*Scolopax minor*) in winter. Because of numerical declines (Bortner 1989) and lower survival rates (Dwyer and Nichols 1982) of the population in the eastern region, increased attention to winter habitats in the East is especially desirable. Several authors suggested that woodcocks in the eastern region winter in the southern Atlantic states (Kletzly 1976; Coon et al. 1977; Krohn and Clark 1977; Wood et al. 1985). High concentrations of woodcocks have been reported in Georgia (Pursglove and Doster 1970), North Carolina (Stamps and Doerr 1977), and South Carolina (Pace and Wood 1979), but data about use of daytime habitats from these areas are few.

Adopting the habitat description process, we must assume that habitats, defined from a small number of general parameters, possess quantifiable vegetative characteristics that are consistent at various scales of examination (Hamel et al. 1986). Descriptions of woodcock habitats have been quantified on the basis of average habitat characteristics of forest stands and from measurements of small plots centered on bird locations. If woodcocks strongly select microhabitats with specific characteristics, average stand conditions may not be comparable with results from bird-centered sampling of vegetation (Larson and Bock 1986). If we are to adequately describe high-quality woodcock habitat (see Dwyer et al. 1988 for some discussion of complications), we must know something of the comparability and dependability of habitat characteristics that we measure (Gutzwiller et al. 1983).

We describe the general vegetational composition and structure of daytime woodcock habitat in bottomland hardwood forest stands in coastal South Carolina. We based our description on bird-centered sampling of vegetation and describe differences in structural characteristics between these sites and average stand characteristics.

Study Area

The study was conducted in the 1,009 km^2-Francis Marion National Forest in the lower coastal plain of South Carolina in Berkeley and Charleston counties (33° 40' N, 79° 10' W). The area has a humid, warm climate with a mean annual temperature of 18.3° C and an average growing season of 294 days. January is generally coldest with a mean temperature of 9.9° C. Precipitation in winter averages 8.4 cm in December, 7.1 cm in January, and 9.1 cm in February. Elevations range from just above mean high tide on the Atlantic Ocean to 27 m. Soil and landforms range from deep sands on ridges to plastic clays in swamps and along creek floodplains. About 98% of the area is forested with a composition of 50% loblolly pine (*Pinus taeda*), 20% longleaf pine (*P. palustris*), 27% bottomland hardwood, and 3% pine hardwood (U.S. Forest Service 1977).

We chose for study that part of the forest where the drainage characteristics of soils and our previous experience suggested the presence of woodcocks. Thus, we limited our work to stands mapped by the U.S. Forest Service and known to have typically moist, poorly drained soils with large amounts of organic matter. These stands usually occurred in what Sheffield (1979) classified as the oak-gum-baldcypress (*Quercus-Nyssa-Taxodium*) type and included flood plains of creeks, hardwood drains, and pond margins.

Methods

We hunted in 7 of the 12 study stands at least one afternoon between 15 December 1977 and 15 February 1978 and in 11 stands at least once between 15 December 1978 and 15 February 1979. Stand sizes were delineated with either the size of the area with contiguous similar vegetation or, for large (>200 ha) areas, the size of area that could be covered by two people with two dogs in one afternoon. Rates of flushing woodcocks in stands were measured as number of flushed woodcocks divided by hours spent hunting (flushes per party-hour). To avoid repeated counting of the same individual, we carefully noted the distance and direction of birds that flushed. Initial locations from which woodcocks flushed (flush sites) were marked with plastic flagging for later relocation.

For comparison, 20 plots were randomly chosen in each of three stands where we hunted in 1977–78 and in which flush sites were most abundant. These plots were selected randomly (equal probability) with a dot grid and were located by pacing with a hand-held compass.

All measurements of vegetation were made during February–June after the hunting season. Nested plots with radii of 3 m and 5 m, centered on the flush point or randomly located point, were used to determine sapling categories. The overstory was sampled with 1X factor metric prism. Vegetation categories were defined as: (1) understory, 0.25–1.0 m high; (2) midstory, >1.0–3.0 m high; (3) saplings, woody stems >3 m high but <12.5 cm dbh; and (4) overstory, >3 m high and >12.5 cm dbh. Plant species names were based on Radford et al. (1968).

Habitat description was based on analyses of flush site characteristics. Overstory and sapling components were characterized by relative density and relative basal area (i.e., equaled relative dominance), calculated for each species on each plot and then averaged over all plots in which that species occurred (Mueller-Dombois and Ellenberg 1974). Frequency of occurrence was the quotient of the number of plots in which a particular species occurred and the total number of plots. Sums of these values rendered the Density-Dominance-Fre-

quency (DDF) Index for each species. Relative density and frequency of occurrence were summed within the midstory and understory categories to yield Importance Value (IV) indices.

Characteristics of flush sites and random sites were compared by a two-way classification ANOVA (unbalanced design). Type of site (two levels—random or flush) and forest stand (three levels) were considered fixed. Habitat variables were normalized by a square-root transformation (W-statistic; Shapiro and Wilk 1965) to ensure independence between sample means and variances (Bartlett 1947).

Results and Discussion

Woodcocks were located in flood plains, swamps (and their upland transition zones), and pond margins in pine stands and clear-cuttings. Oak-gum-cypress was generally the forest type we examined, but the mix of plant species at flush sites ($n = 145$) that we relocated in 11 different stands was more descriptive of the dominant pattern of vegetation of habitat used by woodcocks (Table 1). Based on the DDF value, tupelo-gums (*Nyssa sylvatica, N. aquatica*) were the most important overstory species at flush sites, although both baldcypress (*Taxodium distichum*) and red maple (*Acer rubrum*) occurred more frequently. In the sapling layer, ashes (*Fraxinus* spp.) had a substantially higher DDF value than any other taxon, although tupelo-gums, red maple, and sweetgum (*Liquidambar styraciflua*) also were important components of species compositions (Table 1). In the midstory, only waxmyrtle (*Myrica cerifera*) and greenbriar (*Smilax* spp.) occurred on more than 50% of the plots (Table 2); however, switchcane (*Arundinaria tecta*) had a higher IV index than either of these. In the understory, greenbriar had a higher IV index than all other species; its frequency of occurrence was 95%.

As indicated by stocking of flush sites with trees and composition of plant species, practically all flush sites were in vegetation of middle-to-late stages of succession (Table 3). This contrasts with

Table 1. Composition of overstory and sapling species of 145 woodcock flush sites in the Francis Marion National Forest, South Carolina, during December–February 1977–78 and 1978–79.

Species[a]	Overstory (%)				Saplings (%)			
	Relative density[b]	Relative dominance[b]	Frequency of occurrence[c]	DDF index[d]	Relative density[b]	Relative dominance[b]	Frequency of occurrence[c]	DDF index[d]
Baldcypress *Taxodim distichum*	18.8	22.1	86.9	127.8	21.1	24.4	15.2	60.7
Red maple *Acer rubrum*	19.3	15.9	85.5	120.7	31.2	32.0	45.5	108.7
Tupelo gums *Nyssa* spp.	44.1	43.7	75.9	163.7	34.3	41.7	35.9	111.9
Oaks *Quercus* spp.	13.1	17.4	65.5	96.0	22.1	24.2	14.5	60.8
Sweetgum *Liquidambar styraciflua*	22.5	20.1	63.4	106.0	30.3	30.9	35.9	97.1
Ashes *Fraxinus* spp.	19.0	14.9	55.9	89.9	50.9	48.2	46.9	146.0
American elm *Ulmus americana*	9.0	5.6	35.2	49.8	29.5	27.7	31.7	88.9
Loblolly Pine *Pinus taeda*	13.1	22.9	32.4	68.4				
Waxmyrtle *Myrica cerifera*					31.6	28.7	24.1	84.4
Dogwoods *Cornus* spp.					18.2	13.5	13.8	45.5

[a] Includes species found in ≥10% of sites or averaging ≥30% relative density.

[b] Average at all sites where species occurred.

[c] Number of sites where species occurred/total sites × 100.

[d] Density-Dominance-Frequency Index = Relative density + Relative dominance + Frequency of occurrence.

Table 2. Composition of midstory and understory species at 145 woodcock flush sites in the Francis Marion National Forest, South Carolina, during December–February 1977–78 and 1978–79.

Species[a]	Midstory (%)			Understory (%)		
	Relative density[b]	Frequency of occurence[c]	Importance value[d]	Relative density[b]	Frequency of occurrence[c]	Importance value[d]
Switchcane *Arundinaria tecta*	70.8	31.7	102.5	38.4	29.7	68.1
Waxmyrtle *Myrica cerifera*	36.7	54.4	91.2	15.6	40.0	55.6
Greenbriars *Smilax* spp.	19.0	54.5	73.5	44.6	95.2	139.8
Ash *Fraxinus* spp.	17.1	40.7	57.8			
Palmetto *Sabal minor*	20.5	30.3	50.8	9.2	31.7	40.9
Sweetgum *Liquidambar styraciflua*	12.4	37.9	50.3	5.0	31.7	36.7
Pepperbush *Clethra alnifolia*	32.6	3.4	36.0	33.2	4.1	37.3
Red maple *Acer rubrum*	14.4	20.7	35.1			
Blackberries *Rubus* spp.	21.1	13.1	34.2	10.1	34.5	44.6
Dogwoods *Cornus* spp.	14.3	16.6	30.9	6.2	28.3	34.5
American elm *Ulmus americana*	14.7	15.9	30.6	3.4	30.3	33.7
Alabama supplejack *Berchemia scandens*	9.0	21.4	30.4	3.5	24.1	27.6
Hawthorns *Crataegus* spp.	11.3	10.3	21.6	3.0	16.6	19.6
Tupelo gums *Nyssa* spp.	8.4	11.7	20.1			
Vacciniums *Vaccinium* spp.	5.4	12.4	17.8	8.7	40.0	48.7
Oaks *Quercus* spp.	4.4	11.7	16.1	13.2	57.9	71.1
Jessamine *Gelsemium sempervirens*	5.5	10.3	15.8	6.7	26.9	35.6
Loblolly pine *Pinus taeda*				6.4	14.5	20.9

[a] Includes species with Importance Value ≥20.

[b] Averaged for all sites in which that species was found.

[c] Number at sites where species occurred/total sites × 100.

[d] Importance value index = Relative density + Frequency.

descriptions of Mendall and Aldous (1943), Sheldon (1967), Liscinsky (1972), and Wenstrom (1974), all of whom described summer and fall habitat as being in the early-to-middle stages of succession. We do not imply that vegetation in late successional stages was the only daytime habitat used by woodcocks in coastal South Carolina. We flushed several birds from the margins of a pond with little overstory. There were large acreages of potential woodcock habitat in the Francis Marion National Forest that we did not investigate (Ingram and Wood 1982). Many may have had younger and less dense overstories and may have held abundant woodcocks. Because we did not follow a systematic or randomized sampling strategy to identify potential woodcock habitat, our efforts

Table 3. Values for vegetation variables measured at 145 woodcock flush sites in the Francis Marion National Forest, South Carolina, during December–February 1977–78 and 1978–79.

Variable	Mean	Interval estimate[a]	Range
Height of dominant trees (m)	32	30–34	25–37
Density			
Overstory	0.048	0.044–0.051	0.009–0.135
Sapling	0.081	0.070–0.094	0.0–0.406
Midstory	0.457	0.382–0.538	0.0–5.626
Understory	2.193	1.950–2.450	0.0–7.894
Basal area (m^2/ha)			
Overstory	35.6	33.4–37.9	1.5–70.8
Sapling	10.0	8.7–11.5-	0.0–43.0

[a] Confidence interval (95%) estimated as the retransformed confidence interval about square-root transformed data (Sokal and Rolf 1969).

may have been biased toward stands with well-developed overstories. Nevertheless, we found birds were abundant (Fig. 1), and our observed flush rates are among the highest reported (Pace and Wood 1979; Ingram and Wood 1983). We assume that these rates reflect some degree of selection for these stands by woodcocks.

Analysis of data from 65 flush sites and 60 randomly selected sites in three stands revealed that flush sites had substantially greater overstory basal area ($P = 0.0001$) and greater densities of stems in the overstory ($P = 0.0002$), saplings ($P = 0.0208$), and midstory ($P = 0.0376$; Fig. 2, Table 4).

Conversely, the understory was significantly less dense ($P = 0.0001$) on flush sites than on random sites. Also, except for overstory stem density, we observed differences in structural measurements among stands and detected inconsistencies among random and flush site differences across stands for each examined variable (Table 4). This observation is significant because it demonstrates that woodcocks used microhabitats in a stand despite disparities in structural attributes among stands. Thus, as Larson and Bock (1986) discussed in reference to other species, woodcocks select habitats at different scales.
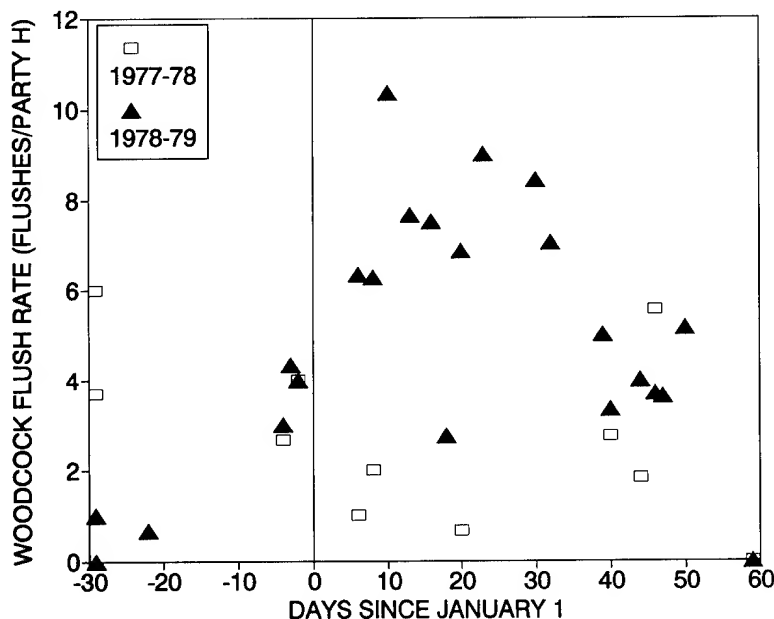
Fig. 1. Flush rates of woodcocks during 35 hunting trips distributed among 11 stands in the Francis Marion National Forest, South Carolina, during December–February 1977–78 and 1978–79.
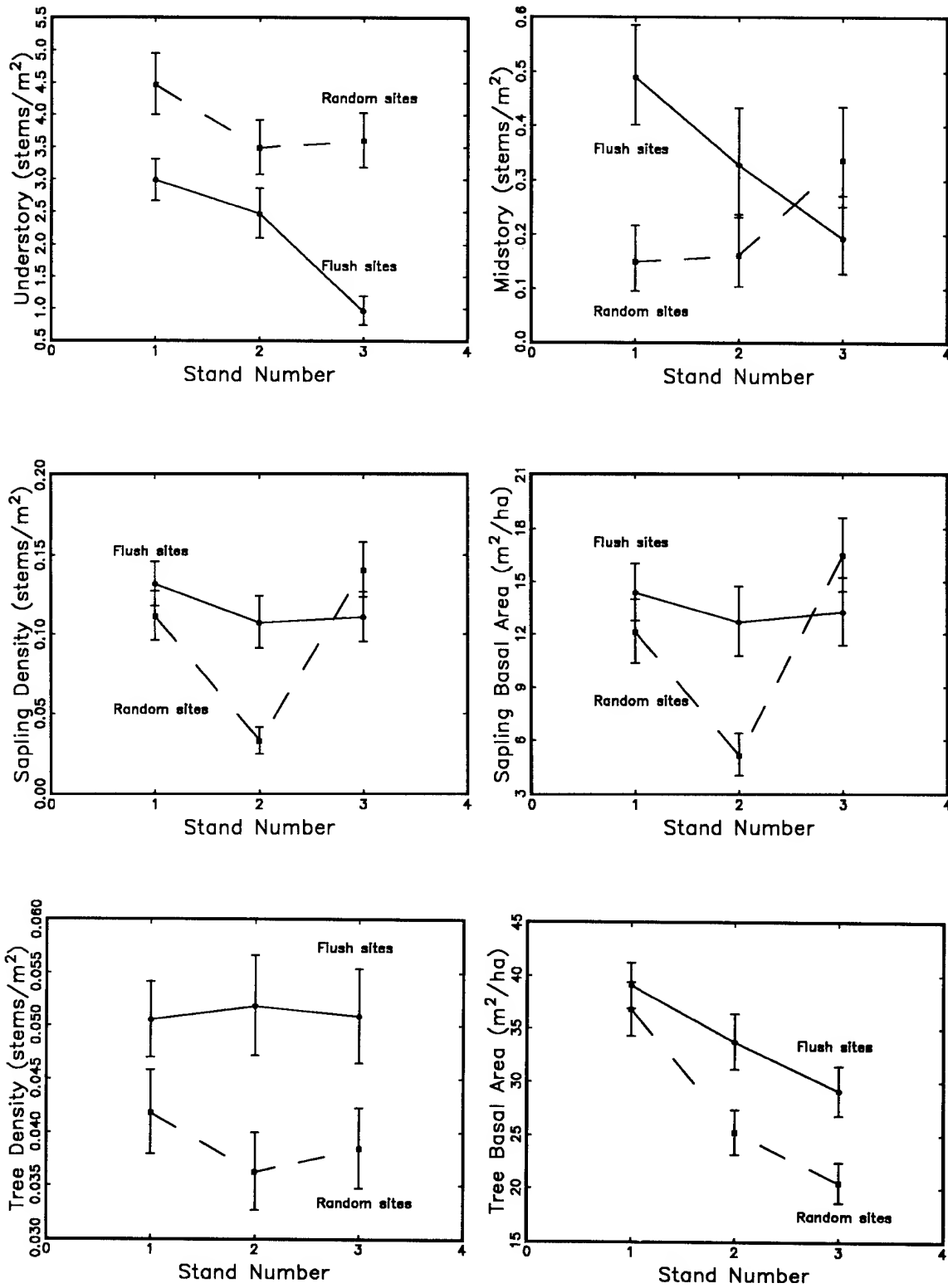
Fig. 2. Comparisons of vegetation structure between flush sites and random sites in three different stands of the Francis Marion National Forest, South Carolina, during December–February 1977–78 and 1978–79. Estimated means and confidence limits (derived from retransformed confidence intervals formed from least-square means and their standard errors determined from two-way analysis of variance) are plotted.

Table 4. Results of two-way analysis of variance used to compare 65 flush sites and 60 random sites in three study stands in the Francis Marion National Forest, South Carolina, measured during December–February 1977–78 and 1978–79.

| Dependent variable	Probability ($F_{calc} > F$)[a]		
	Site type	Stand	Type X stand
Density			
Overstory	0.0002	0.8184	0.6485
Sapling	0.0208	0.0001	0.0007
Midstory	0.0376	0.6906	0.0025
Understory	0.0001	0.0002	0.0216
Basal Area			
Overstory	0.0001	0.0001	0.1021
Sapling	0.0810	0.0032	0.0117

[a] F-statistics were calculated assuming Type III sums of squares.

Dyer and Hamilton (1977) in Louisiana also reported significantly higher basal area of overstory on flush sites than on randomly selected sites. Direct comparison of their data with our data is difficult because they included only trees with dbh greater than 22.9 cm in their overstory class, but differences in dominant vegetation structure between the two studies are evident. We found dominant overstory heights of 32 m on flush sites in contrast to 11.2 m and 18.8 m average tree heights on flush sites described by Dyer and Hamilton (1977). The mean basal areas at flushing points were only 7.7 m^2/ha in Louisiana, which is less than 25% of the 35.6 m^2/ha we observed. Flush sites in Louisiana averaged only 1.1 m^2/ha basal area more than random plots, whereas we found an average difference of 4.0 m^2/ha. Dyer and Hamilton (1977) reported greater densities of understory vegetation on flush sites than on random sites, whereas we found just the opposite. These differences may be attributable to different standards of measurement. Dyer and Hamilton (1977) concluded that the "optimal composition is a dense stand of trees of relatively small diameter," which is not descriptive of our study stands.

Other descriptions of daytime habitat in winter are not directly comparable to ours, but some generalizations are possible. Horton and Causey (1979) reported total midstory stem density (a vegetation size class roughly equivalent to our midstory plus sapling) at activity centers of radio-marked woodcocks in central Alabama as higher

(7,815 stems/ha) than the 5,380 stems/ha that we observed (averaged across $n = 145$) at flush sites. They reported tree (our overstory) densities in preferred habitat of greater than 700 stems/ha, whereas values at our flush sites averaged less than 500 stems/ha. Thus, differences in stand structure reflect the apparent greater age of our than their stands. Horton and Causey's (1979) reported value of 47% cover by plants less than 61 cm high suggested only moderate understory density on their plots.

Numerous authors have quantitatively and qualitatively described woodcock habitat in northern breeding areas and migration stopover areas (Straw et al. 1986; Sepik et al. 1989). Most of this work suggests that woodcocks prefer habitats with early successional vegetation. For example, Liscinsky (1972) recommended that for management of woodcocks the "predominant vegetation (shrubs and small trees) should be less than 30 years old." Structurally, such areas have high midstory and sapling densities and few large (>12.5 cm dbh) trees (Rabe 1977; Sepik et al. 1981; Straw et al. 1986). Thus, our data are in contrast to these descriptions.

Our observation of high use of older stands by woodcocks is not unique. Pearce and Mendall visited typical daytime cover in Louisiana and, as stated in Mendall and Aldous (1943), the "observers' impressions are that the birds usually frequent three main habitats: ..." that include "old growth bottomland hardwood stands of maple, gum, oak and sycamore ... ." Also, Kroll and Whiting (1977) reported that woodcocks used a sawtimber size, mixed pine-hardwood stand but in densities that were evidently lower than two younger stands they examined.

Summary and Conclusions

Stands of the oak-gum-cypress type and their associated transition zones into drier sites were used by woodcocks for daytime habitat during two winters in coastal South Carolina. Woodcocks were abundant in stands that were generally older and somewhat structurally dissimilar than stands described elsewhere as daytime habitats. Several overstory species were important on flush sites, but tupelo gums were the most important. Ash saplings, waxmyrtle, switchcane, and greenbriar also were important components at flush sites. All examined vegetation variables were different between flush sites and randomly selected sites. Our

and others' findings aided in fostering the idea that during daylight hours the American woodcock is a bird of coverts. Given this idea, one might suggest that timber management should foster development of covert. However, data are lacking to support that covert in stands increases survival of woodcocks in winter.

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Responses of Invertebrates to Experimental Acidification of the Forest Floor Under Southern Pines

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Abstract.   We investigated the effects of artificial acidification of the forest floor under southern pines (*Pinus taeda, P. palustris*) on macroinvertebrate populations in Mississippi and in eastern Texas. One-m^2 plots were treated with acid solutions for periods ranging from 1 month to 2 years and were compared with similarly treated control plots. The emphasis was on invertebrates that are important to American woodcocks (*Scolopax minor*). The pH of the spray leachate that reached the soil was approximately 1 unit higher than that applied, although little residual effect on the pH of the litter was detected during the first rainfall after treatment or on the pH of the soil after multiple treatments. Earthworms (*Sparganophilius* spp., *Eudrilus eugeniae*, or *Diplocardia* spp.) were found in greatest numbers during December–April. Generally, the number of

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earthworms decreased substantially after acid treatment. The number of insects was greater in acid-treated plots, but when individuals <50 mg were excluded, mean numbers were similar. Fewer earthworms >50 mg (wet weight) were in the acid-treated plots than in the control plots. Except for earthworms, the biomass of collected invertebrates did not differ by treatment. Earthworms were the most abundant invertebrate in soils in Texas but not in Mississippi.

The detrimental effect of acid deposition on temperate forests is well documented but not thoroughly understood. Most knowledge is based on studies in western Europe, southeastern Canada, and the northeastern United States (Likens et al. 1979; National Academy of Sciences 1983, 1985; Galloway et al. 1984; Johnson and McLaughlin 1986; Klein and Perkins 1988; Schulze 1989). Less information is available for the southeastern United States. In part because of the poor buffering capacity of the soils, southern forests are believed to be sensitive to increased acidification (National Acid Precipitation Assessment Program 1990).

Few researchers have examined effects of acidification on biota of the forest floor. Earthworms, a primary food of the American woodcock (*Scolopax minor*; Sheldon 1971; Miller and Causey 1985; Gregory 1987), seem sensitive to acid deposition. Hagvar (1980) reported that earthworm populations decreased when the forest soil was artificially acidified and speculated that reduced numbers of earthworms were caused by decreased reproduction. Ma et al. (1990) reported that nitrogenous fertilizers lowered soil pH and drastically reduced numbers and biomass of earthworms in grasslands. In eastern Texas, Boggus and Whiting (1982) found that the number of probe holes of woodcocks increased with soil of higher pH. Craft and Webb (1984) reported that acidic sulfate had little effect on forest floor arthropods, although at concentrations of 10× the ambient levels, nonacidic sulfate adversely affected the number of decomposer arthropods. These authors concluded that, because of the buffering capacity of the litter, the hydrogen ion concentration of ambient rainfall should have no effect on forest-floor arthropods and the additional sulfate may enhance numbers of decomposer arthropods in soil.

Here we discuss how experimental acidification of the forest floor alters numbers of macroinvertebrates in soil. These partial results are from two experiments, one in northern Mississippi and the other in southern Mississippi and eastern Texas, on the effect of acid treatment on abiotic and biotic components of the forest floor. Both studies were conducted in southern pine forests that had not been burned for at least 20 years and were, at best, marginal habitat for woodcocks.

Methods

Study Areas

Experiment One

Field studies were conducted in a fully stocked, 45-year-old loblolly pine (*Pinus taeda*) plantation established for erosion control in the Holly Springs National Forest, Lafayette County, Mississippi. A few large oaks (*Quercus* spp.) were present on the site. The sparse understory consisted of flowering dogwood (*Cornus florida*), Eastern redcedar (*Juniperus virginiana*), sweetgum (*Liquidambar styraciflua*), and blackgum (*Nyssa sylvatica*). Large areas of the forest floor were covered with Japanese honeysuckle (*Lonicera japonica*) or poison ivy (*Toxicodendron radicans*). The soil texture was either a Lexington silty clay loam or an Orangeburg-Ruston sandy loam. Total rainfall at the site during the 12 months of the study was 1,082 mm; volume-weighted pH of the precipitation was 4.6 (range = 3.9–5.1). A detailed description of the area is presented in Kress et al. (1990).

Experiment Two

A loblolly pine stand near Bay St. Louis, Mississippi, and a longleaf pine (*Pinus palustris*) plantation near Nacogdoches, Texas, were selected for study. The southern Mississippi site had nearly level, poorly-drained silty to loamy soils of the Atmore and Escambia series. These soils were saturated during wetter months (December–May), and water was at the surface for several days after heavy rains. This site was classified as wetland

(Committee for Wetland Delineation 1989) because of the hydric soil. The mixed-age loblolly stand was naturally regenerated and had a density of 3,660 trees/ha and a basal area of 33.5 m^2/ha. The sparse understory consisted of a few hardwoods and woody shrubs. Rainfall during 1 March–28 February was 1,539 mm in 1987–88 and 1,383 mm in 1988–89. The respective volume-weighted pH of the rainfall during the same 2 years was 4.55 (range = 3.74–6.84) and 4.51 (range = 3.80–6.55).

The eastern Texas site was level and had well-drained Woden fine sandy-loam soil. This 28-year-old stand of longleaf pines had a density of 1,350 trees/ha and a basal area of 36.8 m^2/ha. In June and July 1987, ground vegetation, primarily poison ivy, near some of the plots was treated with a light foliar application of herbicide (glyphosate and 2,4- dichlorophenoxy acetic acid) to reduce contact dermatitis in sensitive personnel. Total rainfall was 749 mm during the 1st year of the study and 1,011 mm during the 2nd year. The volume-weighted pH of the rainfall averaged 4.84 (range = 4.00–6.07) in the 1st year and 4.82 (range = 4.12-6.20), in the 2nd year.

Treatments and Sampling

Experiment One

Information on abundance and diversity of forest-floor invertebrates and their sensitivity to acids was lacking at the onset of the study, thus, two studies were conducted. First, seasonal abundance and relative acid-tolerance of soil invertebrates were determined by applying three different treatments (deionized water, H_2SO_4 at pH 4.0, H_2SO_4 at pH 3.0), replicated on seven 1-m^2 plots. Plots were examined 1 month later for macroinvertebrates. Second, the effect of multiple applications of acid solutions was studied by treating 27 1-m^2 plots (same three treatments, nine replicates each month for 1 year). The invertebrates on these plots were destructively sampled to end the study. Both short- and long-term studies began in April 1985 and were completed in March 1986.

One of three treatments was randomly assigned to 1-m^2 plots of the forest floor. Either 10 L of deionized water (control) or 10 L of acid solutions were sprayed on 1-m^2 plots. The addition of 10 L to a plot was the equivalent of 1 cm of precipitation. The acid solutions were mixed in the field by making a 1:10 or 1:100 dilution of H_2SO_4 at pH 2.0 with deionized water. A 10-L polyethylene garden sprayer fitted with a fan-type nozzle was used to apply all fluids. The nozzle size restricted the rate of flow such that 10 L of fluid were applied in approximately 10 min, thereby allowing sufficient time for the solutions to soak into the soil. The proximity among plots was >3 m. In addition to the 120 mm of deionized water or acid solutions, the uncovered long-term study plots received 1,082 mm of ambient rainfall.

Modified tensionless lysimeters (Jordan 1968) were installed at ground level beneath the fermentation (A_o) layer in 12 of the long-term study plots. Leachate was collected from 0.5 to 2.0 h after treatment and on the day following the first post-treatment rainfall. Ten sets of monthly samples were analyzed for pH from June 1985 through March 1986.

During sampling, litter was removed from each plot and placed on a large plastic sheet, and all macroinvertebrates from it were collected. The entire 1-m^2 plot was then excavated to a depth of approximately 24 cm, and the soil was placed on the plastic sheet for sorting by hand (Axelsson et al. 1971; Walther and Snider 1984). All macroscopic invertebrates, except termites (Isoptera), were collected and preserved in 50% isopropanol. Although the technique for collecting invertebrates was crude, alternatives were few because of the large volume of excavated soil. We assumed some consistency was obtained by having the same individual oversee all sampling. In the laboratory, samples of invertebrates were washed, transferred to clean alcohol solutions, sorted by taxon and age (e.g., larvae, pupae, and adults), blotted dry, and weighed to the nearest milligram.

Experiment Two

Thirty 1-m^2 plots in a randomized-block design with 10 replications (blocks) of three treatments (ambient, pH 4.3, and pH 3.6) were established at each location. In southern Mississippi, the forest floor microrelief was sufficient to permit the placement of 1-m^2 plots in areas that were not covered with water during most rainfalls; standing water was not a concern in the well-drained soils in Texas. At both locations, the plots were placed ≥3 m apart. Nine modified tensionless lysimeters were installed at ground level just below the fermentation (A_o) layer to collect leachate in litter from one plot of each treatment at three randomly selected blocks at each location.

Throughfall was intercepted on elevated, 2-m^2 corrugated fiberglass sheets and collected in plastic containers at each study block. The maximum stored volume per container was 120 L or the

equivalent of 6 cm of throughfall. Three identical collectors also were placed in open areas to provide samples of ambient rainfall at each site.

The acidity of throughfall was adjusted to pH 4.3 or 3.6 with a mixture of HNO_3 and H_2SO_4 (National Bureau of Standards 1984; Irving 1985) and sprinkled on appropriate plots within 7 days of each rainfall. We measured the H^+ activity of rainfall and throughfall with a portable pH meter with automatic temperature compensation. In southern Mississippi, treatment was postponed when standing water was on study plots. Stock solutions of HNO_3 and H_2SO_4 acid were made by adding 90 mL of 70% HNO_3 or 240 mL of 96.5% H_2SO_4 to 1 L of distilled water. One milliliter of each of these acid solutions was added to 1 L of distilled water to yield a solution of approximately pH 2.0. This solution was then used in the field to adjust the pH of the throughfall.

Between applications, plots treated with acid solutions were covered with corrugated fiberglass sheets raised 20 cm above the forest floor to allow air to circulate. Two 1-m long plastic gutters channeled throughfall running off the covers away from plots. Control plots were not covered during the 1st year because the work force was limited. During the 2nd year, both experimental and control plots were covered and additional throughfall was collected to apply to control plots.

One year after treatment, the invertebrates on half (5) of the 1-m^2 plots for each treatment at each site were destructively sampled. Litter and soil were examined for macroinvertebrates as previously described. On the remaining 15 plots at each location, the invertebrates were sampled at the end of the 2nd year.

Statistical Analyses

The effect of treatment on the number of invertebrates within plots was evaluated by a X^2 analysis (Conover 1971). The effect of treatment on the invertebrate biomass within plots was evaluated by a one-way ANOVA; seasonal changes in the invertebrate biomass by treatment were tested by a two-way ANOVA. Log or square-root transformations were applied to biomass data where appropriate (Sokal and Rohlf 1973). Large numbers of dipteran larvae (maggots) occurred in some plots. These maggots always were associated with fungi (*Boletus* spp.), which was in various stages of decay. We believe that numbers of maggots simply reflected the occurrence of this ephemeral food of maggots. Because fly maggots weighed 10–20 mg

wet weight (ww), we analyzed data including and excluding larval insects <30 mg ww to determine if an attraction to fruiting fungi was masking treatment effect. Finally, only invertebrates reported to be important in the diet of the woodcock and of a sufficient size (≥50 mg ww) to be of food value were analyzed independently.

Results

Earthworms found during this study were tentatively identified as Sparganophilidae (*Sparganophilius* spp.) and Eudrilidae (*Eudrilus eugeniae*) or Megascolecidae (*Diplocardia* spp.) Differentiation between *Eudrilus eugeniae* and *Diplocardia* spp. was not possible because only small or immature individuals were collected.

Experiment One

The numbers of millipedes and earthworms decreased significantly with acid treatment (X^2 = 81.92 and 27.21, respectively, df = 2; $P < 0.01$; Table 1). The density of earthworms was reduced in plots receiving a single application of H_2SO_4 at pH 3.0 during all months except April 1986 (Fig. 1). Earthworms were found in greatest numbers during December–April.

The total number of invertebrates did not differ between control plots and acid-treated plots (1,282, deionized water; 1,870, H_2SO_4 at pH 4.0; 1,666, H_2SO_4 at pH 3). The densities in the plots largely reflected the presence of small (i.e., <30 mg ww) larval insects. Irrespective of treatment, the invertebrate biomass, including larval insects <30 mg ww, was greatest in winter and spring and least in summer and fall (ANOVA; $P < 0.01$).

Fewer earthworms >50 mg ww were in the acid-treated plots than in the control plots (X^2 = 13.68, df = 2, $P < 0.01$; Table 1). The total number of insects and millipedes seemed to be greater in the pH 3.0 treatment plots ($n = 614$, $n = 705$) than in the pH 4.0 treatment plots ($n = 256$, $n = 103$) and in the control plots ($n = 289$, $n = 515$). But means were similar when individuals <50 mg were excluded.

The biomass of invertebrates collected in the long-term plots did not differ by treatment (one-way ANOVA, $P = 0.513$; Table 1). The mean (SD) biomass (g/plot) was 6.1 (7.0) of controls, 6.5 (6.9) of invertebrates in the pH 4.0 treatment, and 3.2 (2.9) of invertebrates in the pH 3.0 treatment. Variability among plots was high. When grouped by

Table 1. Abundance and biomass of invertebrates in a loblolly pine forest in northern Mississippi after single or multiple applications of deionized water (control), H_2SO_4 solution of pH 4.0, or H_2SO_4 solution of pH 3.0, 1985–86.

| | Control | | | pH 4.0 H_2SO_4 | | | pH 3.0 H_2SO_4 | | |
Class	%[a]	Number[b]	mg wet wt.[c]	%	Number	mg wet wt.	%	Number	mg wet wt.
Single treatment[d]									
Oligochaeta	63	5.1 (0.9)	809 (132)	65	4.8 (0.8)	852(140)	58	3.8 (0.8)	636(120)
Insecta[e]	70	2.2 (0.3)	414 (63)	69	2.0 (0.3)	468 (85)	70	2.2 (0.3)	414 (63)
Diplopoda	36	1.8 (0.6)	162 (46)	37	0.9 (0.2)	92 (20)	35	0.8 (0.3)	203(115)
Chilopoda	30	0.4 (0.1)	48 (12)	39	0.5 (0.1)	63 (13)	32	0.5 (0.1)	50 (10)
Multiple treatments[f]									
Oligochaeta	100	7.0 (1.8)	1076 (224)	67	4.4 (2.4)	628(393)	78	3.1 (1.6)	507(234)
Insecta[e]	100	3.9 (0.7)	748 (217)	100	3.9 (0.9)	577(113)	100	4.6 (0.9)	667(179)
Diplopoda[g]	56	33.1(33.3)	2100(1900)	56	1.1 (0.5)	71 (30)	44	2.0 (1.0)	148 (68)
Chilopoda	44	0.8 (0.3)	40 (21)	33	0.7 (0.4)	56 (32)	56	1.0 (0.4)	111 (42)

[a] Percent of plots containing each taxonomic group.
[b] Mean number (SE) per plot. Only individuals with a wet weight $\geq$ 50 mg are included.
[c] Mean (SE) wet weight.
[d] Eighty-four (7 plots, 3 treatments, 12 months) 1-m^2 plots were treated once and populations on them were destructively sampled the following month.
[e] Only larvae and pupae are included.
[f] Twenty-seven (3 treatments, 9 plots) 1-m^2 plots treated monthly for 1 year before sampling.
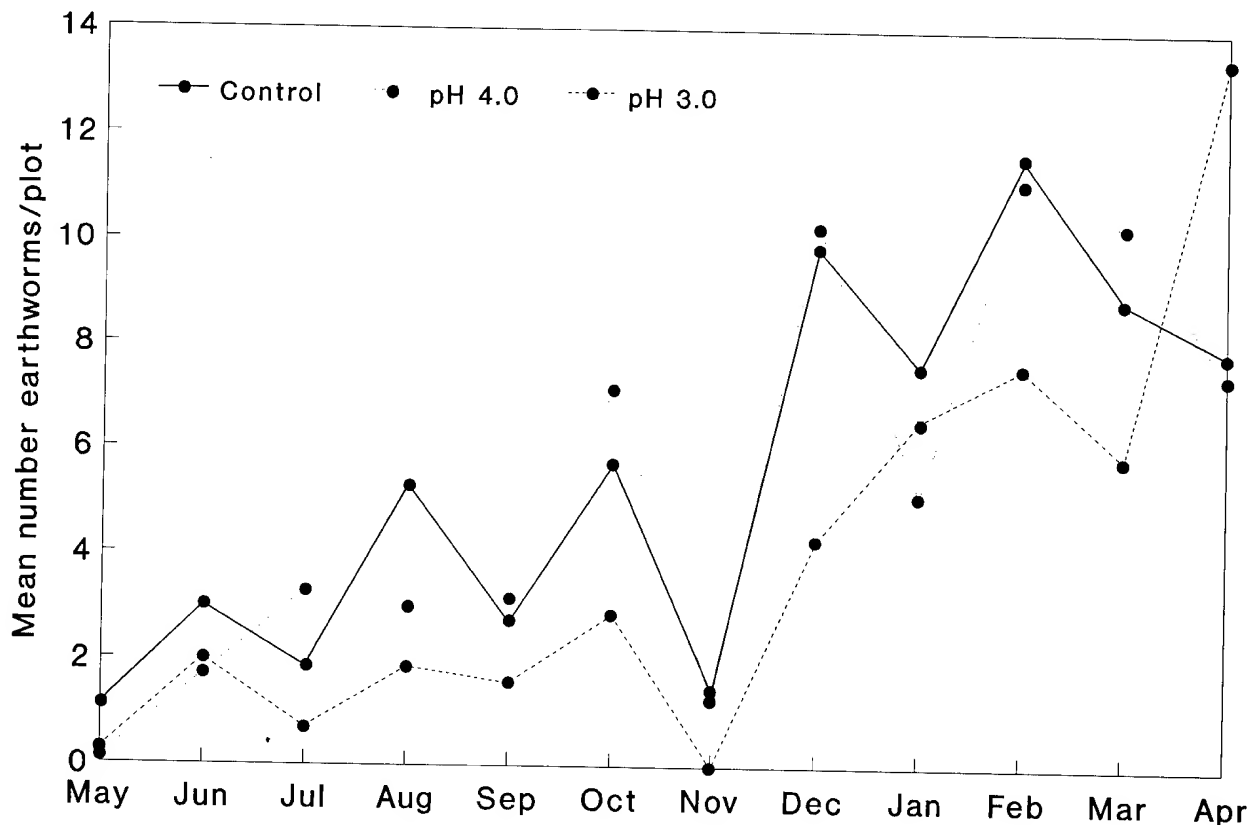
Fig. 1. Changes in the number of earthworms in 1-m^2 plots in a loblolly pine forest in northern Mississippi after a single application of deionized water or pH 4.0 or pH 3.0 H_2SO_4. Data are the mean of 7 plots/treatment/month.

Table 2. Numbers and wet weight of earthworms and other invertebrates excavated from 1-m^2 plots ($n = 5$) in southern Mississippi and eastern Texas after 12 or 24 months of treatment in 1988 and 1989.

| | Earthworms | | | | Other invertebrates | | | |
| | 12 months | | 24 months | | 12 months | | 24 months | |
Treatment	N/m^{2a}	g wet wt.^{b}	N/m^2	g wet wt.	N/m^2	g wet wt.	N/m^2	g wet wt.
Mississippi[c]								
Control	2.0 (2.0)	0.4 (0.4)	1.0 (1.0)	0.3 (0.3)	27.8 (5.1)	1.2 (0.7)	6.6 (1.0)	0.8 (0.3)
pH 4.3	3.4 (3.2)	0.7 (0.5)	0.4 (0.4)	0.1 (0.1)	23.6 (8.4)	0.8 (0.3)	8.2 (2.3)	1.0 (0.4)
pH 3.6	0.2 (3.2)	0.1 (0.1)	0.2 (0.2)	0.1 (0.1)	14.8 (6.1)	0.6 (0.3)	10.4 (2.6)	2.6 (0.9)
Texas[d]								
Control	71.2(21.2)	5.8 (1.9)	20.0 (5.0)	2.5 (0.6)	16.8 (3.4)	0.7 (0.2)	11.8 (1.5)	1.9 (0.2)
pH 4.3	26.2 (4.3)	2.2 (0.6)	24.4 (8.9)	3.3 (1.5)	10.2 (1.6)	0.8 (0.1)	16.8 (6.0)	1.0 (0.6)
pH 3.6	13.6 (5.7)	1.1 (0.4)	18.8 (6.3)	2.3 (0.9)	10.4 (3.3)	1.0 (0.7)	11.8 (0.9)	1.6 (0.5)

[a] Mean number (SE) per plot.

[b] Mean (SE) wet weight per plot.

[c] Because of the saturated condition of the soil at the time of excavation, earthworms were found only in four plots the 1st year and three the 2nd year in Mississippi; other invertebrates were found in all five plots.

[d] Earthworms and other invertebrates were found in all plots in Texas.
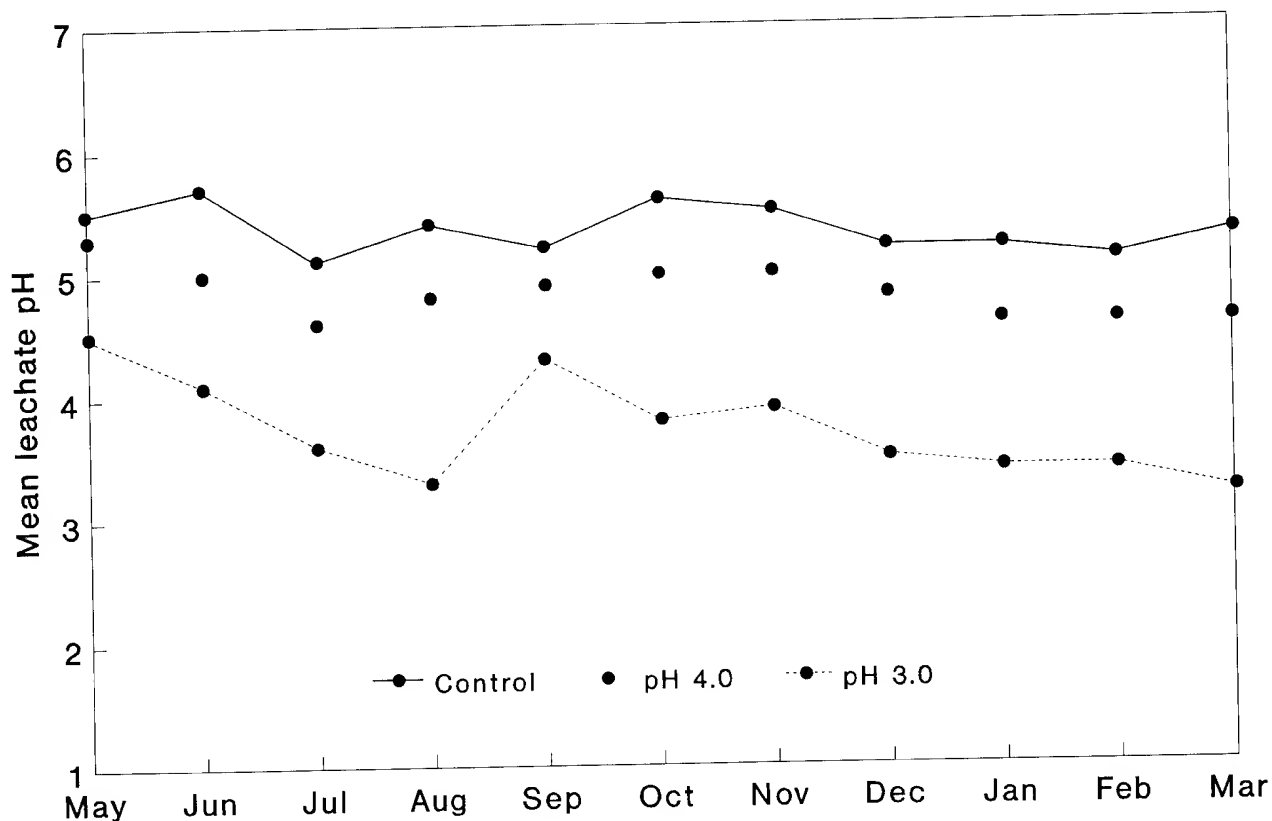
Fig. 2. The pH of spray leachate after monthly applications of either deionized water or pH 4.0 or pH 3.0 H$_2$SO$_4$. Data based on the mean of 4 lysimeters/treatement.

categories of ≤100 mg or >100 mg and compared by treatment, the earthworms did not differ by wet weight. As expected, litter neutralized some of the applied acid solutions. The pH of spray leachate that reached the soil was approximately 1 unit lower than that applied (Fig. 2), although no residual effect of pH was detected during the first rainfall after treatment. The soil pH was slightly higher in the acid-treated plots after 12 monthly treatments. The mean pH of samples of the upper 5–10 cm of the soil was 6.01 (0.21) on the control plots, 5.86 (0.39) on the pH 4.0 H_2SO_4 plots, and 5.59 (0.19) on the pH 3.0 H_2SO_4 plots.

Experiment Two

Because of low numbers, high variability, and small sample sizes (Table 2), the acid treatment had no effect on the larger invertebrates. However, treatment substantially reduced the numbers of earthworms in eastern Texas after 1 year ($X^2 = 248$, df = 2, $P < 0.01$) but not after 2 years ($X^2 = 4.13$ df = 2, $P > 0.10$). Although earthworms were in all plots in Texas, they were rarely found in the often saturated soils in southern Mississippi where only 7 of 30 (23%) plots contained earthworms. In acid-treated plots, the pH of the litter leachate, fermentation layer, and rhizosphere were slightly reduced, but pH of mineral soil was unchanged. These differences were significant ($P < 0.05$) in Texas but not in Mississippi (Esher et al. 1992).

In Texas but not in Mississippi, earthworms were the most abundant invertebrate. Irrespective of treatment, the wet weight of earthworms was greater than the total weight of other invertebrates combined (Table 2). Overall, the biomass of earthworms among plots was variable (0.0–2.7 g/m^2 in southern Mississippi and 0.3–9.5 g/m^2 in eastern Texas).

Discussion

The relation between acid deposition and forest floor invertebrates is complex and poorly understood (Strayer and Alexander 1981; Killham et al. 1983; Coleman 1983; Hagvar 1990). Our results support previous findings that densities of earthworms are lower under acid conditions (Reynolds 1971; Hagvar 1980; Ma et al. 1990; Kuperman 1990) but add to the confusion about effects of acid rain on soil arthropods (Baath et al. 1980; Hagvar and Kjondal 1981; Hagvar and Abrahamsen 1984; Craft and Webb 1984). Aside from earthworms and dipteran larvae, most larger invertebrates in the forest floor seemed unaffected by the treatments we applied. Treatment effects on other soil organisms are reported elsewhere (Esher et al. 1992). Considerable research into the effects of acid deposition on the forest floor community is required.

Overall, the effects of mild acid treatments on earthworm numbers were striking. A single treatment of pH 3.0 H_2SO_4 was sufficient to substantially reduce earthworm numbers under pines, but our studies provided no insight into whether worms migrated from acid-treated plots or simply moved deeper into the soil. Whether the earthworms responded directly to the acid treatments or to the resultant mobilization of metals in the soil is unknown. Certain metals, including brass, are known to be toxic to earthworms (Wentsel and Guelta 1987). The pump-type sprayers used in northern Mississippi had brass fittings that may have introduced small amounts of copper or zinc ions into the acid-treated plots. Whether earthworms could have detected these metals at low concentrations is unknown but unlikely because the plastic watering cans used in southern Mississippi and eastern Texas were free of metal contamination, yet earthworms in those areas responded similarly to the treatment.

Reasons for the low numbers of earthworms in the control plots in eastern Texas during the 2nd year are unknown but may be attributable to inter-plot variation and to small sample size. However, other variables cannot be excluded. Control plots were not covered during the 1st year but were covered during the 2nd year. Covers or increased activity around the plots during treatment may have disturbed the earthworms. Furthermore, the pines in Texas were planted in raised beds, and furrows were still evident at the time of excavation. Small changes in the surface microrelief can drastically affect soil moisture, especially during droughts. A prolonged dry spell occurred in Texas before we excavated the plots. Drier conditions reduce earthworm numbers near the surface (Reynolds 1970).

In general, pine forests seem to be marginal habitat for most soil invertebrates. The density of earthworms was lower in Mississippi and similar in eastern Texas to other forested sites in the South. In hardwood forests in eastern Tennessee, earthworm densities of 1–55 (Reynolds 1970) and 2–96 (Reynolds 1971) individuals/m^2 have been reported. Kalisz and Dotson (1989) reported a density of 2–112 earthworms/m^2 for a variety of habitats in the mountains of eastern Kentucky. The biomass of earthworms in eastern Texas was at the

low end of the range of earthworms in Tennessee forests (Reynolds 1970, 1971). The earthworm biomass in pine forests in Mississippi was well below the average reported from other southern forests (Reynolds 1970, 1971).

Southern 28-year-old or older pine forests seem to be of minimal value to woodcocks seeking invertebrates. However, the density of macroinvertebrates in a site was highly variable. Species like the woodcock, which forage by probing, may be able to locate pockets where earthworms or other invertebrates are relatively abundant. Therefore, pine forests may function as overflow areas when woodcock populations are high or food is scarce. The effect on soft-bodied invertebrates from small increases in acidic deposition may be greater in generally acidic soils, as under pines, than in sites with more alkaline or better-buffered soils. In eastern Texas, where earthworm densities in control plots exceed the threshold level (30–40 worms/m^2) for suitable woodcock habitat (Parris 1986), acid treatment reduced earthworm numbers to levels that do not support woodcocks.

Given the importance of earthworms in the diet of woodcocks, any variable that decreases the biomass of earthworms has a limiting effect on woodcock populations. Preliminary reports of reductions in earthworm densities along pH gradients are consistent with our findings (Reynolds 1971; Kuperman 1990). Recent surveys revealed that woodcock populations are declining (Bortner 1990). If earthworm populations are adversely affected by acid deposition, the number of woodcocks may continue to decline. Although some earthworm species are acid-tolerant (Bodenheimer 1935), pH is of prime importance in determining limits of earthworm distribution (Satchell 1956). Additional studies are needed to determine more about the effects of acid rain on earthworm species preferred by woodcocks (Reynolds 1977).

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The Ruffed Grouse Society—Efforts for Woodcocks—
Past, Present, and Future

by

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The primary goal of the Ruffed Grouse Society is to improve the environment for the ruffed grouse (*Bonasa umbellus*), American woodcock (*Scolopax minor*), and other species of forest wildlife. Obviously, as one of two featured species, the woodcock receives considerable attention from the society. The society's efforts have concentrated on three separate, yet equally important initiatives: research, education, and management.

Since the early 1980's when federal funding under the Accelerated Research Program for Webless Migratory Shorebirds ended, the society has contributed over $160,000 to various research on the woodcock throughout the United States, one of which is still underway on the Upper Peninsula of Michigan. These studies were of habitat use in the breeding and wintering areas. Some information from these studies was presented at this symposium.

Research by volunteers was initiated in Michigan by Andy Ammann in the early 1960's and offers members of the society a unique opportunity to collect information for management. Each year, the Grand Traverse Chapter of the society sponsors a woodcock banding workshop. At this workshop, 4–12 experienced banders introduce 40–100 enthusiasts to the technique of using pointing dogs to capture woodcock broods for banding. In 1989, 1,169 woodcocks were banded by 48 different banders. To date, approximately 11,000 birds have been banded in this manner in the state of Michigan.

From this pool of marked woodcocks, approximately 5% of the bands are returned. These returns provide valuable information on movements and migration. Perhaps more important than the biological data is the interest in the woodcock that is generated by these volunteers. During the symposium many speakers stated that nothing occurs to benefit the woodcock without pressure from the public. Volunteers like the banders generate the interest that creates pressure from the public.

Education by the society is directed at the public and at the managers of natural resources. In 1987, 80 people attended a workshop in Portland, Maine, that was co-sponsored by the society, the U.S. Fish and Wildlife Service, the Wildlife Management Institute, and the American Forest Council. This workshop was designed to promote the incorporation of guidelines for the development of woodcock habitat into land management of publicly owned and, more importantly, industrial forests. The management of industrial forests was emphasized because 47% of the commercial forests in Maine are owned by the forest-products industry. This is the largest aggregate corporate ownership of any state.

The workshop generated several recommendations. Primary among these recommendations was a proposal to have a team of professionals in each northeastern state act as a clearinghouse of information for individuals interested in the development of woodcock habitat.

These teams were identified for several northeastern states. Have they been utilized? Hardly. This lack of activity may be symptomatic of a lack of interest in the woodcock. I certainly hope that this is not the case.

In September 1988, the Grand Rapids, Minnesota, chapter of the society sponsored the Great Lakes Woodcock Management Symposium. Over 150 professionals and woodcock enthusiasts from Wisconsin, Minnesota, and Michigan attended. The primary goal of the workshop was to introduce participants to the concepts of woodcock ecology and to provide examples of habitat management, so that the participants could capitalize on oppor-

tunities to benefit the woodcock through habitat manipulation.

This week we are attending the Eighth Woodcock Symposium, the first such event since 1980. Ten years passed without organized national education specifically devoted to the woodcock. Again, this suggests a lack of interest and a lack of funding. Perhaps the former is an unavoidable consequence of the latter.

In 1985, the society initiated a Management Area Program to foster the development of quality habitat for the ruffed grouse and the woodcock in public forests. Cooperating land management agencies supply the land base, and the society supplies technical and financial assistance. Currently, over 89,000 ha on 120 different areas are enrolled in this program. Projects are being developed in 22 national forests in 17 states. County-owned forests account for 17% of the commercial woodland in Minnesota and for 9% in Wisconsin where the society entered into cooperative agreements with 24 of 43 counties with forest management.

In the Great Lakes region, aspens (*Populus* spp.) are the key to the development of woodcock habitat primarily because of their abundance, distribution, and marketability. The aspens supply much of the region's fiber market, which results in the creation of woodcock habitat. That is a tough combination to beat.

The Ruffed Grouse Society supports the maintenance of aspen forests. The society promotes aspen regeneration through a variety of methods including construction of logging access systems, cuts of noncommercial stands, and regeneration of pre-commercial stands. Aspens are without question the key to production of woodcocks in the Great Lakes region. The Ruffed Grouse Society strives to ensure that aspens remain a viable and abundant resource.

Analysis of data from the singing-ground survey indicates that woodcock populations in the eastern United States have decreased an average of 1.8%/year since 1968 (Bortner 1990). This significant long-term decline is primarily the result of the loss of early successional habitat and changes in land-use patterns.

Unlike the Great Lakes region, much of the Northeast has a relatively small market for wood fiber. The result of this relatively low rate of harvest is intuitively obvious. From 1972–83, the abundance of hardwood seedling and sapling stands decreased 24% in Vermont (Frieswyk and Malley 1985a) and 59% in New Hampshire (Frieswyk and Malley 1985b).

Even in Maine, the nation's second leading paper producer, hardwood seedling and sapling stands decreased 37% between 1971 and 1982 (Powell and Dickson 1984). Much of Maine is devoted to softwood production and, although recently regenerated stands can have a substantial deciduous component and thereby provide suitable habitat for the woodcock, the young softwoods in these stands are often released from this deciduous competition through the use of herbicides (G. F. Sepik, U.S. Fish and Wildlife Service, personal communication). This practice severely limits woodcock production.

Through the Management Area Program in 1991, the society initiated an expansion of habitat development into the primary wintering range of the woodcock. Yesterday's addition of the U.S. Fish and Wildlife Service to the preexisting Memorandum of Understanding between the U.S. Forest Service and the Ruffed Grouse Society should facilitate the establishment of cooperative projects on national wildlife refuges throughout the southern United States. Special emphasis will be placed on the initiation of management in Louisiana.

Changes in the use of land and forests suggest that acreage of aspens will continue to decrease in the Great Lakes region. This loss will be particularly apparent on privately owned forests because aspen stands on these properties are often poorly managed, if managed at all. This loss of aspens will probably level off in 15–20 years as the supply of currently mature, operable stands becomes exhausted and inoperable stands succeed to other forest types. The forest in the Northeast will probably continue to mature. In short, the current decline in the abundance of woodcock habitat throughout the Northeast and the resulting negative effect on woodcock populations is expected to continue.

Recent concerns by a very vocal and politically astute segment of the public may well force a change in management on public lands to one of far less active management. Recent problems by the U.S. Forest Service during the implementation of forest plans is an example of how resource management may indeed be changing. An increasing public with divergent views is demanding that its voice be heard. This in itself is not the problem. The problem arises when the public refuses to recognize the validity of ideas of competing voices.

Increased public involvement in resource management is not limited to national forests. State, county, and local officials are coming under scrutiny by increasingly active, yet not necessarily

informed constituent groups. Perhaps this burgeoning preservationist sentiment is simply a manifestation of a short-term swing to the left of the pendulum that represents public opinion, and in time the use of forest resources through sound management will once again be in vogue.

What can we in this room who are ostensibly at least as concerned with the fate of the woodcock as any other group do to secure the future of the bird? We have to become far more proactive. We must carry the message of resource management to every sportsmen's club, Rotary, Kiwanis, and Lions group. We must become regular contributors to local newspapers and become recognizable faces on local television stations.

If we wait until confronted, we are forced to respond and lose the ability to set the agenda. Neither resource management in general nor specifically the interest of species that require early successional habitats are served by professionals unwilling to become proactive in the public arena. The Ruffed Grouse Society strives to provide resource managers with information necessary to create an informed public.

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The Ecology and Management of Wintering Woodcocks

by

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Abstract.   The southeastern United States is the primary wintering area for most of the continental population of the American woodcock (*Scolopax minor*). Woodcocks are relatively abundant in suitable habitat, but temperature and soil moisture influence yearly patterns of distribution. Most individuals arrive in wintering areas between October and mid-December; northward migration begins in January or February in the southernmost states. Breeding is initiated in wintering areas and, in some years, substantial nesting occurs. Breeding peaks in February and March and is influenced by temperature. Little is known about survival or habitat use after the brood-rearing period. Daytime habitat varies from regenerating forests to mature stands; bottomland hardwoods, pines, and pine-hardwood types are used. Characteristics of the understory have a significant influence on habitat suitability, and vines play a key role. Nighttime habitat includes wet pastures, fallow fields, and agricultural fields. Little is known about habitat management for wintering woodcocks except for inferences from studies that described consistently used areas. Except in Louisiana, there is no tradition of woodcock hunting in the Southeast; most woodcocks are harvested incidentally to other small game.

Key words: American woodcock, habitat, management, migration, reproduction, *Scolopax minor*, surveys, Southeast, wintering range.

Although most of the continental population of the American woodcock winters in the Southeast, less is known about the species there than in the northern breeding range. Before the 1970's, Glasgow (1958) was the primary source of information on woodcocks in the Southeast. Then in 1967, the Accelerated Research Program for Webless Migratory Game Birds (ARP) was established and funded much new research. Although some work continues, the termination of ARP resulted in the cessation of most research on woodcocks in the Southeast. Many of the studies I cite in this review of the ecology and management of wintering woodcocks resulted from ARP.

Distribution

Woodcocks winter from Maryland and Virginia across the South Atlantic and Gulf States to eastern Texas and northward through eastern Oklahoma into southern Missouri (Owen 1977). The northern border of the wintering range excludes most of Tennessee and portions of northern Alabama and Georgia; however, during mild winters, substantial numbers of woodcocks are in Tennessee (personal observation) and northern Georgia (Pursglove 1975). If the wintering range can be defined as "a location in which individuals routinely spend more than a few days in a non-migra-

tory status," the northern border of the wintering range, during some years, extends farther north than depicted by Owen (1977).

Studies of banded birds revealed two relatively distinct subpopulations separated approximately by the Appalachian Mountains (Martin et al. 1969; Krohn and Clark 1977). Although there are exceptions, woodcocks from the Lake States usually winter in Louisiana, Mississippi, and other states west of the Appalachians, whereas those from the Northeast usually winter in the Middle and South Atlantic States. Therefore, two management regions (eastern and central) were established for administrative purposes (Coon et al. 1977). After analyzing data from birds banded during 1929–83, Wood et al. (1985) reported that 94–97% of the birds recovered on the wintering range were originally banded in that same region.

Researchers formerly believed that most of the woodcock population wintered in western Mississippi and central Louisiana, particularly in the Atchafalaya River basin and nearby parishes (Glasgow 1958; Sheldon 1971). After studies were initiated in other portions of the wintering range, however, woodcocks were found to be abundant in Alabama (Causey 1981), Mississippi (Roberts et al. 1984), Texas (Whiting and Boggus 1982), North Carolina (Stamps and Doerr 1976), South Carolina (Pace and Wood 1979; Ingram and Wood 1983), and Georgia (Pursglove 1975). The status of wintering populations in the other southern states is unknown.

Temperature and rainfall are two primary variables that influence the annual distribution of woodcocks during winter. In mild years, some woodcocks remain as far north as Maryland (Sheldon 1971), West Virginia (Kletzly 1976), and Kentucky (Russell 1958) and may be relatively common in North Carolina (Stamps and Doerr 1976) and Tennessee (personal observation). Several consecutive days of below-freezing temperatures force woodcocks to move southward (Roberts and Dimmick 1978; Ingram and Wood 1982; Rushing and Doerr 1984). Mendall and Aldous (1943) cited instances of woodcocks congregating in large numbers in South Carolina and southern Louisiana in response to temperatures below freezing farther north. When freezing conditions extend to the Gulf of Mexico, woodcocks may be forced outside traditional wintering areas into Texas or Florida. M. W. Olinde (Louisiana Department of Wildlife and Fisheries, Baton Rouge, Louisiana., personal communication) reported that few woodcocks were observed in southern Louisiana during December 1989, a period of extremely low temperatures, and he speculated that most had moved into Texas.

Soil moisture influences the distribution of woodcocks by affecting the abundance of earthworms or the birds' ability to forage. Adequate soil moisture is necessary for earthworms to survive and reproduce (Edwards and Lofty 1977) and apparently for woodcocks to probe successfully for them (Boggus and Whiting 1982). Boggus and Whiting (1982) observed that woodcocks were absent from one study plot when it was dry but used the site extensively after heavy rains had saturated the soil.

Much of the remaining forested habitat in some southeastern bottomlands (e.g., the delta in western Mississippi) occurs on soils with a high clay content (personal observation). Because these soils harden when desiccated, woodcocks that arrive in the fall cannot forage effectively. These unfavorable conditions may explain the extensive use by woodcocks of seepage and streamside coverts in upland pine (*Pinus* spp.) or pine-hardwood stands in Louisiana (Glasgow 1958) and Texas (Kroll and Whiting 1977; Boggus and Whiting 1982).

Migration

Sheldon (1971), relying mostly on data from Louisiana (Glasgow 1958), summarized the chronology of woodcock migration. Woodcocks leave northern areas in late summer and early fall, and some arrive on southern portions of the wintering range as early as October. Most birds arrive later, however, and move into the southernmost states during late November (Glasgow 1958). Numbers in the deep South usually peak by mid-December. This pattern of fall migration was confirmed by studies in North Carolina (Stamps and Doerr 1976), South Carolina (Pace and Wood 1979), and Georgia (Pursglove 1975).

The migration from southern portions of the wintering range begins in January during years with above-average temperatures (Glasgow 1958) and is well underway by mid-February in most years. By late February, most woodcocks have vacated coverts in South Carolina (Pace and Wood 1979). In eastern Texas, Tappe et al. (1989) noted that numbers of courting woodcocks usually decline during late February. The migration through Tennessee and North Carolina normally occurs from mid-February to early March (Roberts and Dimmick 1978; Connors and Doerr 1982). Unusu-

ally high or low temperatures may alter this typical pattern by a few weeks.

Local Moves

Our knowledge of winter activity patterns is limited. Horton and Causey (1979) documented that woodcocks wintering in Alabama establish home ranges that may be used for a substantial period. Data for individual birds were not presented, but the average length of radio-monitoring was 32 days; one bird was tracked for 75 days. Daytime home ranges of 12 woodcocks (of different sex and age) averaged 9.2 ha (SD = 2.3 ha). When nighttime habitat was included, home ranges were larger, averaging 14.9 ha (SD = 6.0 ha). Ingram (1981; cited by Wood et al. 1985) reported that the average home range of five woodcocks monitored in South Carolina was 19.6 ha.

Abundance

Although few estimates of population size from wintering areas are available, all indicated that woodcocks are locally abundant. For example, surveys of hunters in South Carolina (Ingram and Wood 1983) and Georgia (Pursglove 1975) yielded identical flush rates of 1.6 birds/h. A study in Alabama, where numbers and quality of searchers and dogs were controlled (Causey 1981), revealed slightly higher rates (2.3 flushes/h). These flush rates are similar to those from northern states but should not be surprising because the entire continental population is concentrated in the Southeast during winter.

Population Monitoring

Surveys to gather information on harvest and the sex and age structure of the population are conducted periodically in a few southern states (Wood 1985; Olinde and Prickett 1991). To date, none of the state fish and game agencies or the U.S. Fish and Wildlife Service has developed a sampling framework to reliably estimate actual numbers or trends of wintering populations.

Monitoring consistently used roosting fields is one method of indexing local wintering populations. Glasgow (1958) experimented with various ways of counting roosting woodcocks and found that surveys by observers on horseback were the most effective. Flushing birds by dragging ropes across fields and by having participants tally individuals flying into fields at dusk produced acceptable results but were less efficient. Data from banding at night could also be incorporated into monitoring.

Surveys of males on singing grounds as conducted by Tappe et al. (1989) in eastern Texas also have potential for monitoring wintering populations. Tappe et al. (1989) recommended that surveys be conducted from January to late February and that males identified during their songs in flight (as opposed to males that were only heard peenting) be included in the sample. A disadvantage of using counts of courting males to monitor local populations is the inability of observers to differentiate between resident and migrant birds. The timing of surveys is also difficult; cooperators have to conduct surveys on short notice when conditions are favorable.

Reproduction

Previous research revealed that male woodcocks initiate courtship in wintering areas (Glasgow 1958), but breeding there was believed to be insignificant. After substantial nesting (3 nests and 10 broods on a single 132-ha farm) in Alabama was documented (Causey et al. 1974), others studied nesting in North Carolina (Stamps and Doerr 1977; Rushing and Doerr 1984), Tennessee (Roberts and Dimmick 1978), South Carolina (Pace and Wood 1979), Texas (Whiting and Boggus 1982), and Louisiana (Olinde and Prickett 1991). Except in Louisiana and South Carolina, researchers documented extensive breeding of woodcocks.

Males in wintering areas may begin displaying as early as November (Roboski and Causey 1981) or December (Glasgow 1958; Stamps and Doerr 1977), but the birds do not reach breeding condition until mid-January or early February (Roberts 1980; Rushing and Doerr 1984). Data on females are less clear, but the presence of spermatozoa in the urovaginal glands of some females confirmed that the breeding condition is reached by late January (Walker and Causey 1982). Nine of 64 (14.1%) females Walker and Causey (1982) collected in January and February contained spermatozoa and, when only those females entering their second breeding season (n = 42) were considered, the percentage was greater (21.4%). Using the presence of yolk in the follicles as indicating readiness to ovulate, it was estimated that 38.5% of the

females collected in February ($n = 39$) had already bred or would soon breed. Timing apparently varies however; during the previous year, the estimate was only 4.3%.

Nesting begins in more southerly portions of the wintering range in late January (Causey 1981) or early February (Whiting and Boggus 1982) and peaks in February (Causey 1981). Dates of nesting are somewhat later farther north (Roberts and Dimmick 1978; Rushing and Doerr 1984).

Besides the well-known effect of photoperiod on avian reproduction, the onset and extent of breeding by woodcocks also seems influenced by temperature. In North Carolina, woodcocks nested in January during mild winters (Stamps and Doerr 1977) but later in years with snow and low temperatures (Rushing and Doerr 1984). Mason et al. (1982) compared serum protein and serum cholesterol levels to ovarian maturation and reported that no females were in the final stages of development during an unusually cold February in Alabama. Causey et al. (1987) reported that an index of the abundance of nests and broods and average January temperatures positively correlated. The authors speculated that warmer temperatures stimulate breeding, whereas low temperatures have a suppressing effect and cause many woodcocks to migrate northward before breeding.

We know little about the species' habits in the wintering range after nesting. The only data on chick survival is from Alabama where Wiley and Causey (1987) reported that the probability of survival of chicks during the first 15 days after hatching was 0.95. After fledging, survival declined to 0.67, but the authors noted that human disturbance may have contributed to the decline. Woodcocks occur in the Southeast throughout spring and summer, but sightings decline after May (personal observation) or June (Horton and Causey 1981). The reason for the decline is unknown but may be due to the exodus from the wintering range by some birds. Two woodcocks (one female with a brood and one chick from another brood) banded in Alabama during spring were recovered by hunters in Michigan that fall (Causey et al. 1979). Furthermore, the longest time that radio-tracked young were followed before dispersing is 8 weeks (Horton and Causey 1981).

Habitat

Much of the research into winter habitat has centered on daytime cover. Species composition and structure of vegetation in the vicinity of flush sites were described in several publications (Dyer and Hamilton 1977; Kroll and Whiting 1977; Causey 1989). Now, some researchers question whether that approach can differentiate among various levels of habitat quality because it is not known whether survival of woodcocks differs by habitat type. Sepik et al. (1989) expressed concern that investigations did not define optimum conditions but simply described the best available habitat in a given area. These authors considered the wide variability in habitat characteristics among sites as support for their contention. Unfortunately, data that relate survival to habitat in wintering areas are unavailable. One unpublished study (U.S. Fish and Wildlife Service) was conducted in Georgia, and another is ongoing in South Carolina and Georgia.

Daytime Cover

Daytime cover that woodcocks use on the wintering range varies widely. Sites range from bottomland hardwoods (Glasgow 1958; Pursglove 1975; Dyer and Hamilton 1977; Horton and Causey 1979; Pace and Wood 1979; Roberts et al. 1984) to upland pine and pine-hardwoods (Glasgow 1958; Kroll and Whiting 1977; Johnson and Causey 1982). In bottomlands, daytime cover is usually in the middle zones of the floodplain (i.e., zones III, IV, and V described in Wharton et al. 1982). Common species in the overstory include sweetgum (*Liquidambar styraciflua*), sugarberry (*Celtis laevigata*), red maple (*Acer rubrum*), American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), and various oaks, (e.g., laurel oak [*Quercus laurifolia*], willow oak [*Q. phellos*], and swamp chestnut oak [*Q. michauxii*]). These zones are above the oxbows typically dominated by baldcypress (*Taxodium distichum*) and swamp tupelo (*Nyssa aquatica*) but at lower elevations than upland forests. Although they favor the middle zones, woodcocks sometimes use other portions of the bottomland complex. For example, Pace and Wood (1979) found woodcocks concentrated in cypress-tupelo swamps in South Carolina. Natural levees where black willow (*Salix nigra*), American sycamore (*Platanus occidentalis*), and boxelder (*Acer negundo*) predominate also may be used, especially when flooding forces woodcocks to vacate other habitats (personal observation).

The use of pine and pine-hardwood stands by woodcocks was noted by Glasgow (1958), but until recently these upland forest types had not been

regarded as important habitat. We now know that wintering woodcocks use pine forests that vary from clear-cuttings of loblolly (*Pinus taeda*) and shortleaf pines (*P. echinata*; Kroll and Whiting 1977; Boggus and Whiting 1982) to sawtimber-sized stands of longleaf pines (*P. palustris*; Johnson and Causey 1982). In these stands, however, the specific areas woodcocks use often are depressions or drainages dominated by hardwoods (sweetgum, redbay [*Persea borbonia*], blackgum [*Nyssa sylvatica*], sweetbay magnolia [*Magnolia virginiana*] and various oaks; Glasgow 1958; M. K. Causey, Auburn University, personal communication; S. D. Parris, Fort Polk, Louisiana, personal communication).

Only a few studies of daytime habitat in wintering areas were quantitative, and different study designs hinder comparison of data. In Louisiana bottomland hardwoods, Dyer and Hamilton (1977) found that dense stands of small-diameter trees provided optimal conditions for woodcocks. The average basal area of trees (dbh greater than 23 cm) near flush sites was 7.7 m^2/ha, and averages in these researchers' four study areas ranged from 7.3 m^2/ha to 8.3 m^2/ha. Kroll and Whiting (1977) reported that in eastern Texas, a high basal area of pines (9.5 m^2/ha) was associated with use by woodcocks. No specific information on the structure and composition of the overstory and midstory was presented in either study.

Causey (1989) reported high variability in habitats used by woodcocks in Alabama's seven physiographic regions. For example, overstory basal area averaged 15 m^2/ha over all the regions but ranged from 10 m^2/ha to 27 m^2/ha. Stem density in the upper portion of the midstory was similarly variable, averaging 2,897 stems/ha in the Appalachian Plateau and 24,455 stems/ha in the Piedmont region. Considering the wide range of conditions (e.g., stem density of 0 stems/ha to nearly 2 million stems/ha in the lower portion of the

midstory; Table), the mean value of any strata probably reveals little about habitat suitability for woodcocks.

Causey (1989) identified proximity to openings or ecotones, pH of soil, and accessibility of the substrate as important features in characterizing woodcock habitat and concluded that woodcocks were tolerant of a broad range of conditions in cover types he termed "moist thickets." His study and those of Kroll and Whiting (1977), Pace and Wood (1979), and Roberts et al. (1984) revealed that wintering woodcocks are adaptable and capable of using a variety of forest types for daytime cover.

A close association between woodcocks and the composition of the understory, particularly the presence of vines, has been observed throughout the wintering range. Important species include greenbriars (*Smilax* spp.), Japanese honeysuckle (*Lonicera japonica*), grape (*Vitis* spp.), poison ivy (*Toxicodendron radicans*), rattan vine (*Berchemia scandens*), and trumpet creeper (*Campsis radicans*). In addition, blackberries and dewberries (*Rubus* spp.) and shrubs, such as switchcane (*Arundinaria tecta*), wax myrtle (*Myrica cerifera*), and gallberries (*Ilex* spp.), are also important in some areas. The understory is a complex of microhabitats that provides woodcocks with daytime cover. Because woodcocks are often where light intensities are approximately 4.5 ft.-candles (Dyer and Hamilton 1977), a diverse understory may contribute to habitat quality because different covers are under different light conditions.

As Sheldon (1971) and Rabe (1977) noted in northern states, the significance of the understory in daytime coverts is not limited to the wintering range. In fact, Rabe (1977) considered the understory the most important structural feature of daytime cover, defining it as "a composite of various elements, including number of saplings and shrubs, horizonal obstruction, and ground cover."

Table. Vegetative characteristics of covers used by American woodcocks in the Lower Coastal Plain of Alabama, 1980–85.

Variable[a]	(Number/ha) N	Canopy cover (%) Mean	Canopy cover (%) Range	Stem density Mean	Stem density Range
Ground cover	125	15	0–100	88,677	0–545,870
Understory	125	29	0–100	102,767	0–832,390
Lower midstory	125	49	0–100	130,469	0–1,991,017
Upper midstory	125	55	0–100	148	0–14,820

[a] From Causey (1989).

When modified by including vines, this definition also is appropriate for wintering areas.

Structure of winter habitat varies from dense, regenerating stands, which are slightly layered or vertically stratified, to open sawtimber stands with a distinct midstory and understory. In some locations, an overstory may not even be present (Causey 1989). Studies revealed a compensatory relation between overstory and understory. If stem density is high in the overstory, only a sparse understory is required; as stem density decreases, development of the understory must increase to provide acceptable cover. This relation, described in the habitat suitability index model for the wintering range of the woodcock (Cade 1985), may partly explain the high variability among key habitat variables.

Two aspects of daytime habitat between the wintering range and breeding range differ. First, wintering woodcocks commonly use stands of mature timber if adequate understory exists (Roberts et al. 1984). In the breeding range, woodcocks use mainly early successional forests (Sheldon 1971; Sepik et al. 1981). Second, vines are an important component of the understory of the daytime cover throughout much of the wintering range but not in the primary breeding areas in the north.

Nighttime Habitat

A shift at dusk from woody cover to more open habitat, primarily pastures and fields, has been reported throughout the wintering range (Glasgow 1958; Horton and Causey 1979; Conners and Doerr 1982). Feeding is presumed to be the primary reason for woodcocks using openings at night (Glasgow 1958; Sheldon 1971; Stribling and Doerr 1985), although increased protection from predators also has been suggested (Dunford and Owen 1973). Woodcocks do not always make these daily movements but sometimes remain in forest habitat throughout the night (Glasgow 1958; Horton and Causey 1979). Although not well studied, movements seem to be influenced by weather and the phase of the moon (Glasgow 1958).

Several habitats, including pastures, fallow fields, agricultural fields, and young clear-cuttings serve as nighttime cover (Glasgow 1958; personal observation). In Louisiana, woodcocks commonly used taller, unmowed sections of pastures and especially wet areas (Glasgow 1958). Fields in which the vegetation was extremely dense often were unused until mowed or until grazing and trampling by cattle created a more open condition. In North Carolina, Connors and Doerr (1982) found that woodcocks preferred untilled soybean fields instead of fields of other crops. This preference may be because of the higher than average nutrient content of earthworms in soybean fields and the favorable microclimate in the furrows (Stribling and Doerr 1985).

Breeding Habitat

Male woodcocks use a variety of openings for singing grounds on the wintering range but seem to prefer brushy fields. Young pine plantations fit this category and are intensively used in some areas (Roberts 1978; Tappe et al. 1989). Early in the breeding season when densities of woodcocks are high, males seem to be relatively nonselective in their choice of singing grounds. They commonly display in a variety of open areas, including abandoned fields, agricultural fields, pastures, and woodland clearings (personal observation). The only detailed description of singing grounds in the wintering range is from the prairie region of Oklahoma (Lambert and Barclay 1975). There, males chose display sites on which percent cover of ground vegetation averaged 46% on mowed test plots and 67% where cattle had grazed. Vegetation cover on unused native prairie averaged 95%. The species of vegetation on the sites did not seem to influence use. This finding was similar to that reported by Sheldon (1971) in the breeding range.

The only studies of nest and brood habitat in the wintering range were conducted in Alabama. Roboski and Causey (1981) reported that woodcocks nested in intermediate-aged pole timber and open sawtimber stands. They described 32 nest sites in various habitats (61% in mixed pine-hardwoods, 17% in hardwoods, 13% in pines, and 9% in open areas) and noted that conditions varied substantially. Basal area of trees ranged from 5 to 37 m^2/ha, and densities of stems of woody seedlings and shrubs ranged from approximately 5,000 stems/ha to nearly 50,000 stems/ha. All nests were less than 1 m from the base of a sapling or were partly concealed by overhead cover. Nests were less often near field edges than reported from northern portions of the range (Bourgeois 1976; Gregg and Hale 1977). Causey (1989) was unable to identify important differences between nest locations and daytime flush sites but found that stem density was generally lower in brood habitat than in daytime cover, particularly in vegetation in the 0.3–3.0 m height range.

Habitat Management

Few studies addressed habitat management techniques for woodcocks in the wintering range. Glasgow (1958) observed that pastures and fallow fields that had been burned to remove dense vegetation were attractive to woodcocks for night roosts. Presumably, the removal of the dense ground-level vegetation facilitates foraging by woodcocks. The effects of prescribed burning on woodcock habitat also were studied in longleaf pine stands in Alabama (Johnson and Causey 1982). Woodcocks used recently burned stands for daytime cover more extensively than stands burned 2 or more years previously, suggesting that reducing ground vegetation improved habitat suitability. Abundance of food did not seem to be a major factor of habitat use by woodcocks because invertebrate densities were similar among sampled areas, regardless of the length of the interval between burnings. Johnson and Causey (1982) concluded that prescribed burning can be valuable for managing southeastern pine forests for woodcocks but urged caution because burned sites had a lower value than nesting cover. Furthermore, burning is often conducted during late winter and early spring when clutches and young broods might be adversely affected.

In Oklahoma, Lambert and Barkley (1975) created singing grounds by mowing openings in brush and prairie habitat. The number of courting males in the area increased because of presumed improved habitat conditions, which is consistent with findings from long-term studies of habitat manipulation in the Northeast (Dwyer et al. 1988).

Hunting

Except in Louisiana, the tradition of hunting woodcocks is not strong in the Southeast; woodcocks are usually harvested incidentally. Wood et al. (1985) noted, however, that changing demographics and a declining abundance of northern bobwhites (*Colinus virginianus*) may generate more interest in hunting woodcocks.

Until the mid-1980's, hunting seasons and the beginning of the breeding period of woodcocks overlapped in several southern states, and the overlap was of concern to some biologists (Stamps and Doerr 1976; Whiting et al. 1985). Late hunting seasons undoubtedly result in the harvest of some nesting woodcocks, although the effect on the overall population is thought to be insignificant (Whit-ing et al. 1985; Olinde and Prickett 1991). One potential effect, however, is that hunting during the migratory period might result in a disproportionate harvest of females because they do not leave wintering areas as early as males (Glasgow 1958). This skewed harvest might reduce the number of females genetically predisposed to breed in the South (Whiting et al. 1985). If such genetic predisposition exists, adverse effects on woodcock populations are probably more important in the southernmost parts of the range.

Beginning in 1985–86 in the eastern region and in 1991–92 in the central region, the hunting season was modified with a closing date on or before January 31. Thus, much of the controversy about late season hunting was averted.

Recommendations

Our understanding of woodcocks in the wintering range has improved considerably during the past two decades, but we still lack the detailed knowledge to formulate management and regulations that ensure the long-term well-being of the species.

More study is needed of the reproduction of the woodcock and of the concept of a distinct southern breeding population. We need to determine the temporal relations among follicle maturation, ovulation, mating, and nesting. We also need to monitor survival and dispersal of fledged young. Presumably some woodcocks, including immatures, remain in the Southeast throughout the summer, but little is known of their behavior or habitat requirements.

Fish and wildlife agencies in the primary wintering states need to develop and implement procedures to survey populations and estimate harvest. As hunting of woodcocks continues to gain in popularity, basic knowledge about the biology of the species must be available. Reliable data on populations will allow examination of the relation between wintering populations and habitat availability. Despite recent changes in the hunting season, the relation between temperature and nesting has yet to be clarified. This knowledge will enable agencies to adjust hunting seasons to coincide with high population levels while minimizing harm to nesting females. If temperature can be used to predict the onset of breeding, long-term weather records can be examined to determine appropriate dates for hunting seasons.

We know the general distribution of woodcocks during winter but need to conduct surveys in areas outside the usual wintering range that may serve as refuges during severe weather. Such areas, if they exist, could be essential to maintaining stable woodcock populations. States also need to initiate monitoring of key habitats to ensure their preservation.

Substantial effort must be devoted to improving our knowledge of woodcock habitat. The best cover may be identified by measuring survival of radio-marked woodcocks in different habitats. These data combined with information on home range and detailed analyses of vegetation should reveal much about the species' requirements. Studies should be conducted in a range of habitats from regenerating forests with little vertical stratification and horizonal diversity to mature forests with considerable structural complexity. Such studies require monitoring large numbers of individuals because cover preferences may vary by sex and age (Horton and Causey 1979; D. G. Krementz, Patuxent Wildlife Research Center, Southeast Research Group, Athens, Georgia, personal communication). The concept of habitat selection by light intensity (Dyer and Hamilton 1977) warrants further study and should be incorporated into these investigations.

Several aspects of habitats for night roosting need additional scrutiny. Monitoring the use by woodcocks of pastures, cropland, and areas set aside under provisions of various agricultural programs will identify preferred nighttime habitat. Research into habitat preference and differential use of roost areas by different segments of the woodcock population (Connors and Doerr 1982) is also needed.

The spatial aspects of habitat and acreages required by wintering populations need to be studied in the context of food. For example, we know that captive woodcocks eat an average of 150 g of earthworms/day, an amount that approximately equals their body weight (Sheldon 1971). It is possible that some coverts, especially small ones, may not sustain earthworm and other invertebrate populations at sufficient levels to support continual use by woodcocks throughout the winter. If true, movements in and among daytime coverts and to fields at night may be, in part, mechanisms to prevent depletion of food resources. Multi-year studies of habitats of varying quality need to be conducted to determine the responses of woodcocks to differing environmental conditions.

Gathering information on management of habitat should be a priority. Silvicultural practices that improve daytime habitat for woodcocks in even-aged and uneven-aged forest stands need to be identified. One approach might be to modify the management of species such as cottonwood (*Populus deltoides*) and green ash , which are grown in plantations in bottomlands. Currently, these plantations do not usually provide suitable habitat for woodcocks because the wide spacing promotes development of an extremely dense understory (Roberts et al. 1984). Pine, pine-hardwood and bottomland hardwood habitats have to be considered. Clear-cuttings planted to pines provide excellent habitat for a few years (Kroll and Whiting 1977), and studies are needed to identify means of improving their quality and longevity. Projects that focus on developing or improving habitat for woodcocks and other species simultaneously need to be vigorously pursued. For example, prescribed burning, which is commonly used for habitat of white-tailed deer (*Odocoileus virginianus*) and northern bobwhites in the Southeast, warrants further study to determine its effect on woodcock habitat.

Managers also should consider innovative means of developing habitat where little cover remains (e.g., in alluvial areas that were cleared for agriculture). One option is the planting of shrubs or even robust herbaceous species to provide daytime cover. Shrubs may be bicolor lespedeza (*Lespedeza bicolor*) and a closely related species (*L. thunbergii*), already widely planted in the South for bobwhites. Woodcocks readily use thickets of bicolor lespedeza for cover (personal observation; G. F. Sepik, Moosehorn National Wildlife Refuge, Calais, Maine, personal communication) and with careful site selection, these shrubs could become the focus of dual species management. Other plants that merit investigation are giant ragweed (*Ambrosia trifida*) and various goldenrods (*Solidago* spp.). These fast-growing species often form dense patches and seem to provide adequate habitat if regenerating hardwoods are not available (personal observation).

Lastly, gathering information on soils has to be included in studies of habitat and habitat management. Well-drained or poorly drained loamy soils are thought to be best for woodcocks, whereas those with excessive sand or clay are thought to pose severe limitations (Cade 1985). These general conclusions, however, are untested. Improving our understanding of the soil's influence on food abundance and accessibility will greatly im-

prove our management and restoration of habitat for woodcocks.

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Critical Review of the Current Knowledge of the Biology of the American Woodcock and its Management on the Breeding Grounds

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Abstract.   We critiqued previous work on the biology and management of the American woodcock (*Scolopax minor*) on the breeding grounds. We determined that little is known about habitat variables and weather extremes that may limit the population. Most investigators who attempted to define habitat requirements of the woodcock used inadequate sample sizes, limited the duration of their studies, did not account for effects of weather, or failed to adequately measure habitat variables. Furthermore, the effects of hunting on local or regional populations has never been adequately studied. We concluded that obtaining data to understand the biology of the woodcock and the effects of hunting is essential before managers can reverse the long-term decline of woodcock numbers.

Key words: American woodcock, breeding grounds, limiting factors, review, *Scolopax minor.*

Since Pettingill (1936) published his classic monograph of the American woodcock (*Scolopax minor*), many scientific studies and seven symposia about the biology of the woodcock have been completed. Special federal funding for research on the biology and the management of the woodcock and other webless migratory birds was established in 1967 (Accelerated Research Program for Webless Migratory Game Birds, U.S. Fish and Wild-life Service) and terminated in 1982. Plans for range-wide management were written (Liscinsky 1966; Owen 1977) and revised (U.S. Fish and Wildlife Service 1990). Yet, woodcock populations in the central and eastern management regions continue to decline (Bortner 1990), and the cause is usually attributed to changes in land use that adversely affect the habitat of the woodcock (Dobell 1977; Gutzwiller et al. 1982; Dwyer et al. 1983).

Although several investigators attempted to define habitat needs of the woodcock, Sepik et al. (1989) concluded that many studies were contradictory and that the validity of conclusions from these studies was doubtful. Despite declining populations, few studies directly addressed factors that limit woodcock numbers. We critically reviewed previous research on the breeding grounds and identified gaps in knowledge and suggest further research.

Breeding Period

The initial 2–3 weeks on the breeding grounds may be extremely critical to the survival of the woodcock. Males and females usually arrive in northern breeding areas at the same time and often on the same date each year, irrespective of weather conditions (Sheldon 1967; Dwyer et al. 1988). Prolonged low temperatures and spring snowstorms can increase mortality and substantially reduce local breeding populations by decreasing the abundance of earthworms and by limiting access to worms (Mendall and Aldous 1943; Sheldon 1967; Gregg 1984; Dwyer et al. 1988; Vander Haegen et al. 1993). Because of their low body mass, males may be particularly susceptible to temperature extremes (Owen and Krohn 1973; Gregg 1984). Although larger than males, females must gain weight after arrival to begin laying eggs.

The woodcock is one of the first migratory birds to arrive in the temperate north, and courtship displays make males conspicuous to predators. The change in the age ratio from older to younger courting males as the breeding season progresses suggests attrition of courting males (Dwyer et al. 1988).

Although several factors could be limiting the population during this period, only recently was work initiated on how habitat use relates to survival (Vander Haegen 1991; Vander Haegen et al; 1993, U.S. Fish and Wildlife Service, unpublished data). The study of the survival of the woodcock in different types of habitat under different weather conditions is needed to determine which habitat types mitigate effects of weather extremes or predation and to develop techniques that create and sustain those habitats.

Several researchers measured the structure and composition of openings that courting males use (Wishart and Bider 1976; Rabe 1977; Gutzwiller and Wakeley 1982; Kinsley et al. 1982;

Rabe and Prince 1982). When an opening was used as a display site, it was assumed to have attributes that attracted the male. In fact, the quality of a display site may have little to do with use by males. Dwyer et al. (1988) postulated that females visit only males that display in openings that are near good nesting cover. Therefore, quantitatively describing and measuring the structure and composition of display areas of males may be of little value. Measurement of variables associated with nesting and brood-rearing habitat would give a more realistic indication of the quality of breeding habitat. Researchers who attempt to predict the value of an area by measuring only the type and structure of openings used by males could be in error.

Although habitat used by woodcocks for brood-rearing and nesting has been studied throughout the breeding range (Roboski and Causey 1981; Coon et al. 1982; Dwyer et al. 1982; Parris 1986; Kinsley and Storm 1989), the results are contradictory (Sepik et al. 1989). Usually, sample size was inadequate and the study too short. Habitat used for nesting might vary among years, depending on the amount and extent of snow cover and frost-free soil. In snow-free years, females can choose the best habitat for nest sites, whereas snow cover in other years limits the choice. Choice of nesting habitat directly influences the habitat used by broods because females do not move young broods far from the nest. Thus, investigators that measure habitat selection by females must account for habitat availability caused by weather conditions when females choose their nest sites. Pooling results of habitat analyses from several years may bias results.

Weather also can affect the survival of woodcock broods (Dwyer et al. 1988; U.S. Fish and Wildlife Service, unpublished data). Females feed young for the first 7 days after the hatch (Gregg 1984) and brood them during inclement weather. If temperatures remain low and are accompanied by precipitation for an extended period, chicks can die of exposure. We think, however, that in certain habitat types the effects of weather can be mitigated. The absence of abundant earthworms in some habitats increases foraging time and may limit chick survival because cool rainy weather during the brooding period is common. Therefore, gathering information on brood and chick survival in different habitats under different types of weather is essential and should have high priority in research.

Post-breeding Period

After breeding and brood-rearing, the activity of woodcocks is largely a recurring pattern of feeding during the day in young, early-successional woodlands and crepuscular moves to and from either a forested opening or a different forested cover. Habitats woodcocks use during the day have been described (Morgenweck 1977; Rabe 1977; Hudgins et al. 1985; Parris 1986; Phelps 1986), but comparisons among these studies revealed that measurements of certain habitat variables (e.g., stem density) vary widely (Sepik et al. 1989). This variability is probably related to several reasons. First, most measurements of habitat components in these studies were made without considering the overall quality of the study site. If the survival of woodcocks is low at a study site because of poor quality habitat, any measure of habitat selection represents use of the best available habitat. Recommendations for management from results of habitat studies on poor sites could lead managers to create inferior habitat. Thus, determining survival rates of woodcocks should be a part of any study of habitat selection.

Measurements of site characteristics that are not essential to habitat choice also may produce variable results among studies. If these components do not affect selection of habitat by woodcocks, site-to-site variation is expected. Protocol for measuring habitat is not standardized. For example, the definition of size classes of forest stands (e.g., shrub, sapling, mature tree) varies among studies. Thus, values of stem density or of basal area for size classes are not comparable among studies. Likewise, some investigators measured site characteristics long after woodcocks used a specific site and when vegetation may have changed (Coon et al. 1982; Gutzwiller et al. 1983; Hudgins et al. 1985; Straw et al. 1986). This may be acceptable for variables (e.g., stem density, basal area) that do not change rapidly over time but can cause spurious results for variables that change rapidly (e.g., earthworm biomass, herbaceous cover, crown cover).

Because woodcocks may use a variety of habitats under usual conditions, results among studies may vary. However, during periods of adverse environmental conditions (e.g., drought), the types of habitat that are usable may be severely limited. Unfortunately, habitat components that are critical for survival during the summer have not been adequately studied.

Although the survival of woodcocks is relatively high during the summer (Derleth and Sepik 1990), periods of extended drought, although rare, may increase mortality because of a decreased abundance of earthworms (Sepik et al. 1983; Dwyer et al. 1988). The change from use of hardwoods to use of conifers during a drought in Maine (Sepik et al. 1983) suggests the importance of conifers; yet, use of conifers is not mentioned elsewhere in the literature. Because severe droughts are infrequent and most studies of habitat were short (2–3 years), the probability of monitoring effects of drought or other rare, weather-related events is small. The effect of drought on a local population can be significant, thus, the need for more information on habitat types that can mitigate effects of drought is great and requires studies of sufficient duration to monitor these events.

Most studies of habitat that woodcocks use at night focused on use of openings as roosting sites (Sheldon 1967; Krohn 1970, 1971; Whitcomb 1974), which include abandoned farm fields, blueberry (Vaccinium spp.) fields, pastures, and log landings (Dunford and Owen 1973; Owen and Morgan 1975; Sepik et al. 1986). Krohn (1971) and Wishart and Bider (1977) reported that some woodcocks do not leave daytime covers at dusk, and Sepik and Derleth (1993a) found that some woodcocks, especially females, move from daytime cover to a different forested cover at dusk and again at dawn. Juvenile males use openings as roost sites at night more often than juvenile females, and adult males use them more often than adult females (Sepik and Derleth 1993a). Although its reasons remain unclear, the use of openings may be an attempt to avoid predators (Dunford and Owen 1973) or competition for singing grounds (Wishart and Bider 1977), whereas females may move to different forested sites to feed (Sepik and Derleth 1993a).

Optimum types of openings (e.g., size, shape, vegetative characteristics, juxtaposition) and forested sites (e.g., stem density, cover type, earthworm abundance) used at night are unknown. Whether the quality of these sites affects survival is also not known. Managers have little information to guide the creation and maintenance of habitat for use at night.

Fall Pre-migratory Period

The migration of woodcocks from the northern breeding grounds does not begin until tempera-

tures at night are consistently less than 0° C (Coon et al. 1976; Sepik and Derleth 1993b). Usually, woodcocks can tolerate these low temperatures and migrate before conditions cause death. During periods of extended drought, however, the molt may be delayed and woodcocks may be unable to accumulate necessary fat reserves for migration and possibly increase mortality. The effect of this mortality on the population and opportunities of mitigating these effects through habitat management are unknown. In fact, evaluation of habitats used before migration has received little attention.

Hunting

Although about 2 million woodcocks are harvested annually by an estimated 700,000 hunters (U.S. Fish and Wildlife Service 1990), the effect of hunting on local or regional populations of the woodcock has received little attention (Goudy et al. 1970; Liscinsky 1972). However, in 1985, bag limits and season length were reduced in the eastern management region because of the long-term decline of the population (Bortner 1990).

There is little evidence that hunting is a major cause of the population decline on a range-wide scale. However, when adverse weather causes significant mortality or reduces recruitment, hunting may have effects. Decisions on annual regulations for hunting are based on information gathered from the wing-collection and singing-ground surveys (Bortner 1990). The singing-ground survey provides an annual index to the number of males but does not provide any measure of the number of females in the population. The wing-collection survey provides information on recruitment, but, because this information is gathered during the hunting season, it can be used only to adjust regulations for the following season. Furthermore, neither survey provides information on changes in the population that occur during most of the breeding season through the hunting season. Thus, there is no mechanism to monitor changes in the woodcock population in the more than 4 months before hunting commences when adverse weather may affect the population. Development of models that estimate survival rates based on weather conditions during this period would allow for alteration in hunting regulations. All the necessary information for such a model, however, is not available.

In Pennsylvania (Coon et al. 1976) and Maine (Sepik and Derleth 1993b), resident woodcocks remain on or near the breeding areas during all or most of the hunting season. This probably occurs in most of the breeding range. Thus, intense, localized hunting could affect local populations, but this has never been adequately evaluated.

Conclusions and Recommendations

In its *American Woodcock Management Plan,* the U.S. Fish and Wildlife Service recommends that a cooperative effort be initiated among all levels of government and private organizations to create, maintain, and manage habitat for the woodcock. Experimental management of habitat has proven that woodcock numbers can be increased in specific areas (Mendall and Aldous 1943; Sepik et al. 1977; Bennett et al. 1982; Sepik and Dwyer 1982; Sepik et al. 1986; Dwyer et al. 1988), but the techniques have been simply to create early successional habitat. Until habitat requirements can be better defined and limiting factors delineated, habitat management remains more art than science (Sepik et al. 1989). If management is to be successful, we must create and manage all essential components of woodcock habitat. Unfortunately, habitat components that are critical for the survival of woodcocks are not well understood, and research should focus on the following:

(1) Information on habitat requirements and the estimated survival of woodcocks under a variety of weather conditions. Sample sizes must be large enough and project duration long enough to detect differences in survival among age-sex classes and among birds that use different habitat types in different weather. Gathering this type of information requires the use of telemetry at several different locations throughout the woodcock's range.

(2) A clear understanding of variables that limit the population to expand management options. We do not imply that current and planned habitat management should cease. In fact, monitoring the response to management of habitat by woodcocks provides information on the importance of different types of habitat (Sepik et al. 1989). Management should be initiated throughout the breeding range to develop and test techniques in management of woodcock habitat. Monitoring the responses of woodcocks to management should be an

integral part of any program. Federal lands (e.g., the national wildlife refuge system, national forests) and state wildlife management areas could serve this work.

(3) A better understanding of the effects of hunting on local populations of the woodcock. The easiest available option to managers to stop the decline of the woodcock population is to restrict harvest. Yet, there is little evidence to support restrictive harvest regulations. In fact, restricting regulations may become a panacea for managers.

Efforts devoted to investigations of the biology and the management of the woodcock during the past 6 decades have been considerable, but critical knowledge is still lacking. Filling gaps in our knowledge requires a large-scale, long-term commitment by federal, state, and private organizations. The *American Woodcock Management Plan* sets the stage for such a commitment, however, strong leadership and a coordinated effort are necessary. Without an expanded base of knowledge, managers do not have the information to manage the woodcock on a sustained basis.

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The American Woodcock Management Plan: Can it work?

by

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Almost anything is possible with a little luck, a lot of effort, and persistence. Implementing the American Woodcock Management Plan (U.S. Fish and Wildlife Service 1990) is no exception.

First, however, a strategic plan, such as we now have, must be rendered into tactical segments, and responsibilities must be agreed upon and assigned. Without that, the plan is a vague wish list.

We have to be forthright and to the point with implementation of the plan. An example of hedging that the public will not buy is on page one of the draft plan, under "Purpose." The point is made that "available data do not indicate that hunting has affected regional population status." What is lacking is admission that neither do the data indicate that hunting has not affected population status. This sort of half-truth rings hollow in the light of later admissions in the document that we have a scant idea of how many woodcocks are killed by hunters each year.

What we do with these less than complete revelations is detract from the grievous need for data on the magnitude of mortality from hunting that is impossible to obtain without a system that provides names and addresses of hunters. Thus, the call for such a system is diluted by our reluctance to depict hunting as a significant factor of mortality. To be up front with this information, of course, provides grist for the anti-hunters. But not to do so draws suspicion from nonhunters. And remember, the former is but 10% of our population, whereas the latter is 80%.

What I am saying is that it is time that professional wildlife management quits obfuscating and faces its problems. We have nothing to be ashamed of for either supporting or controlling hunting. What we should fear most is timidity that keeps us from saying what *is* and thereby generating public mistrust.

I see another potential problem in this effort that may create roadblocks farther along. So far, there is no clear statement that the total authority and responsibility for the woodcock is in the U.S. Fish and Wildlife Service's (Service) pocket. The Service does not have the principal responsibility and authority. It has all of both. The main problem with migratory bird management in recent years is the lack of ability by the Service to accept and implement needed changes in management. And I say this not to reflect on Service personnel. There is plenty of blame to distribute among states, flyways, and private groups.

This simply is the way it has been. This is the way it must *not* be if the woodcock is to benefit from the plan. The Service has to lead by accepting responsibility for the job. It certainly should lure and welcome assistance from other federal agencies, states, and the private sector, yet, it must remember that partnerships are not substitutes for leadership. Partnerships do not realign legal authority and responsibility. Too much has fallen through the cracks in migratory bird management because of diffused responsibilities and resulting acquiescence; the perilous condition of the duck populations is a case in point.

I am overjoyed that finally the Service may have chanced upon an adequate survey system to collect harvest data on migratory birds. After more than 20 years of sweat, swearing, and failure, the Service and the states seem to have agreed upon a permit system that provides names and addresses of migratory bird hunters for conducting statistically valid harvest surveys. The woodcock should be a prime beneficiary of that progressive step. The permit system must be in effect before the plan can succeed. It is a key to reliable population management and, when implemented, will leave habitat management the other priority in need of attention.

Management of habitat is the most basic and toughest part of the conservation of the woodcock, and a good start should be within the existing programs of the Service. Existing national wildlife refuges are logical places for a start. They were established for a variety of specific purposes, but there are many opportunities to accommodate the woodcock. First, the Service needs to subdue the natural-diversity bandwagon that unfortunately seems to be a coming priority in refuges and elsewhere in the Service. The recently reviewed draft strategic plan for operations of the service was replete with this undefined and theoretical toy. Refuge areas are for wildlife and fishes and in, many cases, for specific wildlife and fishes. This means management benefits particular species. Natural diversity requires an absence of management. To manage land and water eliminates natural diversity, which is attainable only in wilderness.

And for refuges, no more off-the-cuff wilderness designations, such as that for the Moosehorn National Wildlife Refuge in Maine. It is irony and a tragedy that part of the refuge that has contributed so much to our knowledge of the woodcock is now off-limits to management of the woodcock because deficient souls in the Department of the Interior and Congress considered a wilderness label nice for that area. Such designations not only detract from the importance of a wilderness designation, they actually threaten resources that the public thinks are protected. I get the uneasy feeling sometimes that many people interested in the refuge system could serve better in national park affairs, where it is acceptable to indulge oneself as a naturalist and to stand back and watch and show others how Mother Nature performs. But refuges exist for one primary purpose, to help the Service perform its mission. That mission, in short, is the conservation of fishes and wildlife, which necessitates on-the-ground activities that create and maintain needed habitats. Wilderness should be limited to the large public domain refuges, such as in Alaska where protection is the primary need and mode of management.

Also in the Service are wildlife research units. They are here, there, and everywhere anymore. They seemingly reproduce like muskrats. Why are these units not ideal for conducting research to fulfill objectives in this plan? Why are white-tailed deer still studied on many of these units? Whitetails are not in trouble! Woodcocks are! This is an opportunity that should not be overlooked.

The potential of partnerships with other federal agencies is a critical part of the plan, and I certainly did not intend to demean it in early statements because the Wildlife Management Institute had a leading role in its creation. The woodcock plan indeed must affect management on lands administered by the U.S. Forest Service, U.S. Army Corps of Engineers, U.S. Armed Forces, and others if it is to be successful. The U.S. Forest Service, for example, manages a lot of woodcock country from the Great Lakes to Louisiana. Admittedly, national forests in the eastern United States appear as small dots and blotches on the map, but nearly 25 million acres are not an insignificant amount of land. These forests could contribute tremendously to implementing the woodcock plan.

The Ruffed Grouse Society's Memorandum of Understanding (Master Memorandum of Understanding between the Ruffed Grouse Society and the U.S. Forest Service, as amended) and subsequent work with the U.S. Forest Service are prime examples of what can be accomplished. Through this partnership, the society is investing hundreds of thousands of dollars on national forests and improving woodcock habitat in an unprecedented manner.

One thing that all of us could do right now to improve woodcock habitat in eastern national forests is to help the U.S. Forest Service fight off growing pressure from extreme environmentalists to eliminate all management of even-aged timber. Touting biodiversity as their newly found cure-all, these extremists are forcing the U.S. Forest Service to abandon maintenance of wildlife openings in the Hoosier National Forest of Indiana. They already eliminated clear-cutting for all wildlife, but endangered species on the Ouachita National Forest in Arkansas. Fortunately seed tree and shelterwood cuttings remain an option there. In this year's appropriations legislation for the U.S. Forest Service, the House attached language that eliminates all even-aged management of timber in the Wayne and Shawnee national forests in Ohio and Illinois. The easiest way that I know to lose several million acres of existing and potential woodcock habitat is to let this kind of simplistic philosophy continue. People on the pseudo-wilderness kick must be confronted, stopped, and preferably deported.

Partnerships with timber companies are excellent. These companies control much woodcock habitat and their interest in the land is compatible with woodcock management. However, contribu-

tions by industry must be made easy. Close and continuous working relations with the companies by state, federal, and private cooperators are needed. Remember that a corporation is an inanimate object. It does not have a conscience. Only those who run companies can have sensitive regard for fairness and justice, which is what woodcock conservation is all about. Right?

One word of advice for approaching industrial America: the higher up on the corporate ladder you can make contact, the more sympathy you will get. Generals never feel as threatened by aliens as lieutenants, possibly because a much higher percentage of lieutenants gets shot.

Acquiring concentrations of woodcocks at strategic locations may help. However, acquisition cannot begin to solve the problem. In fact, habitat acquisition probably is the least cost effective means of helping the woodcock. As on Congress, we should depend on land acquisition sparingly.

Speaking of Congress, among the better ways to win support from private landowners is through tax breaks. We have many examples of tax incentives that work. In Indiana, landowners are entitled to a $1.00/acre tax assessment if they agree to implement prescribed wildlife management. In Michigan, a commercial forest program requires landowners to pay only 30 cents/acre in taxes for forest land. The county government gets an additional 70 cents/acre from the state, which retrieves that money with a yield tax that is collected when timber is sold. The landowner must follow planned timber management that helps wildlife. Minnesota exempts landowners from property tax on portions of their holdings that are maintained in native prairie. In addition, the owner receives a credit against taxes paid on other property as long as the native prairie is maintained. These are examples of innovations that should be part of the tactical efforts for the conservation of the woodcock.

The Service and state agencies have performed magnificently in obtaining and implementing conservation provisions in the Federal Farm Program. The 1990 Farm Act contains forestry provisions that could be used for the management of the woodcock as dictated in the plan. Called the Forest Stewardship Program, the initiative proposed by the National Association of State Foresters seeks to put 25 million acres of non-industrial private forests under conservation plans that enhance soil, water, fishes, wildlife, and timber production. Landowners with approved conservation plans qualify for technical assistance, cost sharing, and tax benefits.

Consequently, it seems to me that the state foresters, who guide this new program, may be good partners of the American Woodcock Management Plan. After all, private non-industrial forests contain this nation's largest amount of actual and potential woodcock habitat. Federal, state, and private foresters are vital contacts for affecting management on those lands.

There is no end to the possibilities of implementing this plan. Any limits are in our minds. Commitment and persistence are musts. Federal agencies, especially the Service, must commit money and people. The states and private organizations must do likewise. This operation cannot succeed on the backs of a few already overworked biologists. This is new, and it requires new resources. I hope we get them.

In closing, I reiterate earlier references to the importance of playing straight with the public. I quote Gilbert and Dodds from their 1987 book titled *The Philosophy and Practice of Wildlife Management:* "A manager in reality only makes recommendations to government regarding action to be taken. If he has scientifically documented the rationale for his recommendations and has adequately shown the impacts on the resource and on the public, government must be prepared to act. It is more likely to act favorably if the management agency has made its case well to the public. Therein lies the secret to successful wildlife management. Scientific knowledge may be the underpinning, but the capability of 'selling' a management scheme to politicians (and their electors) is equally crucial to success. What must be avoided is the temptation to circumvent this legitimate management agency role and this process. Such was the case in a 1983 referendum in Maine to prohibit moose hunting. If the referendum had been successful, the moose management program would have been damaged and a precedent established to manage by public fiat rather than on the advice of professional scientists. If the public had been uninformed and the biological case for the moose season had not been made adequately, wildlife management in Maine would have suffered a serious setback. So in reality the voters sustained the management decision because the management agency had been open and truthful with the public. In a democratic system we, as wildlife managers, must be prepared to defend sound management decisions in any forum, including the political one. Similar challenges are becom-

ing more commonplace. The American system allows for referenda to be placed on the ballot, which usurps the normal governmental process. If managers ignore this reality and operate outside the public arena, they must be prepared to accept the consequences."

Evidence of Leks in the Mating Strategy of The American Woodcock

by

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Abstract.   Preference by displaying male American woodcocks (*Scolopax minor*) for a particular singing ground (i.e., the primary site) was studied in a 130-ha study area in Mason County, West Virginia, during 1981–82. After 16 (89%) changes in occupancy of singing grounds by marked American woodcocks, displaying males occupied singing grounds closer to the primary site. Eight displaying males abandoned singing grounds near the primary site and became primary site occupants. In addition, displaying males performed alternately from adjacent singing grounds and the unoccupied primary site ($n = 5$) and from non-singing grounds near the primary site ($n = 5$). Color-banded males that were not occupants of the primary site roosted on the site at night ($n = 6$). Two of these males displayed at adjacent singing grounds when they were sighted. Observations of color-banded roosting males and of females ($n = 3$) at night were made exclusively on the primary site. Results suggest that the primary site was highly preferred by displaying males. In addition, the primary site seemed to serve as an important nighttime gathering area for woodcocks in the study area. We contend that woodcocks under unique circumstances invoke mating in leks.

Key words: American woodcock, lek, removal, *Scolopax minor*, singing ground, West Virginia.

At dawn and dusk during the breeding season, male American woodcocks (*Scolopax minor*) perform courtship displays in openings called singing grounds. Unless occupancy is disputed, only one male uses a singing ground at a time. Males can occupy a singing ground for as short a time as one crepuscular period or as long as 65 days (M.R.

Ellingwood, West Virginia University, Morgantown, West Virginia, unpublished data). Females in the polygynous mating system of the American woodcock (Oring 1982) visit displaying males on singing grounds to mate.

Males compete for singing grounds (Pitelka 1943; Westfall 1954) and prefer certain singing grounds over others (Sheldon 1967). Weeks (1969) suggested the existence of a hierarchial preference for singing grounds. Godfrey (1974) classified sing-

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ing grounds as either perennial or transitory, and he and Hirons and Owen (1982) observed that males exhibited a strong fidelity for particular sites.

Sheldon (1967) and Whitcomb (1974) reported that singing grounds were quickly reoccupied after removal of displaying males. Redmond (1983) designated singing grounds as high-use and low-use by the rate and frequency with which woodcocks replaced removed displaying conspecifics from singing grounds in New Brunswick.

Shissler (1981) observed that certain singing grounds, which he called primary sites, were occupied longer, had larger numbers of displaying males through the season, and were involved in a disproportionately greater number of changes in occupancy (moves). He speculated that woodcocks display in centers of key sites. Shissler (1981), Hirons and Owen (1982), and Dwyer et al. (1988) suggested that the woodcock is a species that mates in leks.

Our objective was to quantify preference by displaying male woodcocks for a singing ground previously identified as a primary site.

Study Area

The 1,200 ha McClintic Wildlife Area (WA) in Mason County, West Virginia (39°N Lat, 82°W Long), contained a 130-ha area with 15–20 woodcock singing grounds that served as our study area during 1 March–1 June 1981–82. The area is moderately flat, and elevations range from 177 to 265 m above sea level. The McClintic WA is composed of open fields, patches of shrubs, and second-growth forest. Open fields are fallow and cultivated cropland, including hayed fields with red clover (*Trifolium pratense*), timothy (*Phleum pratense*), and broomsedge (*Andropogon virginicus*). Shrubs are primarily multiflora rose (*Rosa multiflora*), and the overstory is black locust (*Robinia psuedo-acacia*). Forests are dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.). The McClintic WA is at the southern boundary of the primary breeding range of the woodcock (Sheldon 1967). The study area could aptly be described as a complex of singing grounds inasmuch as display sites were in a large, insular complex of hayed fields and brushy areas separated by hedge rows and surrounded by woodlands.

Methods

In 1979–80, Shissler (1981) identified a preferred singing ground (primary site) in a complex of singing grounds. His criteria to identify the primary site included the number of displaying males that occupied a singing ground, the number of days a singing ground was occupied, and the number of moves by color-banded males either to or from a singing ground. A move resulted when a male moved his display from one singing ground to another.

In 1981 and 1982, all displaying males in the study complex were captured with mist nets at dawn and dusk (Modafferi 1967) or by nightlighting (Shuler et al. 1986). Captures were started shortly after the initiation of display in early March.

The age and sex of the captured birds were determined by plumage characteristics (Martin 1964). One-year-old birds were classed as second-year birds (SY), whereas >1-year-old birds were classed as after-second-year birds (ASY). We banded each bird with a U.S. Fish and Wildlife Service band and a unique combination of one or two reflective colored leg bands (Shissler et al. 1982). Males were captured throughout both breeding seasons to ensure that all displaying males in the complex were banded. Inadvertently captured females were aged and color banded.

Displaying males that occupied the primary site were removed (i.e., shot) within 3–8 days after they became dominant. We chose not to remove males from all singing grounds for fear of depleting experienced males. Instead, we removed males from a previously identified primary site (Shissler 1981).

Singing grounds were systematically visited to identify displaying males. Displaying males were identified by the color combinations of their bands that were determined approximately every other day by shining them with a hand-held aircraft landing light powered by a 12-V battery. We identified occupants during morning and evening displays, at night while the birds were peenting or performing display flights, and at night after stimulating the birds with a cassette recording of peenting and of songs in flight (Shuler et al. 1986). Observations were made by one to three individuals, and when possible several singing grounds were visited during each observation period.

Singing grounds were numbered by their respective distance from the primary site, which was designated singing ground one. For example,

singing ground five was closer to the primary site than singing ground six (Fig. 1). Logistical constraints prevented a precise determination of starting dates for displays on each singing ground. As a consequence and for comparative purposes, a starting date of 1 March was assigned. This date is consistent with our and Shissler's (1981) observations.

Changes in the occupancy of a singing ground were monitored. With the last known display site of each of 18 moving males as a reference point, the number of inactive grounds toward the primary site and away from the primary site at the time of each move was tallied. The student's t-test was used to compare distances traveled by SY and ASY males.

Results

We monitored the occupancy of 16 singing grounds during 1981 and of 20 in 1982. Ninety-per-

cent ($n = 21$) of the displaying males were captured by 31 March 1981, and 96% ($n = 24$) of the displaying males were captured by 31 March 1982. The males banded during March made the most moves and the most displays. Only three unbanded males occupied singing grounds after 31 March. Migrants appeared and initiated displays in March. Males displayed for 78 days in 1981 and for 85 days in 1982. Twenty-one males were color-banded in 1981 and 24 in 1982. In 1981, 66 color-banded males were sighted during 54 days of observation; 144 males were observed in 1982 during 62 days of observation. Eight displaying occupants (4/year) were removed from the primary site. Four occupants of the primary site became inactive for unknown reasons and were never resighted. Twenty-six of 45 color-banded males were not resighted after initial banding.

Thirteen color-banded displaying males changed singing grounds 18 times; 11 times in 1981 and 7 times in 1982 (Fig. 1). Sixteen (89%) moves brought males closer to the primary site. The average distance of these moves was 327 m (range = 88–1,435, SD = 315), and the average reduction in distance between a male and the primary site was 237 m (range = 18–614, SD = 145). The average distance of the two moves away from the primary site was 185 m (SD = 35).

After-second-year birds ($n = 8$) made 10 (56%) of the 18 observed moves and traveled an average of 230 m (range = 88–525, SD = 128), whereas SY's ($n = 5$) traveled an average of 414 m (range = 210–1,435, SD = 419) in 8 (44%) moves. Traveled differences did not differ by age of the birds. Nine of 10 ASY moves and 7 of 8 SY moves were toward the primary site.

In 1981, 7 of 10 initial occupants of the 10 nearest singing grounds to (and including) the primary site were ASYs, whereas five initial occupants were ASYs in 1982. In 1981, the initial occupant of the primary site was an ASY that had been banded in the complex during a previous study in 1980. The initial occupant of singing ground 2 in 1981 was banded in 1979. No previously banded birds were observed in 1982. In 1981, six males and in 1982, three males moved to the primary site and displayed from it. No displaying male moved from the primary site to another singing ground. Occupancy of singing ground 9 changed six times during the 2-year study. Three of these changes entailed displaying males moving from singing ground nine to the primary site (Fig. 1.)
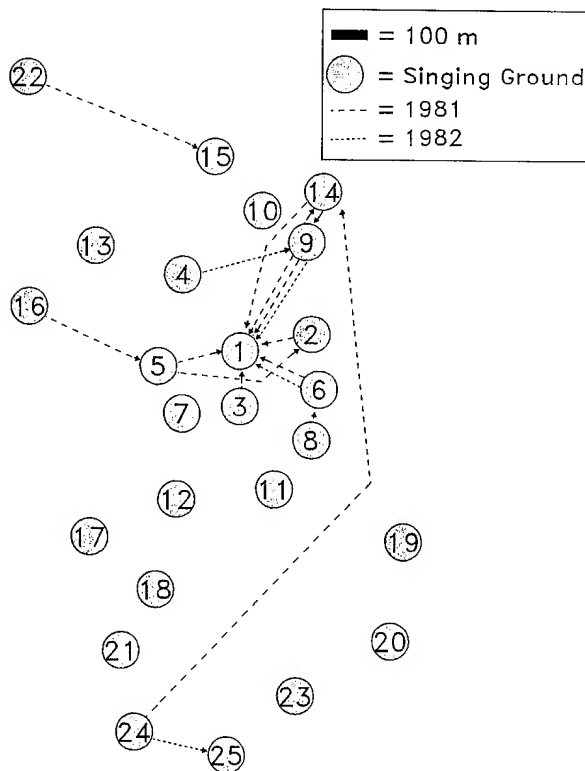

Fig. 1. Moves of color-banded male woodcocks on singing grounds of the McClintic Wildlife Area in Mason County, West Virginia, during March–May 1981–82. Arrows depict the directions of moves.

Beginning on 15 March and progressing by 2-week intervals, the sum of active singing grounds in the study area was 15, 6, 3, 1, and 0 in 1981 and 16, 5, 3, 3, and 1 in 1982. Inactive grounds were available for occupation by displaying males just as the primary site was available after the removal of an occupant. Thirteen moves (81%) toward the primary site occurred while inactive grounds in the opposite direction outnumbered (4:1) those toward the primary site. Two moves toward the primary site occurred while most unoccupied grounds were in the same direction, and one move occurred while an equal number of unoccupied grounds was available in both directions. Both moves away from the primary site occurred when singing grounds were available only in that direction.

Seven (39%) males were identified on their new singing grounds within 1 day of occupation and 11 (61%), within 5 days. Eighty-nine percent of all males that moved were identified within 15 days of their move. Moves to the primary site tended to be direct; 67% of these moves were uninterrupted. A lack of observers prevented us from determining the timing of some moves.

Including birds that were removed, 12 different males occupied the primary site during the 2-year study; 7 in 1981 and 5 in 1982. During this study, six different birds occupied singing ground 9 and five different birds occupied singing grounds 2 and 15. No other singing ground was occupied by more than four different birds.

The ratio of ASY to SY occupants of the primary site was 0.8:1.0 in 1981 and 4.0:1.0 in 1982. The ratio of captured ASY males to captured SY males was 1.2:1.0 in both 1981 and 1982. Male ASY's were initial occupants on 91% of the singing grounds that were active after 1 April and on 43% of the other grounds.

Males displayed during a greater span of time per year on the primary site than on any other singing ground. During 1981, the primary site was active 63 days; singing ground 9, 57 days; singing ground 15, 48 days; and singing ground 2, 45 days. In 1981, displays ended when a displaying male was removed from the primary site. In 1982, the primary site was active for 69 days, singing ground 9 was active for 73 days and singing ground 18, for 76 days. In 1982, a displaying occupant was removed from the primary site in late April. After the removal, occupants of singing grounds 9 and 18 intermittently displayed on the primary site active for another 14 days.

After removal of the primary site occupants, five color-banded males alternately displayed on their own singing grounds and on the primary site. Each male performed from one to several alternating displays during 1–14 days. Three males that made alternating displays were occupants of singing grounds adjacent to the primary site. Two males that made alternating displays eventually became occupants of the primary site. One male performed an alternating display on a ground other than the primary site.

In eight instances, color-banded males displayed from non-singing ground positions near the primary site. These exploratory displays lasted only a portion of a display period and were made at 50–300 m from the primary site (Fig. 2). Exploratory displays involved intermittent displays from non-singing ground positions by males that otherwise displayed from recognized singing
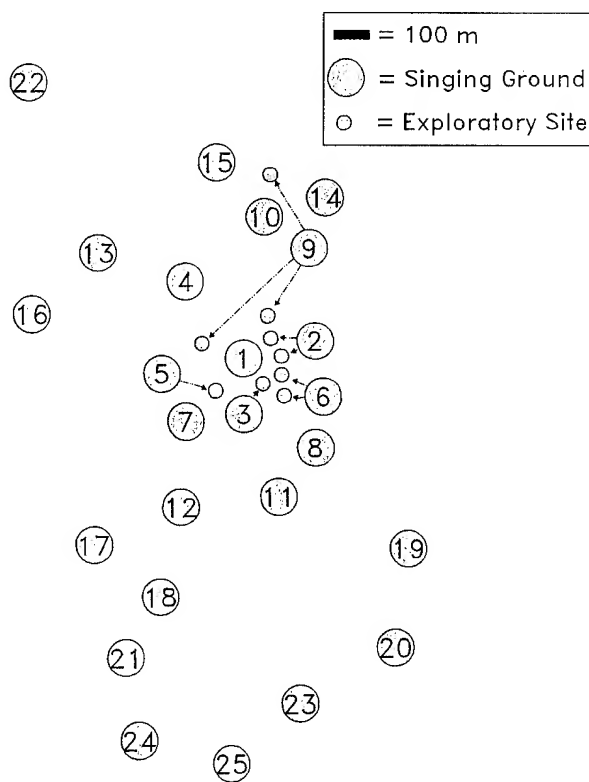

Fig. 2. Exploratory courtship displays by color-banded male woodcocks in the McClintic Wildlife Area in Mason County, West Virginia, during March–May 1981–82. Arrows depict the source of displaying males that briefly left their singing grounds to perform exploratory displays.

grounds. The five males that performed exploratory displays were occupants of singing grounds adjacent to the primary site and three of these males eventually occupied the primary site. Only one exploratory display was performed in a location away from the primary site.

On six different occasions, color-banded males that were not occupants of the primary site roosted at night on the primary site. Two of these roosting males were active occupants of adjacent grounds at the time. Several untallied sightings of males with indiscernible color-band combinations were also made on the primary site at night. These males did not occupy the primary site at the time. Once, three different color-banded males were flushed from the primary site in the same night. Sightings of banded non-occupants at night were made only on the primary site although all occupied grounds were visited at an average rate of once every 2 days.

During 1982, two female ASYs were captured and color-banded on the primary site at night. One of these birds was sighted later in the breeding season within 50 m of the primary site. No other females were captured at night in the study area. Two females were captured on other grounds during crepuscular periods.

Discussion

We expected the removal of occupants from a preferred singing ground (primary site) would solicit moves of males from adjacent singing grounds to the primary site.

Reports of a spatial relation between singing grounds and nocturnal roost sites (Sheldon 1967; Dunford and Owen 1973; Nicholson et al. 1977; Shissler 1981) coupled with reports of quasi-courtship behavior (Sheldon 1961; Krohn 1971; Godfrey 1974; Whitcomb 1974) and a disproportionate presence of juvenile males on nocturnal roost sites (Sheldon 1967; Krohn 1971; Godfrey 1974; Whitcomb 1974) suggest that males may establish an affinity for particular singing grounds through experience or through visits to active singing grounds late in the breeding season.

Consistent moves by color-banded males toward the primary site revealed a proclivity by displaying males for the primary site. In one instance, a male moved away from the primary site by moving from singing ground 4 to singing ground 9. This move seemed to improve the bird's access to the primary site by improving his ability

to communicate and interact with the primary site occupant. This is possible because factors in addition to distance, such as vegetation and topography, probably influence communication among birds on adjacent singing grounds. The bird that moved away from the primary site by moving from singing ground four to singing ground nine, seemed to improve his position relative to the primary site by reducing the density of hedgerows and trees between himself and the primary site. Three occupants of singing ground 9 eventually occupied the primary site. Occupants from singing ground 9 had routine aggressive cackling interactions with primary site occupants. No moves or interactions were observed between males on singing ground 4 and the primary site. The move of a male from singing ground 9 to singing ground 14 (Fig. 1) resulted from aggressive cackling flights by a competing bird.

We suggest that singing grounds near the primary site were preferred over more distant sites and that closer sites were used as staging grounds in attempts to occupy the primary site. This point is best exemplified by the occupancy of singing ground 9. It was occupied for extended periods during both field seasons, had relatively high occupation rates, and served as the source of several male occupants of the primary site.

Sheldon (1967) and Godfrey (1974) asserted that non-displaying males are a reservoir of potential displaying males. Despite frequent untallied encounters with non-displaying birds on the periphery of occupied singing grounds, only three unbanded males occupied singing grounds after initial banding was completed (31 March) each year. We had anticipated that non-displaying males would serve as principal replacements of removed males in our study. Instead, displaying occupants from other singing grounds almost exclusively replaced removed birds. This result prompts us to question the breeding potential of non-displaying males in our study area. At the very least, males that failed to display from singing grounds during March lacked the ability to successfully compete for singing grounds later.

Removal of displaying males from the primary site may have inflated the occupancy rate of the site. The systematic removal of occupants from the primary site in short time intervals created an opportunity for greater turnover on the site than was otherwise probable. Still, 9 of 10 males that occupied the primary site (excluding the initial occupant of the primary site each season) moved

from adjacent singing grounds, thus demonstrating a preference for the primary site over previously held singing grounds.

The rapid and consistent replacement of occupants on the primary site was atypical of the occupancy of other singing grounds. Seventy-one percent of the singing grounds were unoccupied by 1 April and 91% were unoccupied by 1 May. These abandoned grounds were available to displaying males but remained unoccupied. At the time of documented moves by males, unoccupied singing grounds in a direction away from the primary site outnumbered those toward the primary site by a factor of 4. Nevertheless, 89% of the moves were toward the primary site.

In both years, the primary site was occupied into May, despite the removal of eight males. Summed over both years, the primary site was occupied longer than any other singing ground although, in 1981, activity on the site was concluded with the removal of an occupant. In 1982, a primary site occupant was removed in late April, but occupancy of the primary site continued for 14 days because males from two remaining active singing grounds intermittently displayed from it.

We believe that fidelity to the primary site was less pronounced in 1982 than 1981. Replacement of birds shot at the primary site was less predictable and more tentative in 1982. In 1981, two males banded during 1979 and 1980 were recaptured in the study area, whereas none was observed in 1982. Observations indicated that in 1981, males on the primary site consistently displayed from the same approximately 10×10 m location. During 1982, the display location varied as far as 35 m among occupants. If male woodcocks develop an affinity for certain singing grounds through observation and experience (Shissler 1981) and removals in 1981 eliminated experienced males and curtailed displays, the absence of recaptures and inconsistency in the locations of displays in 1982 are explained. We note that the abundance of experienced males could be influenced by natural mortality or hunting and that there was a decline (20.8%) in the number of singing males in West Virginia from 1981 to 1982 (Tautin 1982).

Shissler (1981), Hirons and Owen (1982), Oring (1982), and Dwyer et al. (1988) suggested that woodcocks mate in leks. Some (Shissler 1981; Hirons and Owen 1982; Oring 1982) implied that leks of the woodcock are nonresource based, whereas Dwyer et al. (1988) suggested that they are resource-based and driven by the proximal

relation between singing grounds and nesting habitat. In our study area, the primary site, which was more or less central in an open-field complex with some interspersing hedgerows, seemed to be farther from nesting habitat than most other singing grounds in the complex.

Redmond and Keppie (1988) proposed that vegetative characteristics that affect light intensity or acoustics determine the quality of singing grounds and that males recognize superior vegetative structure. These investigators dismissed the importance of experienced males, noting that preference was demonstrated in the apparent absence of such males.

We hypothesize that occupants of the primary site at the McClintic WA had an acoustical advantage over occupants of adjacent grounds. Anecdotal observations from project personnel indicated that the occupant of the primary site could be heard from all other grounds in the complex, whereas his peers lacked such an advantage. We speculate that this advantage was due to the central location of the primary site, moderate elevation, and relative vegetative openness. Superior acoustical characteristics of the primary site would provide the primary site occupant with a competitive edge in attracting females. Visitation rates of females were greater on the primary site than on other sites. High rates of visitation of females would explain intense competition for the primary site by males.

We reject the notion that the male's recognition of indices of either the quality of proximal nesting habitat or of the light and sound characteristics of a singing ground play a significant role in competition for the site. Instead, we submit that males respond to the relative presence of females on singing grounds and that the preference of sites by females determines the competition for the site by males. We believe that the suspected high visitation rate of the primary site by females is a response to superior acoustical characteristics that enhance the performance by males. The primary site did not seem to have a unique vegetative character or proximity to nesting habitat. We also believe that the experience of adult and juvenile males contributes to the development of a preference for a singing ground. Finally, males may recognize cues in the display of primary site occupants (i.e., frequency and intensity of display) that imply high visitation of the ground by females.

Conclusions

Several scolopacids are known to mate in leks. We suggest the woodcock population in the McClintic WA mated in a lek. The males favored a primary display site as evidenced by their distinct pattern of moves toward the primary site. Further evidence of this preference included exploratory and alternating displays in almost exclusive association with the primary site. Roosting color-banded male non-occupants and the presence of females at night on the primary site were also particularly noteworthy. Finally, agonistic encounters and suspected non-displaying males suggest that the primary site was highly preferred. These data and observations prompt us to conclude that mating of woodcocks at the McClintic WA was in a non-resource based, dispersed lek.

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Behavior of Radio-marked Breeding American Woodcocks

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Abstract.   During spring 1986–89, we equipped 175 male and 89 female American woodcocks (*Scolopax minor*) with radio transmitters. Radio-marking had little effect on behavior; within 1 day of marking, 37 of 64 (58%) displaying males were dominant and within 7 days, 138 of 157 (88%) were dominant. All females marked before nesting proceeded to nest, and marked females with broods remained with broods after release.

Dominance of males declined from 73% in April to 69% in May and to 26% in June as breeding activity waned. In all years, after-second-year (ASY) males were dominant more often than second-year (SY) males (67.5% vs. 58.9%). Most males displayed at more than one (range = 2–12) site. Distances that males moved between the primary singing ground and subsequent singing grounds averaged 775 m in all years and ranged from 618 m (1986) to 966 m (1988).

Females visited males at singing grounds throughout the breeding cycle; some females visited more than one site. During prenesting, females remained in daytime covers during the crepuscular period (55%), flew to different feeding covers (22%), visited singing grounds (14%), or flew from daytime covers to unknown locations (9%). During nesting, females left nests during the crepuscular period (72%) and moved to singing grounds (5%), to feeding areas (59%), and to undetermined locations (7%). Females with broods remained with their broods during the crepuscular period (62%), flew to feeding areas (30%), visited singing grounds (1%), or flew to undetermined locations (6%). The woodcock mating system is similar to a resource-based polygyny. Males compete for singing grounds near high-quality nesting areas. The fitness of males is expressed by dominance at more than one singing ground. Woodcocks are not monogamous; females may visit more than three different males during a single courtship period but do not visit males regularly. Most females leave nests during the crepuscular period to feed in a different cover.

Key words: Breeding behavior, courtship, move, *Scolopax minor*, telemetry, woodcock.

The breeding behavior of the American woodcock (*Scolopax minor*) has been characterized in several ways. Hirons and Owen (1982) described males as promiscuous with a system of singing grounds (sites where males display) analogous to dispersed leks. They suggested that these leks are non-resource based and females are attracted to a singing ground only by the male's presence. Oring (1982) believed that male woodcocks have a male-dominance-polygyny mating system with an intermediate dispersion of display areas. In this system, males do not defend resources essential to females but compete for females by attaining relative positions of dominance or by demonstrating quality through display (Oring 1982). Dwyer et al. (1988) suggested that the woodcock mating system is a resource-based polygyny that revolves around nest sites, wherein females choose males on display sites near high-quality nesting habitat.

Previous researchers of behavior of male woodcocks used direct observation of birds (Pettingill 1936), banded individuals (Mendall and Aldous 1943; Sheldon 1967), and color-marked individuals (Richter and Liscinsky 1955; Westfall and Weeden 1956; Shissler et al. 1982). Early attempts to use telemetry were unsuccessful because either transmitters or harnesses reduced courtship activities (Hudgins et al. 1985) and caused abnormal behavior (Ramakka 1972; Horton and Causey 1984). Because female woodcocks are more difficult to observe and capture, observations of females at singing grounds and of females leaving and returning to nests were limited (Pettingill 1936; Mendall and Aldous 1943; Sheldon 1967). The principal objective for this study was to observe and document the behavior of breeding woodcocks. Secondarily, the study served to identify behavior by woodcocks that might be attributed to the radio transmitter.

Study Area

Woodcocks were marked on the 6,850-ha Baring unit of the Moosehorn National Wildlife Refuge (NWR) near Calais, Maine. Before management, refuge land was mostly mature second-growth forest, interspersed with natural wetlands, constructed impoundments, meadows, and blueberry (*Vaccinium* sp.) fields. The forest was composed of pure stands of spruce (*Picea* sp.) and balsam fir (*Abies balsamea*) infested with spruce budworm (*Choristoneura fumifera*). Hardwoods, consisting of birch (*Betula* sp.), red maple (*Acer rubrum*), and

aspen (*Populus* sp.), were common but being replaced by conifers. Also, there were some extensive areas of riparian alder (*Alnus* sp.) habitat, mostly along the Moosehorn Stream in the southern portion of the refuge and around some wetlands and impoundments. Dwyer et al. (1988) described the area in detail.

Since 1979, blocks of 2 ha and strips of 0.2–0.4 ha were cut at a rate of 40–60 ha/year. Larger (≤ 24 ha) clear-cuttings were created in spruce-fir stands to salvage timber damaged by spruce budworm. Under this program, 7–57 clearings have been created each year (Sepik and Dwyer 1982). The refuge now contains patches of the original forest interspersed with clear-cut blocks and strips ranging in age from 0 to 10 years.

Methods

During spring 1986–89, female and displaying male woodcocks were captured in mist nets (Sheldon 1967) during morning and evening courtship periods. Females on nests or with broods were located by a pointing dog and captured with either hand-held nets (Ammann 1974, 1977) or with mist nets near the nest. Birds were banded with U.S. Fish and Wildlife Service leg bands and reflective color bands (Shissler et al. 1982) to identify sexes and radio-marked individuals. Sex and age were determined by characteristics of wing-plumage (Martin 1964), and birds were classified as 1-year-old (SY) or ≥2-years-old (ASY). We weighed each bird and attached a 3.5–4.0 g radio transmitter to its back with livestock-tag cement and a single-loop wire harness that was secured with a metal crimp (McAuley et al. 1993). We radio-marked dominant males, females caught in mist nets during the prenesting and nesting periods, nesting females, and females with ≤6-day-old broods.

Courtship of woodcocks at the refuge usually begins on about 25 March and extends through mid-June. We monitored woodcocks from 1 April to 15 June 1986–89. Females were marked during April and May each year. All males were captured before 16 April, except in 1986 when they were captured in April and May. We located and followed birds with scanning receivers and hand-held antennas from vehicles or on foot. We attempted to obtain the exact location of each radio-marked bird during the morning (1.5–0.5 h before sunrise) or evening (0.25–1.50 h after sunset) and once during the day.

A male woodcock was considered dominant when he was the only male that peented at a

display site or if he performed courtship flights and peented when other males were peenting nearby. The dominance of some males was determined by monitoring radio signals from points of higher elevation around the study area. A male was considered dominant if for at least three repetitions the radio signal was heard for about 1 min (courtship flight presumed) and was followed by the absence of a signal for about 3 min (ground display presumed). A male was considered subdominant when he visited a singing ground and did not peent or if he peented intermittently but did not perform courtship flights near a display site where another male was performing. The site where a male was observed most often was considered the primary singing ground. We used the analysis of variance (ANOVA) to test for differences in moved distance among years. We used a significance level of $P = 0.05$.

We determined the magnitude of dominance of males that we monitored for 2 or more weeks by dividing the number of crepuscular periods during which a male was dominant by the number of crepuscular periods in which he was monitored. We recorded the number of different singing grounds each male used and tested for differences in the average number of singing grounds a male used each year. We used ANOVA to compare the average proportion of times males were dominant among years and to examine differences between age classes in the average proportion of times males were dominant.

Females were monitored similarly to determine their moves in relation to courting males. We divided the breeding cycle into three periods: prenesting (including the period between loss of nest or brood and renesting), nesting (including egg laying), and brood rearing. We located females in daytime feeding covers, in brood-rearing habitats, or at nest sites and followed them during crepuscular periods to determine whether they visited a singing ground, went to feed (active signal), or remained in daytime cover. Our main measure of transmitter effects was related to behavioral changes in dominance of males and mating, nesting, and brood-rearing of females. If dominant behavior of males (i.e., performing courtship displays on the site where captured) was affected, we assumed that attachment of the transmitter caused the behavioral change. If something else (e.g., sickness of the bird) caused the behavioral change, we could not measure the effect.

Results

We captured and attached radio transmitters to 175 male woodcocks (24 in 1986, 54 in 1987, 51 in 1988, 46 in 1989) and 89 female woodcocks (11 in 1986, 31 in 1987, 27 in 1988, 20 in 1989). We lost contact with 11 males (4 in 1986 and 7 in 1987) within 7 days of marking. We were unable to follow most females for the entire monitoring period because more than 70% of them were captured during nesting or brood-rearing. Also, females that lost nests often left the study area and moved as far as 15 km or farther from the original nest sites (McAuley et al. 1990). Males were monitored during 3,286 crepuscular periods (Table 1) and females during 945 periods.

Radio Transmitters and Behavior

Within two crepuscular periods after having been marked, 58% (37 of 64) of the males that we observed were dominant (Table 1). Within 7 days of radio-marking, 88% (138 of 157) of the males that we observed were dominant (Table 1). In

Table 1. Behavior and dominance status of male woodcocks within 1 and 7 days after radio-marking at the Moosehorn NWR, 1986–89.

Year	Males	Number Crepuscular periods	Monitored crepuscular periods	% Dominant (n) within: 1 day	7 days	% Never dominant (n)
1986	24	1,037	580	45 (10/22)	71 (17/24)	0
1987	47	3,592	889	50 (5/10)	91 (39/43)	0
1988	51	4,008	968	59 (10/17)	92 (46/50)	2 (1/51)
1989	46	3,166	849	80 (12/15)	90 (36/40)	2 (1/46)
Total	168	11,803	3,286	58 (37/64)	88 (138/157)	1 (2/168)

1987-89 when males were marked during only the first 2 weeks of April, 91% (121 of 133) were dominant within 7 days of marking. During the 4-year study, only two males (1 each in 1988 and 1989) did not reestablish dominance after they were marked (Table 1).

All females that were radio-marked before they initiated nesting and remained in the study area nested (n = 24). No female that was radio-marked after having been captured with a brood (n = 24) abandoned her brood. Six radio-marked females that abandoned or lost clutches to predators and 9 that lost all their chicks to either predators or inclement weather renested (McAuley et al. 1990). One radio-marked female and her chick died in 1986 when the transmitter's antenna became entangled in the band of the chick.

Frequency of Dominant Behavior

During the 4-year study, we monitored radio-marked male woodcocks during 27.8% of the crepuscular periods, 1 April-15 June. We monitored males during 580 (56%) crepuscular periods in 1986, 889 (24.7%) in 1987, 968 (24.1%) in 1988, and 849 (26.8%) in 1989 (Table 1). During all years combined, radio-marked males were dominant during 72.6% of the observation periods in April, 69.2% in May, and 25.7% in June (Fig. 1), and radio-marked males were subdominant during only 4.6% of the observation periods (Fig. 1). During the remaining periods, birds either did not visit a singing

ground or their status was unknown. In each year, ASY males were dominant more often than SY males (DF = 1, F = 3.94, P = 0.049; Table 2). In 1987-89 when males were radio-marked only during 1-15 April, more ASY males than SY males (78 vs. 39) were captured. Overall, ASY males were dominant during 67.5% and SY males during 58.9% of the observation periods.

Each year, most radio-marked males displayed at more than one singing ground (Fig. 2). The percentage of males that used more than one singing ground was 94% in 1986, 71% in 1987, 68% in 1988, and 60% in 1989. Occasionally, we could not determine the exact location of a display site although we could determine from radio signals that a male was making courtship flights. The mean number of singing grounds by males that used more than one singing ground was 5.6 (SE = 0.70, range = 2-12) in 1986, 3.2 (SE = 0.33, range = 2-8) in 1987, 3.0 (SE = 0.24, range = 2-9) in 1988, and 3.1 (SE = 0.21, range = 2-6) in 1989. The mean distance males moved from the primary singing ground to secondary singing grounds did not differ (DF = 3, F = 1.46, P = 0.23) among years (Table 3).

Moves by Females

Visits to Singing Grounds

During 1 April-15 June 1986-89, 30 radio-marked female woodcocks visited singing grounds during the crepuscular period (6 in 1986, 5 in 1987,
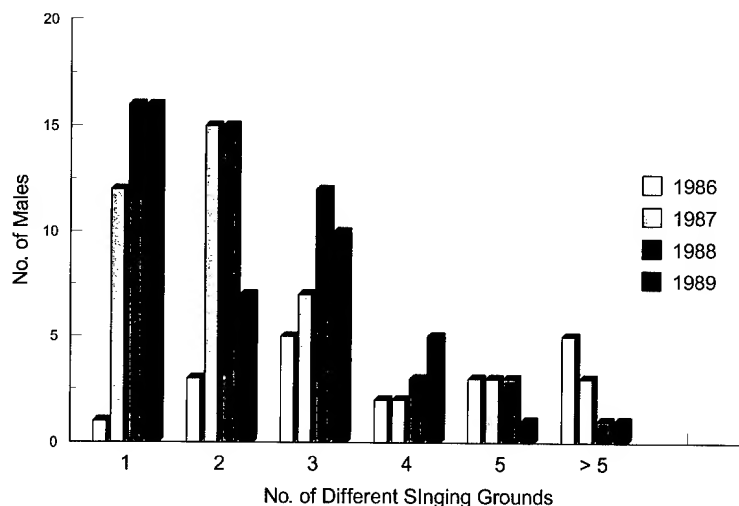

Fig. 1. Frequency of dominant (by month) and subdominant (seasonal) behavior by radio-marked male woodcocks on the Moosehorn National Wildlife Refuge during 1986-89. Frequency of dominance (subdominance) was calculated by dividing the number of times a male was observed dominant (subdominant) by the number of observations.
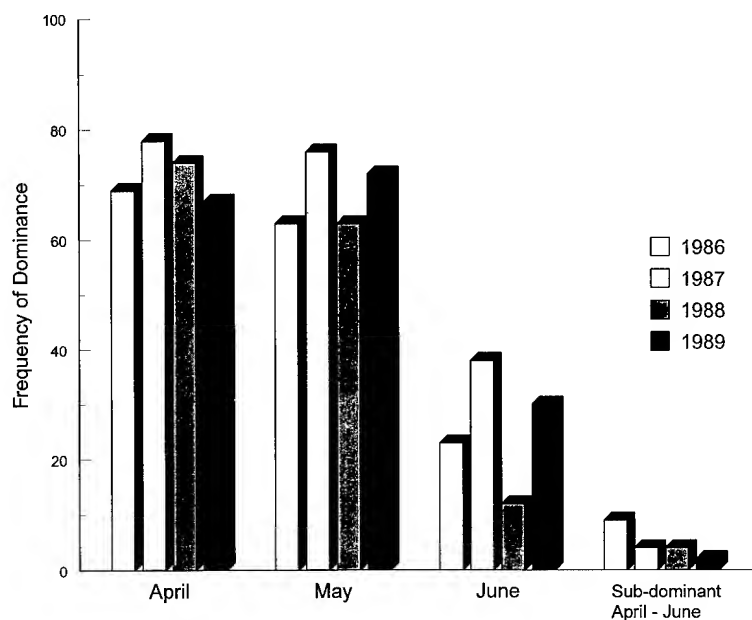
Table 2. Frequency of dominance of second-year (SY) and after-second-year (ASY) radio-marked male woodcocks at the Moosehorn National Wildlife Refuge, 1986–89. Includes only males monitored ≥ 2 weeks.

	Mean frequency of male dominance[a]			
	SY		ASY	
Year	n	% (SE)	n	% (SE)
1986	13.0	52.9 (7.0)	6.0	60.1(11.7)[b]
1987	16.0	67.6 (6.6)	22.0	74.4 (4.9)[b]
1988	13.0	63.8 (5.7)	29.0	66.8 (3.6)[b]
1989	10.0	51.3 (6.6)	27.0	68.6 (3.1)[b]
1986-89		58.9	67.5	

[a] Number of periods a male was dominant divided by the number of periods the bird was observed.
[b] ANOVA, Year: DF = 3, F = 2.50, P = 0.062; Age: DF = 1, F = 3.94, P = 0.049;
Year•Age: DF = 3, F = 0.78, P = 0.505.

Fig. 2. Number of different singing grounds used by radio-marked, dominant male woodcocks at the Moosehorn NWR during 1986–89.

Table 3. Mean distance between the primary (most often used) display site and alternate sites (A) of each dominant, radio-marked male woodcock, and mean distance of all moves combined (B) by all male woodcocks at the Moosehorn National Wildlife Refuge, 1986–89. Includes only males that used ≥ 1 singing ground and exact locations.

	A		B	
	Number	$\bar{X}$ Distance (SE)	Number	$\bar{X}$ Distance (SE)
Year	of males	(m)	of moves	(m)
1986	17	618 (144)	64	711 (165)
1987	23	839 (145)	44	756 (109)
1988	29	966[a] (135)	49	894[b] (96)
1989	25	775 (162)	43	714 (110)

[a] Excludes one male that moved 7,297 m; if the value is included, distance = 1,022 m (SE = 1,125).
[b] Excludes one male that moved 7,297 m; if the value is included, distance = 1,177 m (SE = 215).

7 in 1988, and 12 in 1989). In each year, one or more females visited at least two different singing grounds (range = 2-4). The average number of different singing grounds a female visited was 2.7 (SE = 0.49) in 1986, 1.2 (SE = 0.20) in 1987, 1.6 (SE = 0.30) 1988, and 1.3 (SE = 0.14) in 1989.

Pre-nesting

During the prenesting period, we followed 27 female woodcocks (Table 4), 19 of which visited singing grounds during 44 (14%) crepuscular periods. Collectively these females visited 35 different singing grounds, and several of these females visited at least 4 different singing grounds. During 172 (55%) crepuscular periods, the females did not leave daytime cover, and during 70 (22%), females flew to another feeding cover. During 29 (9%) crepuscular periods, females left their daytime cover and moved to an undetermined location.

Nesting

We monitored 46 female woodcocks on nests (Table 4). During 23 (5%) crepuscular periods, 14 females left their nests and flew to 20 different singing grounds. Most moves (249, 59%) were to

feeding areas. Females remained on their nests during 118 (28%) crepuscular periods, and females left the nest and moved to undetermined locations during 30 (7%) crepuscular periods.

Brood-rearing

We followed 28 female woodcocks with broods (Table 4). Two females left their broods during the crepuscular period and visited singing grounds (1%). During 64 (30%) periods, females flew to feeding areas, and during 131 (62%) periods, they remained with their broods. During 13 (6%) crepuscular periods, females left their broods and moved to an undetermined location.

Discussion

Male Behavior

Male woodcocks that were dominant at the start of the breeding season displayed throughout the breeding season. During April and May when most birds nested and renested (Dwyer et al. 1982; U.S. Fish and Wildlife, unpublished data), males were

Table 4. Crepuscular moves by radio-marked female woodcocks during pre-nesting (includes pre-renesting), nesting (includes laying), and brood-rearing at the Moosehorn NWR, spring 1986-89.

Year	Females	Number Females visiting males	Different visited SG[a]	Movements to: SG[a]	Feed[b]	Unk[c]	None[d]
Prenesting							
1986	3	3	9	9	11	14	0
1987	1	1	3	4	6	0	52
1988	12	5	9	10	30	8	45
1989	11	10	14	21	23	7	75
Nesting							
1986	7	4	9	11	9	13	59
1987	11	5	6	6	39	14	33
1988	18	4	4	4	92	2	14
1989	10	1	1	2	109	1	12
Brood-rearing							
1986	4	1	1	1	3	3	41
1987	4				13	1	28
1988	15	1	1	1	44	6	46
1989	5				4	3	16

[a] SG = singing grounds.
[b] Feed = feeding areas.
[c] Unk = undetermined destiny.
[d] None = no movement.

dominant during most of the observation periods. In June when breeding was waning, courtship by radio-marked males declined to only 26% of the observation periods. After-second-year males were dominant more often than SY males. Also, several males were more dominant than others. These more dominant males displayed at more than one singing ground during a single crepuscular period. When these males moved to an occupied singing ground, they either displaced the resident dominant male or were confronted by him and driven off. Such aggression was manifested by cackling flights (Pettingill 1936). By moving and exerting dominance over several singing grounds in an area, a male probably increases his likelihood of mating.

Mendall and Aldous (1943) believed woodcocks are monogamous. Pettingill (1936) and Sheldon (1967) reported woodcocks are polygamous, whereas Hirons and Owen (1982) reported male woodcocks as promiscuous. On two occasions, we observed males mate with two or more females during a single display period. Because most males displayed at more than one singing ground, at least 63% of the prenesting females visited more than one male, and some females on nests visited at least three different singing grounds, we conclude that woodcocks are not monogamous but polygynous and that males are promiscuous.

Female Behavior

We believe that our data are minimum estimates of the number of moves by females because the average number of observations per female per year is relatively low (range = 8–18). In 1986 when females were observed more often (average = 18 observations/female vs. 8, 12, and 15 in 1987–89), we observed females visiting more singing grounds (DF = 3, F = 5.05, P = 0.007). Therefore, the number of visited males should be considered minimum estimates.

Pre-nesting

The pre-nesting period at the Moosehorn NWR usually is shorter than 2 weeks (U.S. Fish and Wildlife Service, unpublished data). Females did not visit males regularly during the pre-nesting period. Females remained in daytime cover during 55% of the crepuscular periods and visited a singing ground during only 14% of their moves. If moves to undetermined locations were classified as moves to singing grounds, they would increase visits to singing grounds to only 25%. Females

probably visit several males to assess some quality of male fitness before selecting a mate. However, because females usually visited males in only a limited area and only few males were visited, females are probably using some proximate cue such as habitat as a basis for choice of males. Infrequent visits to males also suggests that females can retain viable sperm for several days. Ruffed grouse (*Bonasa umbellus*; Bump et al. 1947) and sage grouse (*Centrocercus urophasianus*; Gibson and Bradbury 1986) require only one mating to fertilize an entire clutch of 8–12 eggs, and mallards (*Anas platyrhynchos*) can retain viable sperm as long as 17 days (Elder and Weller 1954). Therefore, one mating is probably sufficient to fertilize the three to four-egg clutch of a woodcock.

Nesting and Brood-rearing

Incubating females commonly leave their nests at dusk, presumably to feed, and return after dark (Pettingill 1936). Mendall and Aldous (1943) noted that female woodcocks did not feed in the vicinity of their nests. Our data support both observations because nesting females left their nest sites to fly to different covers to feed during 72% of the observation periods. Even females with broods left during 37% of the observations and flew to different covers to feed. This behavior may enhance the survival of eggs and chicks. Nesting and brooding females leave large, conspicuous droppings that, if deposited in the vicinity of the nest or brood, would probably attract mammalian predators. Furthermore, by flying to different areas to feed, females do not compete with their chicks for food in the brood-rearing area.

Nesting females maintained limited contact with males. We do not know whether females on nests mated with the male that displayed closest to the nest site. However, some females on nests did not always visit the male that was displaying closest to the nest site, and one female left her nest to visit three different males, including the male closest to the nest, during a 20-min period. One-third of the females on nests visited one or more singing grounds. If the undetermined moves (7%) were visits to males, 12% of the observed moves of females during nesting were visits to males. Also, two females with broods visited males. Because nesting success is 50–67% (Gregg 1984; Mendall and Aldous 1943) and survival of broods can be poor in some years (Dwyer et al. 1988; U.S. Fish and Wildlife Service, unpublished data), renesting by woodcocks is common (McAuley et al. 1990).

Females probably visit males during nesting and brood-rearing to encourage males to continue displaying in the area. Keeping males displaying near their nest and brood-rearing sites provides females with ready access to males for renesting if a clutch or brood is lost.

All visits of males by females did not result in copulations. Often, we observed nesting females land near displaying males, remain on the singing ground for several minutes, and leave without copulating. The intensity of display by males (loudness, rate of peenting, and frequency of display flights) increased after visits by females. These visits probably strengthened fidelity of males to display sites and encouraged them to continue displaying. The necessary frequency of visits or copulations to keep a male on a particular display site is unknown.

Effects of Radio Transmitters

Attaching transmitters during the courtship period affected some woodcocks only briefly because 88% of the radio-marked males performed normal courtship within 7 days of receiving a transmitter. Because 12% of the males had not re-established dominance within 7 days after attaching transmitters suggests that either attachment of the transmitter or trapping and handling of the bird temporarily disrupted courtship behavior. Female woodcocks did not seem to be affected by the transmitter. Radio-marked females visited males at singing grounds, nested, raised broods, and even renested. We think that abnormal behavior reported in previous studies was caused by transmitters that were too large, by poor harness design that restricted flight (Ramakka 1972; Horton and Causey 1984), by marking birds too late in the breeding season, and by inadvertent radio-marking of subdominant males (Hudgins et al. 1985).

Woodcock Mating System

Hirons and Owen (1982) stated that the American woodcock mates in a dispersed lek. When birds mate in leks, males gather at traditional sites to which females come to be inseminated (Avery 1984). Males often defend territories, but territories are too small to contain sufficient resources to influence choices by females (Avery 1984). Although the mating pattern of the woodcock resembles mating in leks, the spacing of singing grounds and the distance that males moved from primary to other singing grounds seem too far and too random to support the existence of a dispersed lek. Moves by males to new singing grounds were without a discernable pattern. The mean distance between the primary singing ground and the new site was greater than 700 m. In mating systems with leks, females that are ready to breed make special journeys to mate with one or more males clustered at a lek (Wrangham 1980). Although one or more subdominant males may come to a singing ground, usually only one male displays.

During our study, the most dominant male woodcocks displayed at more than one singing ground and most (63%) prenesting females visited more than one male. The number of used singing grounds is probably greater than we report because, in 1986 when males were observed twice as often (56%) as in other years (25%), males used nearly twice the number of singing grounds (DF = 3, F = 13.0, P = 0.0001). Males probably move among display sites to increase their chances of mating with more than one female. Robel (1966) reported that male greater prairie-chickens (*Tympanuchus cupido pinnatus*) that controlled the largest booming territories mated with the most females. Although the average distance they moved was highly variable, male woodcocks probably have a finite area or number of sites they can defend successfully.

Females visit more than one male to assess fitness of males and to select a mate. But on what basis do females select a mate? Dwyer et al. (1988) discussed sexual selection in relation to size and age of male woodcocks. They concluded that male dominance is a result of age and experience. "Therefore, females generally have an opportunity to select older experienced males, but may differentiate between the quality of some resource around a display area" (Dwyer et al. 1988).

Most woodcock nests are within 137 m of a singing ground (Mendall and Aldous 1943; Sheldon 1967; Gregg 1984); this fact has led researchers, who believed that males first select specific types of sites and then attract females to these sites to mate, to investigate characteristics of display sites. Gregg (1984), however, stated "this apparent relationship between singing ground locations and nest site selection was probably not a result of females selecting sites within the territories of males ... but a similarity in habitat preference between males and females." Under the male-dominance polygyny systems (Oring 1982) and the mating systems with leks (Emlen and Oring 1977; Avery 1984; Gibson and Bradbury 1986), males do

not defend resources essential to females (e.g., nest sites or feeding areas). The critical distinction between resource-defense polygyny and both the male-dominance polygyny and mating in leks is whether or not mates or critical resources can be monopolized economically (Emlen and Oring 1977). Under the resource-defense polygyny, a female's choice of a mate should be influenced by the quality of the defending male and the resources under his control (Emlen and Oring 1977).

Dwyer et al. (1988) described the woodcock mating system as resource-based and males as competing for display sites surrounded by the available best nesting covers. Dwyer et al. (1988) believed that male woodcocks select openings that are surrounded by the available best nesting habitat and compete for these sites where they have a higher probability of attracting females. Under resource/mate-defense polygyny, nests are clustered in territories of males, whereas under male-dominance-polygyny, the distribution of nests should be random in territories of males (Cartar and Lyon 1988).

Our findings indicate that home ranges of most prenesting and nesting females included one or more singing grounds (U.S. Fish and Wildlife Service, unpublished data). When they left nests and daytime covers, most females flew over or past singing grounds to feeding areas, and many fed in covers adjacent to singing grounds (U.S. Fish and Wildlife Service, unpublished data). The highest densities of displaying males were in areas with the highest densities of broods and nests (U.S. Fish and Wildlife Service, unpublished data). Furthermore, nesting and brood cover were interspersed with display sites. The characteristics of display sites in these areas seem of little importance, for example, most sites were on recent clear-cuttings, gravel roads, and skidder trails. Therefore, our data more closely support Dwyer et al's. (1988) characterization of the woodcock mating system. Female woodcocks use proximate habitat cues and select males that are dominant on singing grounds surrounded by good nest and brood cover. If more than one male is using habitat of equal quality, the female chooses the most fit male (based on ultimate cues that we could not determine).

Conclusions

Woodcocks are not monogamous; males may mate with more than one female, and nesting females may visit three or more different males during a single crepuscular period but do not visit males on a regular basis. The mating system of the American woodcock is similar to a resource-based polygyny. We believe that male woodcocks compete for singing grounds near high-quality nesting areas. The fitness of males is expressed by dominance at one or more display sites. Females visit males most often during prenesting and occasionally during nesting (laying and incubation) and brood-rearing. Males probably stay on a singing ground as long as it is visited by females. When visits by females become infrequent or cease, male woodcocks leave their primary singing ground to display at other sites. Most males display at more than one site. Females visit males during nesting and brood-rearing to mate and possibly to encourage males to display if renesting is necessary. Most females leave nests during crepuscular periods to feed in a different cover. Our estimated numbers of singing grounds used by males and numbers of males visited are probably low because, when males were monitored twice as often, the number of different singing grounds increased nearly two-fold.

Acknowledgments

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Age-ratios, Radioactivity, and Foods of Eurasian Woodcocks in Italy

by

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Abstract.   The age-ratio of Eurasian woodcocks (*Scolopax rusticola*) from 6,085 wings was 69.5% (SD = 7.6) juveniles. The mean radioactivity from 79 samples of pectoral muscle was 70.0 Bq/kg (SD = 110.2). Samples collected after mid-December showed a uniform lower level of radioactivity. Foods of 48 woodcocks were not different among birds collected from the different geographic belts, however, Simpson's standardized niche-breadth index was greater of adults than of juveniles. Hypotheses are tested that birds crossing central and northern Italy have a different geographical origin from birds crossing southern Italy.

The breadth of the Eurasian breeding range of *Scolopax rusticola* poses difficulties for determining the origin and places of overlap of populations in wintering areas and along migration routes. This is particularly evident in the southwestern Palaearctic area where hunters kill the most woodcocks. Nesting areas of woodcocks that winter in France and in Great Britain were identified by ringing. In central Mediterranean countries, however, the task is more complicated because, in regions that harbor woodcocks from farther east, few woodcocks have been ringed. Conversely, because woodcocks are subject to extremely high mortality from hunting in the Mediterranean basin, especially in Italy, these data suggest that birds originate from different populations, which are exploited differently. Italy is on the southern boundary of the breeding range and only a few nests have been found. Italy, however, is at the center of migratory routes (autumn peak between 20 October and 20 November, spring peak between 1 and 31 March) and offers grounds for wintering, mostly in southern areas and on the islands (Sicily and Sardinia).

Hunting mortality is substantial (ca. 1–2 million birds/year) and probably related to the long season that opens in October and extends to December in most areas and through February in other areas. The daily bag limit is from two to five, and the number of days allowed for hunting per week is from 3 to 5 and varies among regions.

We use age-ratios, presence of radioactivity, and food use to address probable differences in the origin of woodcocks bagged in Italy.

Methods

Age-ratios

Wings, which were submitted by hunters during 1976–88 throughout Italy, were used to age 6,085 woodcocks according to methods of Clausager (1973). Two age classes (juvenile and adult) were identified by the wear of the tips of the three longest primaries.

Radioactivity

Because of the fallout from the nuclear reactor at Chernobyl, Ukraine, in 1986, we measured the radioactivity of Cesium^{137} in samples of pectoral muscle from 79 woodcocks collected from 18 October 1986 to 6 January 1987. Radioactivity was

measured with an intrinsic Germanium gamma-spectroscope with anticoincidence to sodium iodine (Leo 1987) and provided a resolution of 3 keV and a sensitivity as high as 0.37 Becquerels (Bq). Moreover, background radioactivity was measured in six frozen woodcocks that were bagged in 1984-85 before the accident at Chernobyl and served as controls.

Foods

The contents of gizzards from 48 woodcocks (Table 1; 18 males: 4 adults, 11 juveniles, 3 unknown age; 26 females: 8 adults, 14 juveniles, 4 unknown age; 3 unknown sex: 2 juveniles, 1 adult; unknown age and sex: 1) from various regions of Italy (northern zone, $n = 27$; central zone, $n = 14$; southern zone, $n = 7$) were examined with a stereomicroscope. Whenever possible, partly digested organisms were assigned to taxonomic orders according to taxonomic keys of Imms (1970) and Hoffman (1979). If specimens could not be identified to Order, they were assigned to a higher taxa. Although some of the remains were identified to Family, suitable data for statistics were obtained only by analyzing mean numbers of prey ranked by Order or higher.

Soft-bodied prey were partly missed even under careful stereomicroscope examination. This bias, however, becomes negligible if data on presence or absence instead of total biomass are considered. A t-test was used to compare differences in age-ratios and amounts of radioactivity. Simpson's niche-breadth and Spearman's rank test (As; Barbault 1981) were used to evaluate differences in taxa of prey of woodcocks. To evaluate geographic differences, the Italian regions were grouped into three geographic belts: north, central, and south, each characterized by a homogeneous migration (Fig. 1).

Results

Age-ratios

The mean percentage of juveniles, although variable, was substantially lower in central Italy (63.6%, SD = 3.1) than in other areas (north: 71.6%, SD = 8.9; south: 75.9%, SD = 4.0; Table 1), especially in the south (south–central, $P = 0.0001$ vs. the north–central, $P < 0.05$). Mean percentage of juveniles did not differ ($P > 0.05$) between the south and the north. The overall mean percentage of juveniles was 69.5% (SD = 7.6).

Table 1. Percent occurrence of prey in 48 woodcock gizzards collected in three zones of Italy, 1984-87.

| Taxon | Zone and sample size | | |
	North $n = 27$	Central $n = 14$	South $n = 7$
Nematoda	1.3	—	—
Oligochaeta	15.2	17.1	15.6
Arachnida	2.0	2.1	2.2
Crustacea	2.0	—	—
Isopoda	2.0	—	—
Insecta	29.8	27.7	37.7
Unidentified	0.7	2.1	2.2
Thysanura	0.7	—	—
Dermaptera	3.3	2.1	2.2
Lepidoptera	0.7	—	—
Diptera	8.6	10.7	13.3
Coleoptera	14.5	12.8	20.0
Hymenoptera	1.3	—	—
Chilopoda	6.6	2.1	2.2
Unidentified	0.7	—	—
Geophilomorpha	2.0	—	—
Scolopendromorpha	3.3	2.1	—
Lithobiomorpha	0.7	—	—
Diplopoda	5.3	14.9	6.7
Polydesmida	0.7	—	—
Julida	4.6	14.9	6.7
Unidentif. larvae	1.3	2.1	—
Stones	10.5	12.8	13.3
Vegetable remains	17.1	10.6	15.6
Mud/Amorph. matter	4.6	—	—
Feathers	4.0	10.6	6.7

Radioactivity

In woodcocks exposed to fallout from Chernobyl, radioactivity from Cesium[137] averaged 70.0 Bq/kg (SD = 110.2) and peaked at 500.4-610.5 Bq/kg. These values are about 10× higher than values of controls before the nuclear accident at Chernobyl (average 7.9 Bq/kg, SD = 4.4). Moreover, Manunta (1963) in a previous study detected no radioactivity in woodcock tissue.

The standard deviation of amounts of radioactivity in woodcocks was higher in central Italy than in the other two geographic belts, but mean values did not differ ($P > 0.05$). All woodcocks
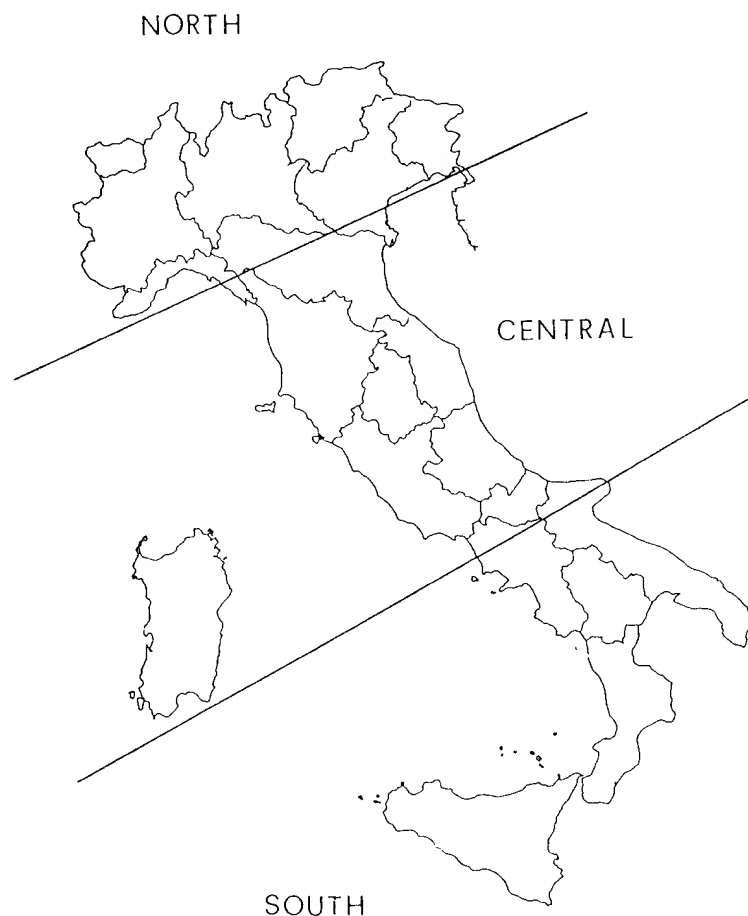
NORTH

CENTRAL

SOUTH

Fig. 1. The three geographic belts of Italy in the analyses of the difference in occurrence of radioactivity and age-ratios of woodcocks.

bagged after mid-December contained less (<31.1 Bq/kg) radioactive contamination (Fig. 2).

Foods

Foods in the gizzards did not differ among birds by areas, but the diets could not be compared with reported diets of woodcocks in Italy, especially in Sicily (Lo Valvo 1986), because of different methods of analyses. Percentages of prey of woodcocks either among the various geographic belts (north-central: $n = 18$, $r^s = 0.787$ vs. south-central: $n = 10$, $r^s = 0.763$ vs. north–south: $n = 18$, $r^s = 0.637$) or between adults and juveniles ($n = 12$, $r^s = 0.930$) were not different. The number of types of prey (disregarding inorganic material, feathers, and vegetable matter) was greater in adults (As = 0.4608) than in juveniles (Table 3; As = 0.3529).

Discussions and Conclusions

Irrespective of a possible different migratory behavior between adult and young birds, the higher percentage of young birds bagged during the post-reproductive migration in southern Europe and in the Middle East than in northern Europe (Chelini and Spanò 1983; Spanò 1988) indicates a difference in origin between these populations. This difference also exists between north–central and southern Italy, suggesting that diverse populations overlap.

Different data support different origins of the birds. First, fairly uniform observations during several years revealed that the numbers of woodcocks did not decline in spite of intense hunting (Kalchreuter 1979), perhaps, because different populations are represented and mortality is lower elsewhere. Second, the net decrease in radioactivity after mid-December in all woodcocks from the central zone suggests they belong to a population that migrates later and most likely originates in eastern areas (i.e., southern Ural, eastern Volga region) where radioactive fallout is lower (Il'icev 1985). However, to achieve confirmation of diverse overlapping populations in central Italy, extensive ringing has to be undertaken in eastern Europe when woodcocks nest.

Table 2. Percent of juvenile woodcocks shot by hunters by region and zone of Italy, 1976-88.

Zone and region	Percent of juveniles (mean)	Standard deviation
North		
Piemonte	72.8	9.6
Valle d'aosta	75.0	25.0
Liguria	63.4	14.5
Lombardia	62.6	29.9
Triveneto	84.0	21.2
Combined regions	71.6	8.9
Central		
Emilia	65.2	13.1
Toscana	60.3	21.8
Umbria	67.3	15.5
Marche	65.3	11.6
Abruzzo-Molise	58.5	29.7
Lazio	63.6	18.3
Sardegna	64.4	13.8
Combined regions	63.5	3.1
South		
Campania	73.8	7.9
Puglia	70.5	27.9
Lucania	75.6	18.7
Calabria	79.3	12.2
Sicilia	80.3	10.7
Combined regions	75.9	4.0

Table 3. Occurrence (%) of prey in woodcocks by age-class in Italy, 1984-87.

Taxon	Age and sample size	
	Adults $n = 13$	Young $n = 21$
Nematoda	—	0.8
Oligochaeta	16.7	16.8
Arachnida	2.8	2.3
Crustacea	1.4	2.3
Isopoda	1.4	2.3
Insecta	30.6	31.0
Unidentified	1.4	0.8
Dermaptera	4.2	1.5
Lepidoptera	—	0.8
Diptera	8.3	10.4
Coleoptera	16.7	16.0
Hymenoptera	—	1.5
Chilopoda	4.2	5.4
Unidentified	—	0.8
Geophilomorpha	1.4	1.5
Scolopendromorpha	2.8	2.3
Lithobiomorpha	—	0.8
Diplopoda	6.9	8.8
Polydesmida	1.4	—
Julida	5.5	8.8
Unidentif. larvae	—	0.8
Stones	13.8	9.6
Vegetable Remains	19.4	12.7
Mud/Amorph. matter	2.8	2.3
Feathers	1.4	7.2
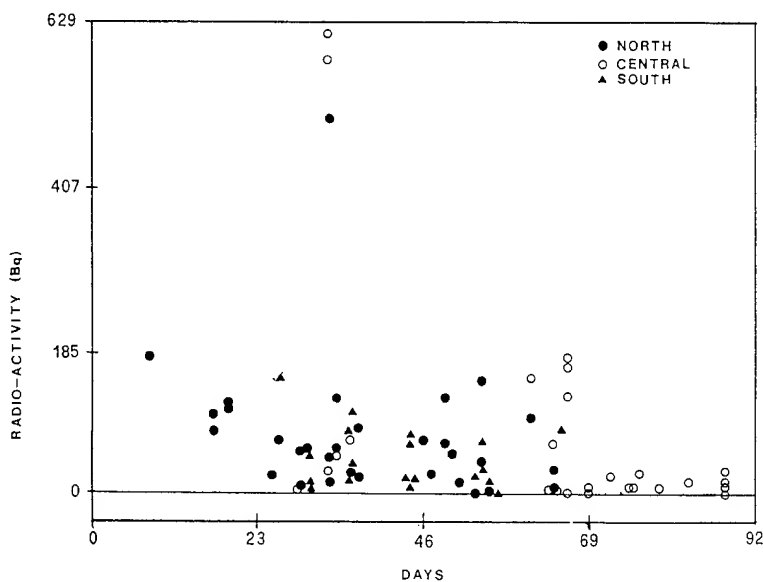
Fig. 2. Radioactivity (Becquerels) in samples of pectoral muscle of woodcocks in the geographic belts of Italy, 1986-87 (Day 0 = 10 October 1986, Day 92 = 10 January 1987).

The distribution of the amounts of the radioactivity measured in woodcocks and coming from the Chernobyl nuclear accident was extremely variable, but radioactivity in Italy rarely exceeded the tolerance levels (600 Bq/kg) established for foodstuff by the European Community (Mallet 1988; Spanò and Salvo 1988). Food analysis suggests no ecological variations in woodcocks frequenting different zones of the Italian peninsula. The higher niche-breadth values of adults than of young birds reflect a greater adaptability of the older individuals to fluctuations of food resources caused by variations in weather and climate (Fadat and Landry 1983).

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Assessment of 1-2-year-old Aspen Stands as American Woodcock Habitat in Michigan

by

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Abstract.   American woodcock (*Scolopax minor*) populations were studied to describe features of their habitats and changes in their populations 6 years before and 2 years after (1982-89) a 95-ha mature aspen (*Populus* sp.) forest in the Upper Peninsula of Michigan was clear-cut. Clear-cutting reduced the mean tree densities from 1,038 to 40 stems/ha and the shrub densities from 3,485 to 1,078 stems/ha. The occupied singing grounds increased from 1-2 prior to cutting to 6 in the first spring and to 7 in the second spring after cutting. Late in the first summer, flush counts during a systematic search of a 16-ha plot increased from 0-2 flushes/plot before clear-cutting to 6-19 flushes/plot. In the second summer after cutting, a density of >3.0 birds/ha (probably including some early arriving migrants) was estimated by line-transect method. The birds seemingly colonized the clear-cutting primarily through immigration in the first 2 years because reproduction could not account for the magnitude of the increase. Use of the clear-cutting by woodcocks was not continuous, however, because in dry periods birds moved to nearby wetter areas. The soil moisture was lower in the regenerating stand in the clear-cutting than in adjacent uncut areas, and earthworm biomass averaged below optimal levels. Recommendations for silviculture include clear-cutting across a gradient of soil moisture or cutting near swamps and spacing clear-cuttings temporally to provide tree and shrub cover for woodcocks during early aspen regeneration.

Habitats and Foods of the Eurasian Woodcock During Migration Through North Dobrogea, Romania, 1970-1989

by

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Abstract.   For 16 years (1970-89) habitat use and foods of Eurasian woodcocks (*Scolopax rusticola*) during autumn migration were determined at the Danube River delta in the vicinity of North Dobrogea, Romania. We collected 1,361 woodcocks from seven habitat types. Most woodcocks used aspen (*Populus* sp.) plantations with dense understories (n = 539, 39.1%) and mixed plantations of cutover black locust (*Robinia pseudoacacia*) and ash (*Fraxinus ornus*; n = 324, 23.1%). Only 325 (24.0%) woodcocks were collected in unmanaged forests. The contents of the stomachs of 208 woodcocks were examined. The primary invertebrate foods were *Jules* spp. (17.9%), *Harpalus* spp. (16.4%), and *Amara anenea* (11.7%). Ingested plant parts were unidentified plant fragments (7.1%) and seeds of *Stearia viridis* (4.6%). Ingested foods did not differ between sexes or among habitats.

Habitat Use and Survival Rates of Wintering American Woodcocks in Coastal South Carolina and Georgia

by

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Abstract.   Habitat use and survival rates of radio-marked American woodcocks (Scolopax *minor*) were studied during the winter in coastal South Carolina (1988–89) and Georgia (1989–90). Soon after they arrived, woodcocks were captured in mist nets or in modified shorebird traps or by nightlighting. Each bird was weighed, aged, sexed, and fitted with a 4-g radio transmitter and monitored daily until it died or could not be located or until its radio failed. During the day, the woodcocks in South Carolina frequented seasonally flooded stands of gum-oak-willow (*Liquidambar-Quercus-Salix*) >75 % of the time and <15-year-old pine (*Pinus* spp.) plantations during the remaining time. The predominantly used understory vegetation was switch cane (*Arundinaria gigantica*). In Georgia, woodcocks used bottomland hardwoods, young pine plantations (<15-years-old), mature pine-hardwood stands, and clear-cuttings that had regenerated naturally. Wax myrtle (*Myrica cerifera*) dominated the used understory species at these sites. The woodcocks in South Carolina rarely made daily moves between daytime and nighttime cover, whereas the birds in Georgia made regular flights. At both sites, the daily survival rates of females were low, especially in the absence of losses from hunting. Daily survival rates of females ranged from 0.992 in adults to 0.994 in young. Daily survival rates of males ranged from 1.0 in adults to 0.996 in young. We determined no significant differences in the daily survival rates of woodcocks by age or sex in either South Carolina or Georgia. Probable predators of radio-marked woodcocks included bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), and barred owls (*Strix varia*).

Survival of Eurasian Woodcocks Estimated from the Age Ratio of Specimens in Hunting Bags at Wintering Sites

by

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Abstract.   Analysis of their spatial and temporal distribution in daytime wintering habitats suggests that Eurasian woodcocks (*Scolopax rusticola*) are territorial during winter. Daytime sites are small and occupied by one individual and are usually used for the entire winter unless unfavorable weather causes a decline in the abundance of prey. Ringing revealed that woodcocks are also faithful to nighttime sites, implying that the length of time a woodcock spent in the wintering range was determined by the bird's own survival. Consequently, the survival of woodcocks can be obtained from the estimated mean length of time birds spend on their wintering grounds, from recovery rates of banded birds, or from the mean age of birds taken by hunters. The mean age is directly proportional to the percentage of young (age ratio) taken by hunters. Thus, the survival of woodcocks is low in hunted areas in France because 70% of the harvested birds are juveniles. Survival rates may vary widely and require annual monitoring.

Importance of Meadows for Wintering Eurasian Woodcocks in the West of France

by

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Abstract.   Earthworms (Lumbricidae), which supply 87.7% of the energy in foods Eurasian woodcocks (Scolopax rusticola) ingest, were sampled in forested and agricultural areas in western France. Earthworms were collected at sites used by woodcocks during the day and at night. Soils were wetted with formaldehyde and dug to a depth of 20 cm. At forested sites (n = 36) used by woodcocks, the biomass of earthworms averaged 38 kg/ha (SD = 30) and included nine species of earthworms. Permanent meadows and temporary meadows (>2-years-old, n = 33), which represent 80% of the nocturnal habitat of woodcocks, contained more species (n = 21) and greater biomass ($\bar{x}$ = 1,450 kg/ha, SD = 800) of Lumbricidae than cultivated areas (11 species, $\bar{x}$ = biomass = 230 kg/ha, SD = 355) that were not used by woodcocks. The high densities of woodcocks in western France in the winter is linked to the mild, wet climate that favors Lumbricidae. High densities of earthworms in meadows explain the high use of these areas as night-time feeding sites by woodcocks.

Management and Research on the American Woodcock at the Moosehorn National Wildlife Refuge

by

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Abstract. The Moosehorn National Wildlife Refuge (NWR) borders New Brunswick, Canada, in northeastern Maine and is the only national wildlife refuge dedicated to research and management of the American woodcock (*Scolopax minor*). Research and management in cooperation with the Patuxent Wildlife Research Center of the U.S. Fish and Wildlife Service and with the Ruffed Grouse Society were initiated in 1976 to determine the causes of the decline in woodcock numbers in eastern North America and to develop techniques to stem this decline. Because its history of wildfire, farm abandonment, and reforestation is representative of many areas of the Northeast, the Moosehorn NWR is an ideal location for this work. By the mid-1970's, the woodlands of the Moosehorn NWR were dominated by mature stands of birch (*Betula* sp.), maple (*Acer* sp.), aspen (*Populus* sp.), white pine (*Pinus strobus*), spruce (*Picea* spp.), and balsam fir (*Abies balsamea*). Populations of many species of wildlife, including the American woodcock, that require an early-growth forest were declining. Thus, management was initiated to increase the diversity of the age and the vegetation of the forest. Approximately 2,400 ha of forest were selected for cutting during 40 years (60 ha/year). Rectangular blocks (2 ha) and strips (30 m × varying lengths) are clear-cut in several forest stands of different types and ages. Not more than 20% of a stand is harvested at one time. A new series of blocks or strips is cut in a stand every 8–10 years; a rotation takes 40–50 years. Prescribed burning is used to improve aspen regeneration on a few clear-cut sites. Research at the Moosehorn NWR has been on management that improves habitat for woodcocks, the time and cause of woodcock mortality, and the influence of habitat management on the survival of woodcocks. Results are encouraging. Numbers of courting males in the spring increased from 44 in 1982 to 109 in 1989. The woodcocks' use of some areas managed as feeding habitat increased by 500%. Some forest stands that harbored few woodcocks before management now have some of the highest densities of woodcocks on the refuge. Most notably, high-quality habitat for woodcocks is being redefined. For example, fields with formerly large numbers of roosting woodcocks are

now frequented by only a few because the birds moved to newly created clear-cuttings. Studies of the causes of mortality revealed that drought, low temperature, deep snow, and predation reduce the number of woodcocks but that habitat that lessens the severity of these effects can be provided.

Isolation of a Reovirus from American Woodcocks

by

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Abstract.   Following an episode of subzero weather in December 1989, about 60–80 American woodcocks (*Scolopax minor*) were found dead at Cape May, New Jersey, and another 17 at Eastern Shore of the Virginia National Wildlife Refuge. Twelve of the 17 carcasses from the refuge were submitted for diagnosis to the National Wildlife Health Research Center of the U.S. Fish and Wildlife Service. No significant lesions were seen during the necropsy, however, a virus was isolated from the cloaca, brain, intestine, and lungs of four of the eight examined birds. All the viral isolates produced the same characteristic effect in cell culture, and thus far five have been determined to be nonenveloped RNA viruses. A representative isolate examined by electron microscopy was identified as a member of the Reoviridae family. This is the first report of a virus isolated from a woodcock. Further work is required to determine the prevalence of this virus in the eastern woodcock population and whether it causes morbidity or mortality in woodcocks.

Recognition of Individual Roding Eurasian Woodcocks and Its Application to Census Analysis

by

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Abstract.   Quantitative and qualitative analysis of data from censuses of roding woodcocks (*Scolopax rusticola*) is difficult without the identification of specific individuals. To address multiple counts in a census, I attempted to distinguish individual males by recordings of calls of free-flying males. Recordings were made of eight males at times and locations that ensured that no individual was recorded more than once. The duration of the roding calls (time between two notes) was recorded on tape and on sonograms. Seven variables were measured, and discriminant analysis revealed that three triplets of variables allowed a correct classification of 89.7% of the eight males. Yet, the analysis of the sonograms of the roding calls of a bird equipped with a radio transmitter during 1.5 months showed some fluctuations in the variables.

This technique for the recognition of roding individuals was used to analyze a series of 25 daily recordings. Of the 229 recorded calls, 140 (61%) were usable and indicated that 10 different males were present. Some of these males seemingly took up a greater part of the roding period. Other males displayed in a sporadic manner. The number of different individuals roding at an observation point and the number of recorded contacts correlated ($r^2 = 0.74$, F = 65.35). Thus, the number of recorded contacts is a valid index of relative abundance.

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