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HABITAT AND ENERGETIC RELATIONSHIPS OF AMERICAN WOODCOCK IN MICHIGAN

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HABITAT AND ENERGETIC RELATIONSHIPS OF AMERICAN WOODCOCK IN MICHIGAN

By

Dale Leslie Rabe

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

1981

ABSTRACT

HABITAT AND ENERGETIC RELATIONSHIPS OF AMERICAN WOODCOCK IN MICHIGAN

By

Dale Leslie Rabe

Studies were undertaken to examine 1) the role of interspersion and food availability on habitat utilization by breeding woodcock (Philohela minor), 2) the proximal cues of habitat used to locate feeding sites and the foraging strategies used to capture earthworms (Lumbricidae), and 3) the impact of weather on food availability and bioenergetics of breeding woodcock.

During the springs of 1978 and 1979, 23 aspen (Populus tremuloides) community habitat complexes were censused for singing males and intensively searched with a pointing dog to locate nests, broods, and solitary birds. At the same time, data were collected on habitat structure and earthworm abundance. Thirty-two solitary birds and 31 broods were located during 78 h of searching in the two years. Singing male woodcock used 17 and 20 of the habitat complexes in 1978 and 1979, respectively. Three of the complexes were never used by woodcock during the study. Between-year comparisons of each habitat complex revealed that use by singing males and solitary birds was much more consistent than brood use. Numbers of broods using a complex were correlated (P<0.10) with numbers of singing males in 1979. Earthworm abundance was correlated (P<0.10) with brood use in both years; correlations to males were weaker. Structural measures of the habitat complexes (ie. size, shape, and interspersion) were not consistently correlated with any woodcock use between the years.

In a series of laboratory experiments, the foraging behavior of live-trapped adult woodcock was examined in order to test specific hypotheses about the proximal cues of habitat used to select feeding sites and foraging strategies used to capture earthworms. Foraging trials were conducted in a circular arena where the birds were allowed to probe among eight soil trays containing various soil types, soil moistures, and earthworm size classes and densities. Color, which tends to be correlated with soil types and moisture regimes preferred by earthworms, was found to be the primary proximal cue used by woodcock for selecting feeding sites in these experiments. Birds concentrated searching effort in areas of relatively high prey density, but exhibited no size selectivity. Following the capture of one earthworm, birds tended to concentrate additional searching in the immediate area. This non-random search pattern seems to account for the greater efficiency of capture when prey are aggregated.

A simulation model was used to study the potential impact of weather on the the bioenergetics of breeding and post-breeding woodcock. The model included the effects of temperature and precipitation on the energy requirements of the bird and the availability of its primary food source, earthworms. When energetics data on woodcock were not available, data from similar species were substituted. Earthworm availability was modelled from field data collected in northern Michigan. Results suggest that energy stress on woodcock is potentially greatest during the brood period, with egg laying being the second most critical time. Even though earthworm availability is generally low in mid-summer, this does not appear to be a stressful period because energy requirements of the bird are also relatively low. Simulated earthworm availability during the brood period was compared with reproductive success data and indicated that the impact of spring weather on earthworms is a contributing factor to chick survival. Management implications of the model are discussed.

ACKNOWLEDGMENTS

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I am indebted to my major advisor, Dr. Harold H. Prince, Department of Fisheries and Wildlife, and Carl L. Bennett, Michigan Department of Natural Resources, for their valuable contributions in all phases of the study. I also wish to thank my other committee members, Dr. Donald L. Beaver, Department of Zoology, Dr. Erik D. Goodman, Department of Electrical Engineering and System Science, and Dr. Stanley J. Zarnoch, Department of Fisheries and Wildlife, for their assistance and professional advice.

Special thanks are in order for Dougles Inkley, Tim Reis, Gildo Tori, and James Hudgins, for their dedicated assistance in data collection.

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BREEDING WOODCOCK USE OF MANIPULATED FOREST-FIELD COMPLEXES IN THE ASPEN COMMUNITY TYPE

Researchers have long recognized that woodcock habitat includes a forest and a field component during both breeding and non-breeding seasons (Pettingill 1936, Mendall and Aldous 1943, Blankenship 1957). In recent years considerable information has accumulated concerning the preferred structural elements of singing grounds (Maxfield 1961, Dyer and Hamilton 1977, Kroll and Whiting 1977, Rabe 1977). To apply this information effectively, it is also necessary to understand how bird use relates to spatial associations of these habitat components. The objective of this study was to investigate breeding woodcock response to various habitat interspersion patterns.

METHODS

The Habitat Complex

The study was done within relatively homogeneous aspen plant communities in the Houghton Lake State Forest located in the northern lower peninsula of Michigan. The sapling-size age class of aspen was selected because it is a preferred diurnal cover in that region (Blankenship 1957, Rabe 1977). A habitat complex was defined as the total area of a clearing, or cluster of clearings, plus a 50-m strip of surrounding aspen habitat (Fig. 1). Diurnal cover was limited to this amount based on results of Bourgeois (1977) and Rabe (1977), who found that more than 90% of all diurnal contacts with woodcock (including nests, broods, and solitary birds) were within 50 m of a clearing.

Twenty-three habitat complexes were selected for this study. Areas were rejected if any other clearings were within 150 m of a defined complex. Clearings in the complexes were created with a rolling chopper to remove trees and destroy root systems. Five of the clearings were created in March 1978 and had only sparse plant cover during the study. Of the remaining clearings, 12 were created 3-4 years before the present study and planted to rye grass as part of a deer management program, and 6 were 8-10 years old and dominated by natural grasses and scattered shrubs, primarily sweet fern (<u>Comptonia</u> <u>peregrina</u>).

Variables measured for each habitat complex included size, shape and number of clearings, and the amount of aspen (Table 1). Shape (S) was calculated as a ratio between the length of the perimeter of a clearing (L) and the circumference of a circle of equal area (A) and is based on a shoreline development formula presented by Wetzel (1975):

$$S = L/2\sqrt{\pi A}$$

Discrete openings were defined as clearings larger than 0.1 ha that were separated by a barrier of aspen trees

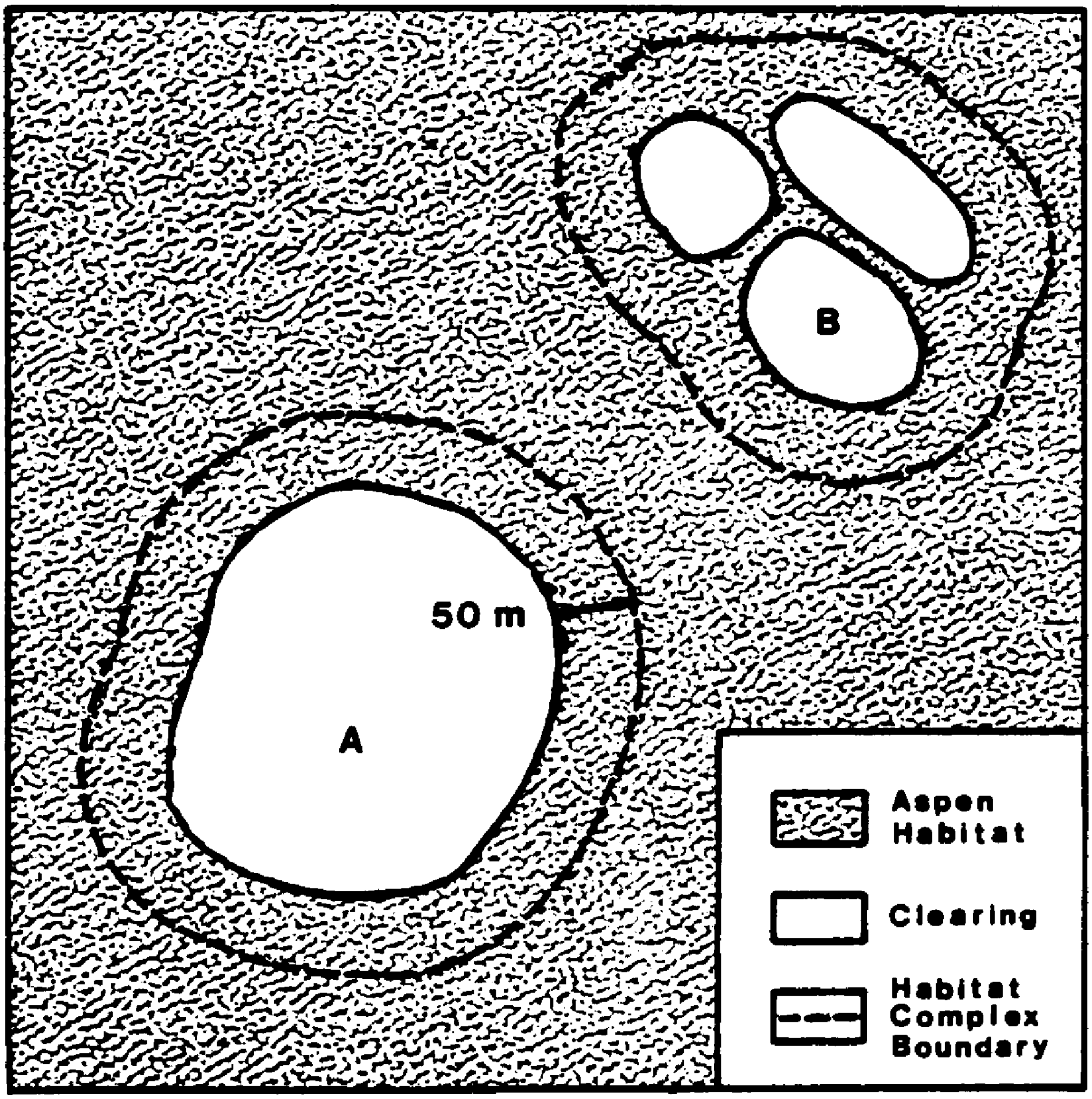

Figure 1. A diagramatic representation of experimental forest-field complexes with one (A) and three (B) discrete openings (see text for definition). The dashed line indicates the area of diurnal habitat included in each complex.

Table 1. Mean and range of variables measured for each of the 23 habitat complexes.

Variable	Mean	Range
Area of aspen habitat (ha)	5.7	0.9 - 14.0
Area of clearing (ha)	2.5	0.1 - 10.9
Number of discrete openings	2.3	1 - 5
Shape of clearing[a]	2.2	1.1 - 3.4

[a] Based on a formula for shoreline development by Wetzel (1975).

(Fig. 1). Area and perimeter measurements were taken from aerial photographs using a computer digitizer.

Measurement of Soil and Earthworm Abundance

Earthworm abundance and soil moisture were monitored because of their potential impact on woodcock use of the areas. Since most feeding activity takes place in the diurnal habitat (Miller 1957, Dyer 1976), sampling was done at nine random locations in the aspen portion of each complex during May of both years. Earthworm abundance was measured in 0.25-m^2 plots using a formalin extraction technique (Reynolds et al. 1977). Soil moisture determinations were made at the same sites by a gravimetric method (percent moisture by weight). Average values of soil moisture and earthworm abundance for each complex were used in comparisons with woodcock utilization.

Woodcock Use

Measurements of woodcock use included an evening census of singing males and diurnal searches of the surrounding aspen habitat with a pointing dog to locate broods and solitary birds. Singing-ground counts were done twice each year between 25 April and 15 May. Starting time and weather conditions for censusing followed guidelines established by the U.S. Fish and Wildlife Service which are based on studies by Westfall (1954), Blankenship (1957), Goudy (1960), and Duke (1966). The average of the two censuses was used in comparisons with other bird uses and habitat variables.

Three diurnal searches of the habitat complexes were made each year during the major hatching period, 1 May to 7 June. Searching was discontinued during rainy periods or when ambient temperatures exceeded 27° C, conditions that would impair a dog's ability to locate woodcock. An attempt was made to standardize searching effort among habitat complexes. Total contacts with broods and solitary birds for the three searches were used in comparisons with other variables. When possible, all members of broods were banded to avoid recounts.

RESULTS

Woodcock Use of Habitat Complexes

Numbers of singing male woodcock and broods using the complexes increased between 1978 and 1979 whereas contacts with solitary birds declined slightly (Table 2). Similar trends were documented for the percentage of habitat complexes used by the respective components of breeding woodcock. The greatest change between years occurred in brood usage, where equivalent searching effort resulted in almost twice as many brood contacts in 1979.

Correlations between singing male, solitary bird, and brood use of the habitat complexes in 1978 and 1979 produced four statistically significant associations (Table 3). Between the two years, numbers of singing males and solitary

Table 2. Maximum number of active singing grounds (based on two censuses) and total number of solitary birds and broods found in 39 h of searching each year. The value in parenthesis is the percentage of the 23 habitat complexes used by woodcock.

Woodcock use	1978	1979
Singing males	26 (74)	35 (87)
Solitary birds	18 (39)	14 (35)
Broods	10 (26)	21 (43)

Table 3. Correlation matrix of woodcock use among the habitat complexes (n=23).

	Singing males		Solitary birds		Broods	
Woodcock use	1978	1979	1978	1979	1978	1979
Singing males						
1978	1.0					
1979	0.48*	1.0				
Solitary birds						
1978	0.25	0.23	1.0			
1979	0.50*	0.20	0.44	1.0		
Broods						
1978	0.21	0.24	0.01	0.05	1.0	
1979	0.41	0.54*	0.16	0.25	0.20	1.0

*Significant at $P<0.05$.

birds were correlated ($r=0.48$ and 0.44, in 1978 and 1979 respectively). Brood use between the two years was not significantly correlated ($r=0.20$). Also, in 1979, numbers of singing males were correlated with brood use of the habitat complexes. The fourth correlation, between singing males in 1978 and solitary birds in 1979, has no biological value.

Woodcock-Habitat Relationships

Average soil moisture content in the complexes increased slightly from 1978 to 1979 (Table 4). Although yearly averages of earthworm numbers did not change, numbers within some individual habitat complexes did fluctuate.

Correlations between woodcock use and habitat variables produced few significant ($P<0.01$) associations (Table 5). The number of broods using a habitat complex was correlated with earthworm abundance in both years and with the area of clearing in 1978. Although numbers of solitary birds correlated with size of clearing in a habitat complex in 1978, this relationship was not repeated in 1979. None of the correlations between singing males and habitat variables were significant.

The different ground covers in the clearings were also evaluated to determine their importance to singing-male use of the areas. Numerical comparisons showed that 3 of 5 bare-ground, 1 of 12 rye grass, and 2 of 6 shrubby clearings were not used in 1978, and that each clearing type had one fewer unused habitat complex in 1979. Statistically, these

Table 4. Average and range (in parenthesis) of soil moisture and earthworm abundance for all 23 habitat complexes combined.

	Soil moisture	Earthworms/0.25-m^2 plot	
Year	(%)	Number	Biomass (mg)
1978	12.5 (7.3 - 24.1)	2.67 (0 - 13.0)	540 (0 - 4,130)
1979	16.7 (9.7 - 32.1)	2.87 (0 - 17.2)	480 (0 - 4,070)

Table 5. Correlations between woodcock use and habitat variables (n=23).

	Singing males		Broods		Solitary birds	
Habitat variables	1978	1979	1978	1979	1978	1979
Area of aspen habitat (ha)	0.30	-0.02	0.47*	0.17	0.26	0.06
Area of clearing (ha)	0.20	0.01	0.37*	-0.01	0.45*	0.17
Number of discrete openings	0.25	0.28	0.20	-0.11	-0.32	0.09
Shape of clearing	0.21	-0.27	0.11	-0.14	-0.09	0.16
Number of earthworms	0.19	0.29	0.35*	0.35*	-0.06	-0.06
Soil Moisture	-0.07	-0.15	-0.19	0.07	-0.09	0.13

*Significant at P<0.10.

differences were not significant when corrected for sample size.

DISCUSSION

Male Woodcock

Most of the singing grounds used in 1978 were used again in 1979. A high degree of fidelity to singing grounds by male woodcock is well documented (Sheldon 1971, Liscinsky 1972, Whitcomb 1974). The between-year correlation of singing males reported in this study (r=0.48) would probably have been higher had it not been for the nine new singing males in 1979. There is no data to indicate why singing males increased on these areas between the two years.

Singing males are known to use openings which contain a wide variety of vegetative structures. Observations during the present study indicate that in the bare-ground and rye clearings, males had a tendency to select singing sites close to aspen edges. However, in clearings with scattered shrubs, singing sites were located throughout the openings. Wishart and Bider (1976) believe that shrubs offer predator protection for displaying males. In open fields, the proximity of singing sites to edges of clearings may be one way woodcock compensate for lack of shrubby cover in the clearing.

Correlations of singing males with size of clearings and numbers of discrete openings suggest that smaller discrete openings more easily accommodate multiple singing grounds than a single large opening. Wishart and Bider

(1976) noted frequent aggression between territorial males not isolated by a structural barrier. Maxfield (1961) found that minimum size of a singing field was directly related to the height of surrounding vegetation.

The weak correlation between singing and solitary birds in both years and the relatively small number of diurnal contacts suggest that, in general, singing males were not using adjacent aspen habitat as diurnal cover. In contrast, Mendall and Aldous (1943) and Sheldon (1971) documented numerous instances where diurnal cover was immediately adjacent to singing fields and males walked to courting sites.

Broods

Current methods for evaluating woodcock population trends are based on censuses of singing males (Artmann 1977) and assume that the proportion of displaying males in a population is constant through time and under differing habitat conditions. Data in support of this assumption are limited. However, the correlation between singing males and broods in 1979 provides indirect supporting evidence. It is felt that the lack of significance for the same correlation in 1978 was partly due to the smaller sample size. Additional supporting evidence has been reported by Whitcomb (1974) who found a correlation between the numbers of singing males and the total spring male population on High Island, Michigan, as derived from summer mist net data over a five year period. Because of the lack of sufficient field data to support the assumption that singing males are proportional to total breeding population size, Godfrey (1975) recommended abandoning singing-ground censuses in favor of other survey methods. Although singing-ground counts are an efficient means of censusing, additional research is needed to verify that a constant proportion of males in a population display, independent of changing habitat conditions and population levels.

The association between woodcock use of habitat and earthworm abundance has long been suspected. Not until recently, however, has a strong dependency been demonstrated (Reynolds et al. 1977). The significant correlation between brood use and earthworm abundance in this study supports those findings; male usage had a much weaker correlation to earthworm abundance. I suspect that when females are caring for broods, they spend a greater amount of time in feeding areas because of high energy requirements and restricted mobility. The importance of earthworms in a habitat complex is further emphasized by the fact that the three habitat complexes never used by woodcock were also devoid of earthworms, based on our sampling.

MANAGEMENT CONSIDERATIONS

Enough research has been done on woodcock habitat preference so that conceptual models can be developed to guide management practices. Habitat requirements of breeding woodcock can be grouped into three major components: food, diurnal cover, and singing grounds. By using the range of suitable conditions for each of these components as an indicator of their importance, the following ranking seems appropriate:

Food > Diurnal Habitat > Singing-Ground Habitat.

Also, since areas used as singing grounds are frequently used for summer roosting fields (Whitcomb 1972, Wishart and Bider 1976), the model is probably appropriate to the post-breeding season as well.

Food habits analyses (Aldous 1939, Sperry 1940, Glasgow 1958, Dyer 1976) have shown that earthworms are an important part of the woodcock diet. Reynolds (1977) found that only two species of earthworms are commonly eaten by woodcock in Maine. This high degree of specialization limits woodcock to habitats that can support suitable and sufficient earthworm populations. Data from Reynolds et al. (1977) suggest that a strong association exists between vegetation types and earthworm abundance because of differential palatability of leaf litter, with aspen and alder being most preferred (Reynolds and Jordan 1975).

Diurnal habitat requirements are somewhat broader than food requirements based on the wide range of woodcock-associated vegetation types that have been reported in the literature (Sheldon 1971). More recently, structural analyses (Bourgeois 1977, Kroll and Whiting 1977, Rabe 1977) have suggested that understory features are better indicators of diurnal habitat suitability than species composition. Even from a structural standpoint, however, diurnal habitat requirements can be met in a variety of forest community types.

Although the literature describes a variety of singing-ground habitats (Maxfield 1961, Sheldon 1971), studies have generally been unsuccessful in predicting their use on the basis of structural or species composition. Bennett et al. (1981) found that adjacent forest habitats were a better predictor of use than features within a clearing. Fields with scattered shrubs seem to be preferred (Sheldon 1971), but woodcock will use practically any opening if there is enough area to take-off and land. These data indicate that singing grounds have the most general requirements of the three components.

Based on this model, selection of sites to be managed for woodcock should consider food availability as the top priority, then diurnal habitat, and finally the characteristics of the singing ground. Attempts to manipulate earthworm populations in the field are generally impractical, yet habitats that support adequate populations can easily be manipulated using normal forestry practices to produce suitable diurnal and singing-ground habitats for woodcock.

FEEDING SITE SELECTION AND FORAGING STRATEGIES OF AMERICAN WOODCOCK

Woodcock obtain most of their food by probing in the soil. Because this method of foraging does not allow visual contact with prey items before capture, birds are limited in their ability to assess food abundance at a particular site. When prey are not evenly distributed in the environment, as generally is the case, woodcock are likely to expend time and energy searching in unprofitable areas unless they are able to use some proximal cue (Baker 1938) of the habitat to aid in locating more profitable sites.

Food habits studies indicate that woodcock consume a variety of soil invertebrates but depend to a large extent on earthworms (Pettingill 1936, Aldous 1939, Sperry 1940, Glasgow 1958, Dyer 1976). The amount of earthworms vary with seasons and geographic location, but generally comprise 60 to 90% of the diet. Because of their specialization on one particular prey, it seems likely that woodcock would use environmental factors which affect the distribution and abundance of earthworms as proximal cues for locating them. This premise led to a study of earthworm ecology in an effort to identify critical habitat components that might be detectable by woodcock. Soil properties were considered most likely because of their direct affect on earthworm abundance and distribution.

Because of limitations on the depth that woodcock can probe, availability of earthworms is not only a function of their horizontal distribution but also their vertical distribution in soil. Murchie (1958) classified variables affecting their horizontal distribution into three categories: 1) physio-chemical including soil temperature, moisture, pH, inorganic salts, aeration, and texture; 2) the availability of food including herbage, leaf litter, and consolidated organic matter; and 3) the reproductive potential and dispersive powers of the species. Vertical distribution, on the other hand, is influenced primarily by species ecological preferences and by soil moisture and temperature conditions (Reynolds and Jordan 1975). When temperature or moisture conditions become unsuitable, earthworms respond by moving to more suitable areas or aestivating until favorable conditions return (Edwards and Lofty 1977:127-131). In general, high surface temperature and dry soil are more limiting to earthworms than low temperature and water-logged soil (Nordstrom and Rundgren 1974).

Reynolds et al. (1977) found that over 90% of the earthworms consumed by woodcock in Maine were of two species (<u>Aporrectodea</u> <u>tuberculata</u> and <u>Dendrobaena</u> <u>octaedra</u>) even though several others also occurred in woodcock habitats. The partial or total exclusion of these earthworm species was due to their scarcity or preference for deeper soil strata rather than an avoidance by the woodcock. Liscinsky (1972) found that captive woodcock readily consumed earthworm species not normally found in their diet.

A. tuberculata and D. octaedra have been found to occur in soils ranging from gravelly sand to clay, but highest densities are consistently associated with light loam soils (Guild 1948). Reynolds (1977) reported that optimal temperature and moisture conditions for these species are between 10 and 18° C and 15 to 80%, respectively. Earlier studies (Olson 1928, Guild 1948), however, referenced a considerably narrower range of 15 to 40% for moisture. Gerard (1967) found that several species of Aporrectodea generally occur within 10 cm of the soil surface except when soil temperature falls below 5° C or soils become dry, forcing individuals deeper in the soil.

This information indicates that earthworm availability differs not only on the same site between seasons but also between sites at the same point in time. Thus, if woodcock are to forage efficiently they need to be responsive to both the static and dynamic components of soil which affect earthworms. The objectives of this study were to examine soil properties as possible cues for selecting feeding sites and the strategies used to capture earthworms.

METHODS

The Birds

The same six woodcock were used as subjects in all the experiments except the last two, where injuries resulted in only four birds being tested.

Upon capture, woodcock were wing-clipped and placed in individual holding cages (0.6x1.0x1.0 m) constructed of woven-wire with cloth ceilings. Wing-clipping did not seem to impair normal activities, yet helped to reduce injuries while birds adjusted to captivity. Woodcock were kept indoors under a natural light regime, maintained on an *ad libitum* diet of live earthworms (*Lumbricus terrestris*), and provided with water. This species of earthworm, commonly referred to as night-crawlers, was selected because it was commercially available in large quantities. I found, as did earlier studies (Stickel et al. 1965, Liscinsky 1972), that woodcock had no problem eating them even though they were larger than species normally found in their diet. Earthworms fed to woodcock in the holding cages were covered with moistened sphagnum moss (*Sphagnum* sp.). This helped to prevent rapid dehydration of the earthworms and also avoided introducing a potential bias from the use of soil to cover the food.

Woodcock were allowed at least 10 days to adapt to captivity before being used in experiments. This proved to be sufficient time for them to adjust to the frequent handling, reestablish a normal feeding pattern, and regain most of the weight lost immediately after capture.

The Testing Arena

Foraging experiments were conducted in a 1.5-m circular arena (Fig. 2) having a 0.5-m woven-wire sidewall, plywood floor, and an open top. Eight soil trays (23x33x10 cm) were positioned symmetrically around the perimeter of the arena, recessed flush with the floor, and filled with firmly packed soil.

The arena was isolated in a 2.4-m^2 room with sound absorbing walls. This was necessary because extraneous noise and motion tended to interrupt the foraging activity of birds being tested. Observations were made from outside the room through a 20-cm^2 one-way glass window. Room lighting was adjusted to approximate the crepuscular conditions when woodcock normally feed.

Testing Procedures

Standardized test procedures were used for all experiments. Prior to experimentation, birds were familiarized with the arena while testing their movement patterns. Soil conditions in each tray were identical for this test. One woodcock that did not exhibit a random probing pattern (equivalent probing in each tray) under these conditions was excluded from further testing.

Experimental treatments were randomly assigned tray locations within the area for the duration of an experiment.

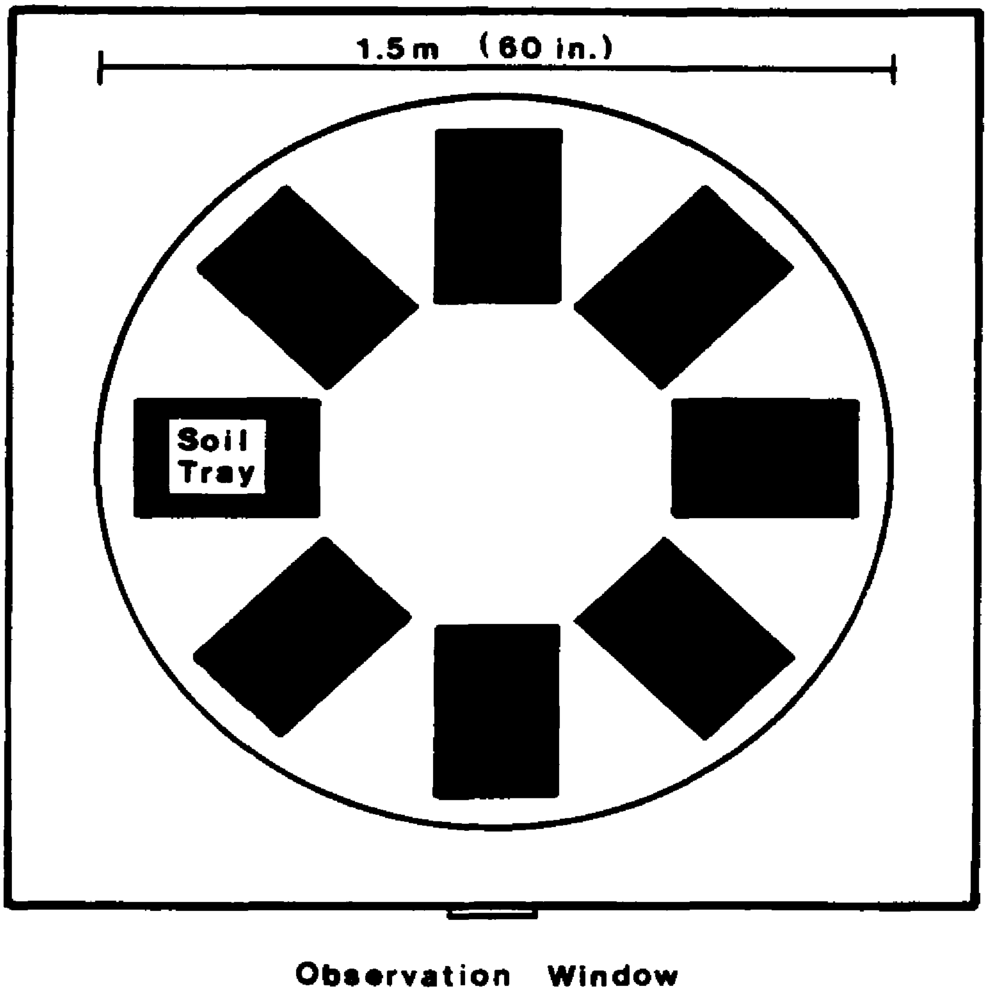

Figure 2. Layout of the testing arena used for the foraging experiments.

Each experiment consisted of three replicate trials for each bird on different days. Woodcock were deprived of food for a 12 h period before each trial. During a trial, a bird was allowed to forage among the trays for a 10-min period while an observer recorded its movement patterns and the number of probes and earthworm captures in each tray. At the end of a trial, birds were returned to their holding cages and fed.

Analysis

Although data are presented as percentages of total probing activity, statistical analysis for each experiment was performed on the number of probes per tray using a two factor mixed model analysis of variance (ANOVA):

$$Y_{ijk} = U + a_i + B_j + (aB)_{ij} + E_{(ij)k}$$

where Y_{ijk} is the number of probes per trial, U is the overall mean of probing activity, a_i is the fixed effect of the i-th treatment (the various soil or prey conditions in trays), B_j is the random effect of the j-th individual woodcock, $(aB)_{ij}$ is the treatment-bird interaction term, and $E_{(ij)k}$ is the random error. Because individual woodcock varied considerably in probing activity during a trial, including them as a main effect in the analysis improved the test of treatment differences. The first-order interaction was used to evaluate the consistency of treatment response between individuals. Data were transformed with $\log_{10}(X+1.0)$ to improve among group heterogeneity. When overall treatment differences were found to be significant, a Tukey HSD test (Gill 1978:179) was used to test for individual treatment differences. In all cases statistical significance was set at the 0.05 probability level.

RESULTS AND DISCUSSION

Selection of Feeding Sites

These experiments were designed to investigate the role of soil characteristics as proximal cues in woodcock feeding site selection independent of other habitat parameters. Specifically, they attempt to determine if woodcock monitor not only stable physio-chemical components of soil (ie. texture, pH, organic matter) which affect earthworm site suitability, but also the more dynamic components (ie. moisture and temperature) which influence seasonal availability of earthworms. Because many characteristics of soil may provide potential cues, I decided to first examine naturally occurring soil types to determine if woodcock exhibit any overall preferences before proceeding to more detailed investigations. Among the dynamic components of soil, it was felt that moisture was generally more limiting and possibly more detectable by woodcock than soil temperature which tends to be more uniform over a broad area. For these reasons, the first two experiments evaluated probing activity in relation to selected soil types and moisture conditions.

In the first experiment, woodcock were given a choice of four soil types: sand, sandy loam, loam, and clay loam (Table 6). All soils were obtained from the same general

Table 6. Classification, texture analysis, and associated earthworm populations of the four soil types used in the experiments.

	Texture [a]			Earthworm Density [b]
Soil type	% Sand	% Silt	% Clay	(Number/m^2)
Sand	94	2	4	0
Sandy loam	58	32	10	78 ± 21
Loam	42	36	22	108 ± 38
Clay loam	32	32	36	69 ± 22

[a] Based on hydrometric determination (Foth and Turk 1972).

[b] Samples at the site where soils were collected using a formalin extraction technique (Reynolds et al. 1977).

geographic area as the birds being tested. Sampling (using the formalin technique of Reynolds et al. 1977) at the soil collection sites indicated that all except the sandy soil type were supporting earthworm populations. Soils were air-dried to standardize moisture content and screened to remove large debris. Each of the four soils were used in two trays in the testing arena. In the second experiment all trays contained the loam soil but differed in moisture content. Water was added to each of two trays to achieve 10, 25 or 50% moisture levels. The remaining two trays were left with air-dried soil. Earthworms were not used in either experiment.

Woodcock showed pronounced discrimination between basic soil types (Fig. 3). All six birds exhibited similar patterns of preference as indicated by the nonsignificant (P>0.25) bird-treatment interaction term in the analysis. Comparisons of individual treatments showed that probing activity was significantly different between each soil type except sand and clay loam. The ranking of woodcock preference documented in this experiment correlate well with the ranking of earthworm abundance at the locations where these soils were collected.

Liscinsky (1972) reported somewhat different findings in a similar study of woodcock probing activity and capture success in sand, clay and loam soils. He found that when soils contained earthworms the highest capture rate was in loam, yet the greatest number of probes was in clay.

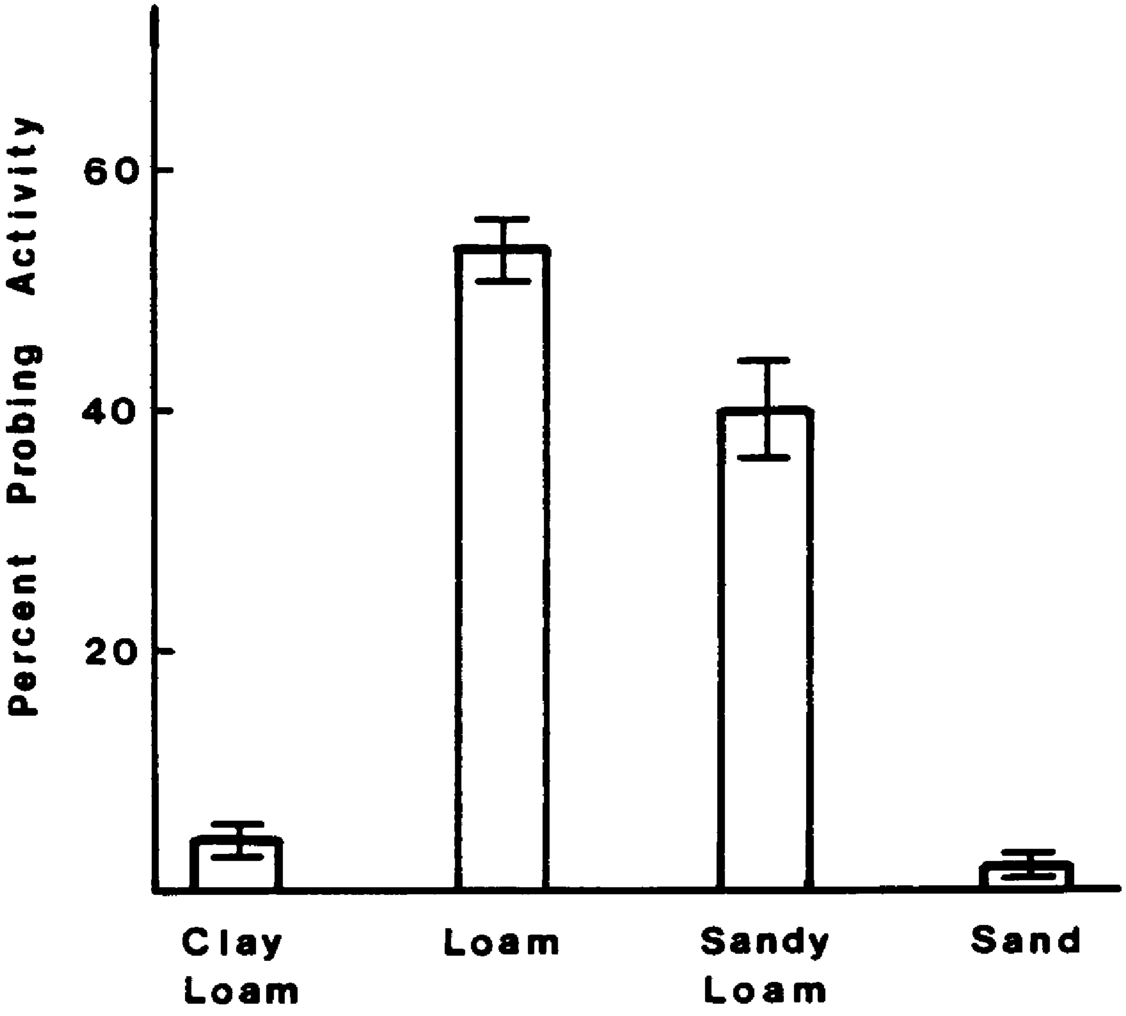

Figure 3. The average (±S.E.) percentage of probing activity by six woodcock among the four soil types tested.

However, when soils contained no earthworms, probing activity was nearly equal among the three soils, with only slightly more probing in sand. I suspect the outcome in the latter case results from the fact that Liscinsky (1972) measured probing activity over a 24-h period, and that when birds were unsuccessful in obtaining food from loam soils they began to search all others available.

Woodcock showed significant overall preferences in terms of soil moisture content, with 50% of all probing activity occurring in the wettest soil (Fig. 4). It should be pointed out, however, that moisture conditions on the wet side (>50%) of the optimal range for earthworms as reported by Reynolds et al. (1977) were not tested. Although differences between the three drier soils were not statistically significant, they do show a trend of increasing activity with increasing moisture content. All six birds tested showed equivalent patterns of preference. There is a close parallel between the amount of woodcock probing activity and moisture conditions preferred by earthworms.

These findings suggest that woodcock use both moisture content and some physical property of soil to select feeding sites. However, the variables are confounded because there were perceivable color differences associated with the soil types and moisture regimes tested, and in each case greater probing activity was associated with the darker soil conditions. Among the four soil types, the loam and sandy

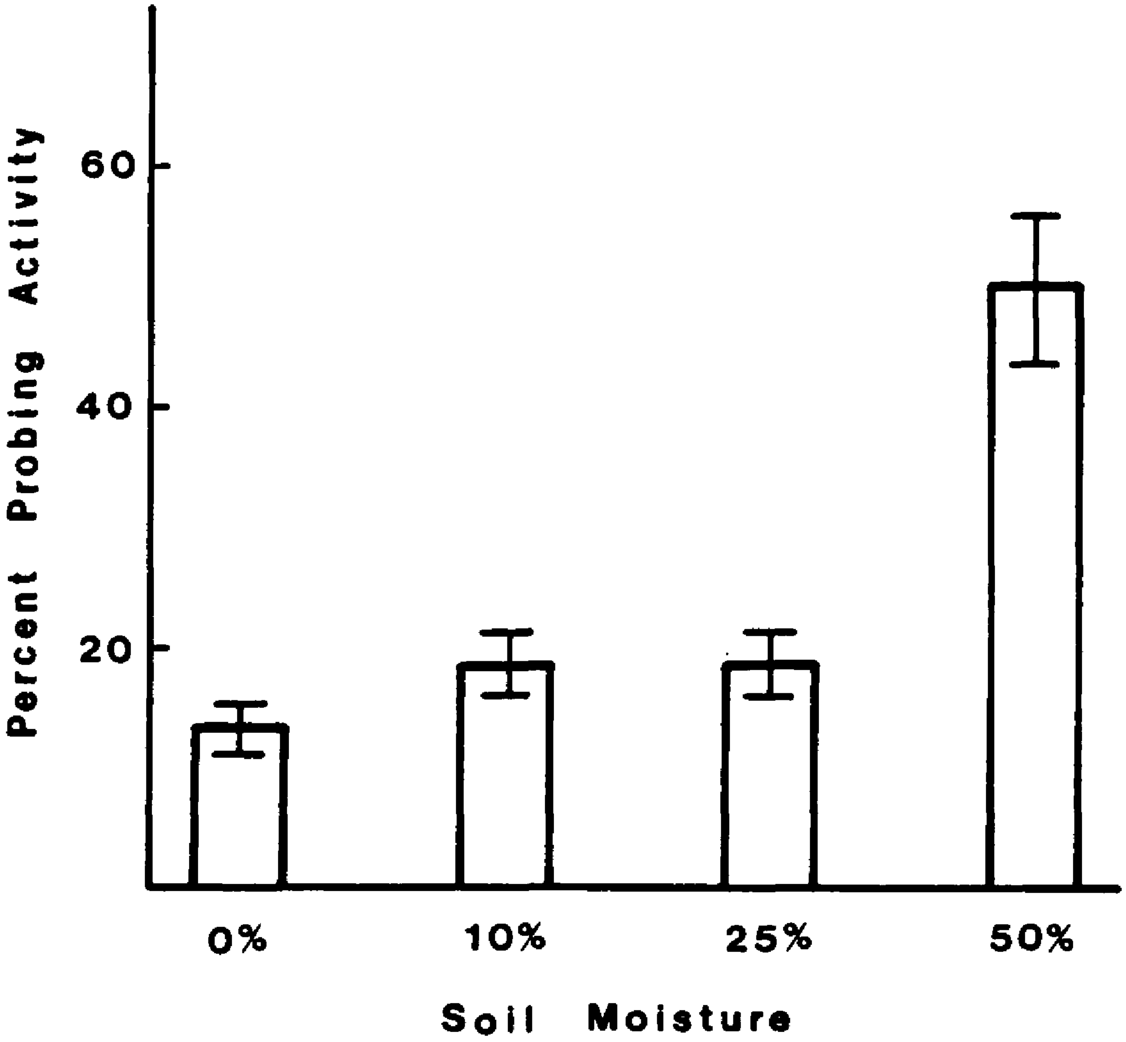

Figure 4. The average (±S.E.) percentage of probing activity by six woodcock in loam soils of varying moisture content.

loam were much darker than either the sand or clay loam. Differences were less obvious between the two lighter and two darker soils. In general, I found that soils became darker in appearance as the moisture content was increased.

The Role of Soil Color

In this experiment it was necessary to modify natural soil conditions in order to dissociate color from moisture content and soil type. This was accomplished by coloring sandy soil with fabric dye. The colors selected represent a continuum from light to dark and included a yellow which closely matched the natural color of sand, a medium green and brown, and black. Two trays of each colored soil were randomly positioned in the arena. Fifty percent moisture was added to the yellow soil and 25% to both the green and brown, while the black soils were left air-dried. In this way, physical properties of the soil were held constant among the trays while creating opposing gradients for color and moisture. If woodcock are cuing primarily on soil type, they would be expected to exhibit random probing under these conditions, whereas reliance on color or moisture would result in concentrated probing activity in the darkest or wettest soils, respectively.

Woodcock exhibited a strong preference for the darkest soils (Fig. 5). In fact, 70% of all probing activity occurred in the air-dry black soil while only 4% took place in the yellow soil with 50% added moisture. Nearly equal amounts of probing took place in the green and brown soils.

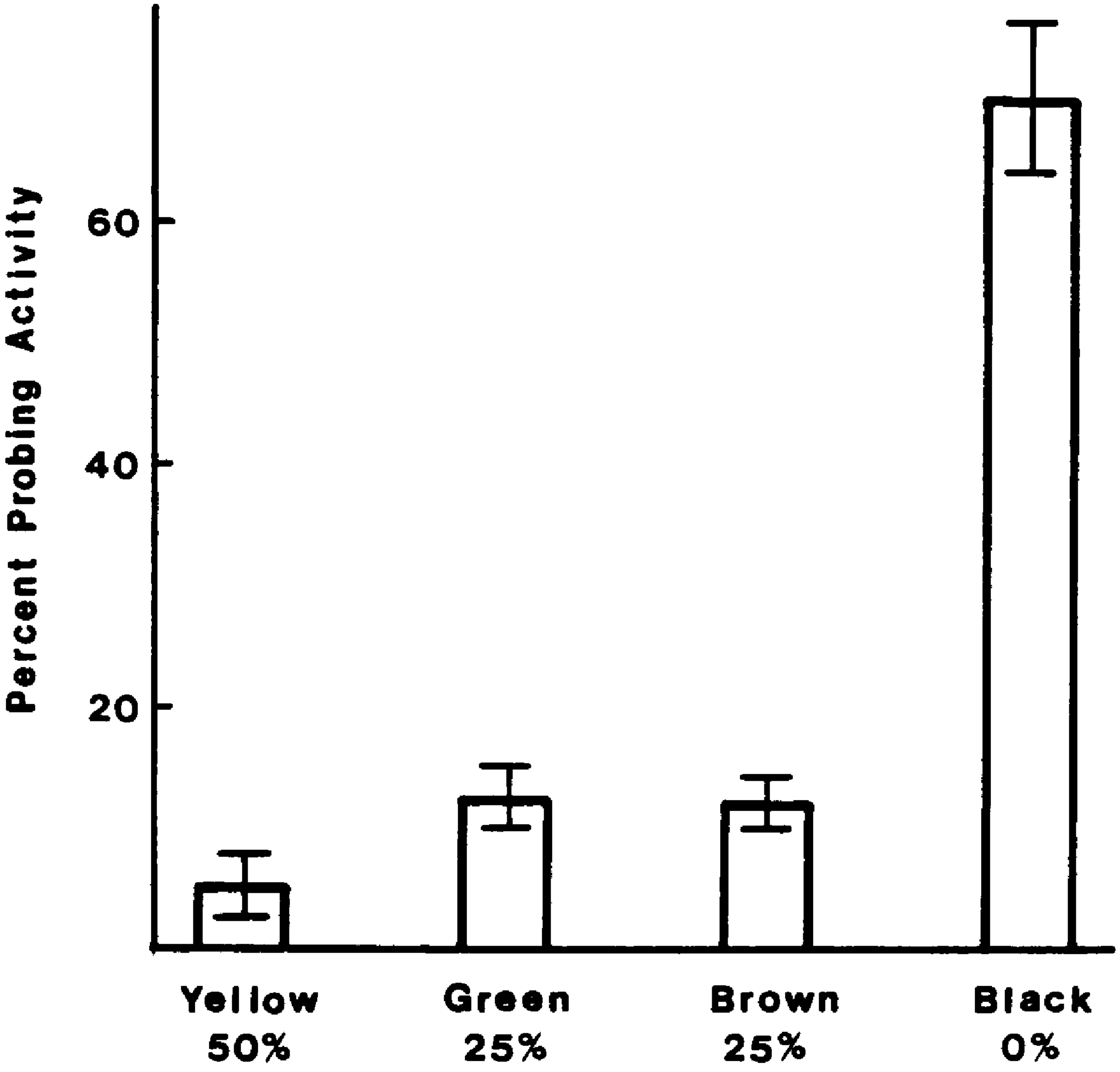

Figure 5. The average (±S.E.) percentage of probing activity by six woodcock in color-dyed sandy soil with varying moisture content.

As in the first two experiments, all six birds showed equivalent patterns of preference among the various color-moisture combinations. These results indicate that woodcock put greater emphasis on color than either soil type or moisture content as a basis for selecting feeding sites. The nearly equal probing activity in the green and brown soils also suggests that color value (the brilliance of a color, Foth and Turk 1972) may be a more decisive factor than hue (color wavelength) in evaluating soil.

Color would be particularly useful for locating prey within the range of habitats used by woodcock because darker soils, for the most part, are associated with the soil types and moisture content preferred by earthworms. In addition, use of color allows the birds to monitor only one soil characteristic and yet have a basis for evaluating both site quality and seasonal availability of earthworms. Because of the dynamic nature of moisture in soil, and therefore earthworm availability, I suspect that woodcock regularly sample new areas in order to monitor changing conditions.

Under experimental conditions, with all soil choices in close proximity to each other, woodcock rarely showed complete avoidance of any tray during a trial. Instead, they appeared to apportion searching effort according to the relative darkness of soils. Under natural conditions, when foraging covers a much larger area, I suspect that woodcock allocate searching effort among various soils in a similar manner. It may be that soil sampling is done in reference to some sort of color search image.

It is possible that under certain environmental conditions the reliability of color as an indicator of good site quality may break down (e.g. when soils become overly saturated with water) or mislead birds. Field observations of woodcock probing in mud puddle basins along sandy trail roads appears to be an example of the latter case (Rabe, unpublished). The basins were much darker in appearance than other parts of the roadbed because of a thin layer of silt accumulation from water runoff. It was assumed that the birds were searching for food at these locations, yet earthworm sampling was unproductive. Because probing was always concentrated only in the basins, I dismissed the possibility that the birds were simply in search of grit.

The fact that woodcock use soil characteristics as a means of locating earthworms does not exclude the possibility that vegetation, ground litter, or other habitat features may also play an important role. For example, Reynolds and Jordan (1975) found that earthworm abundance was determined in part by vegetation cover types because of differences in the palatability of their leaf litter. Thus, it is possible that woodcock also use plants to aid in the location of earthworms.

Foraging Behavior Within Feeding Sites

Foraging studies on other animals have shown that some predators concentrate feeding in areas of relatively high prey density when prey size is held constant (Smith and Dawkins 1971, Simons and Alcock 1971, Krebs et al. 1974), while others even become size selective when prey are sufficiently abundant (Werner and Hall 1974, Krebs et al. 1977, Goss-Custard 1977, Bengston et al. 1978). In the latter studies, predators were able to make some visual assessment of prey conditions. I was particularly interested in finding out how efficient woodcock are considering their visual limitations for locating and pursuing prey. Two additional experiments were used to evaluate how woodcock forage relative to variations in prey size and prey density.

Loam with 40% moisture was used in all trays for both experiments. Live _L. terrestris_ were used as prey and were randomly placed in the trays 2 to 6 cm below the soil surface. In the first experiment equal numbers of two size classes were used with the larger size class approximately three times the biomass of the smaller. Four trays were given two small prey and the remaining trays received two large prey. In the second experiment, prey size was held constant (using the larger size class) and the density of earthworms varied among the trays. Each of two trays were given either 0, 2, 4, or 8 earthworms.

Probing activity and capture success were not significantly different between trays containing large or small prey (Table 7). Equivalent analyses (ANOVA's) on capture efficiency and number of probes per capture,

Table 7. Summary of probing activity and capture success ($\bar{X}$ ± S.E.) of four woodcock in response to equal densities of two size classes of prey.

Prey size	Percent probing activity	Total captures	Capture[a] efficiency	Probes per capture
Small	46 ± 4	22	23 ± 3	38 ± 2
Large	54 ± 4	14	15 ± 4	74 ± 13

[a] Capture effeciency is the percent of prey caught out of the total number available.

however, showed that significantly more probes were used to capture larger earthworms, yet there was no overall difference in the efficiency of capture between the two sizes. On the average, woodcock caught only 19% of the available prey during each ten minute trial.

Significant differences in probing activity did occur relative to variations in prey density with the greatest amount of activity in trays containing the largest numbers of prey (Table 8). Tests of individual treatment differences showed that significantly less probing took place in trays containing no prey, significantly more in trays with eight prey, and nearly equal amounts in trays containing two and four prey. As reflected by the similarity of capture efficiency data, total numbers of prey captured were approximately proportional to the initial densities of prey in the trays, yet the number of probes needed per capture declined significantly as the density of prey increased. In this experiment, woodcock caught 48% of the available prey, on the average. It is not clear why the same birds were so much less efficient in capturing earthworms in the first experiment compared to the second, or why so many more probes were needed per capture even when prey conditions (size and number of prey per tray) were equivalent. Individual birds exhibited equivalent patterns of selectivity in both experiments.

Observations of probing behavior during these experiments indicated that woodcock use a fairly well-

Table 8. Summary of probing activity and capture success ($\bar{X}$ ± S.E.) of four woodcock in response to various densities of equal-sized prey.

Prey density	Percent probing activity	Total captures	Capture[a] efficiency	Probes per capture
0	17 ± 1	0		
2	25 ± 1	7	45 ± 11	22 ± 3
4	24 ± 2	12	43 ± 12	12 ± 2
8	37 ± 1	17	56 ± 21	9 ± 3

[a] Capture efficiency is the percent of prey caught out of the total number available.

defined search pattern to locate and capture prey. The pattern includes two distinct types of probing: exploratory and pursuit. Birds searched new areas by making shallow exploratory probes along and on either side of their path of movement (in the experimental arena this tended to be a circular path around the perimeter). With each probe birds paused momentarily before advancing. Because woodcock were never observed capturing prey with exploratory probes, I concluded that they were used primarily for detecting the presence of earthworms in the soil. Both Liscinsky (1972), studying captive birds, and Glasgow (1958), observing wild birds, also concluded that woodcock were able to detect earthworms without actual contact. Sheldon (1971) speculated that nerve endings concentrated at the tip of the bill allowed the bird to sense earthworm movement, however, to my knowledge this has not been verified.

When an earthworm was detected with an exploratory probe, the woodcock followed with one or more pursuit probes in the immediate area. Pursuit probing was generally much deeper than exploratory probing and generally occurred in rapid succession. If unsuccessful in capturing the food item, birds simply continued searching along their original path. When successful, however, they nearly always concentrated further exploratory probing in the same area as the capture. Only after extensive searching without additional success did birds once again begin searching in new areas.

Woodcock did not exhibit any size selectivity for earthworms while foraging . By the time a bird is able to visually assess a prey item, it has already expended energy to locate, capture, and withdraw the earthworm from the ground. From an energetic standpoint, the additional cost of ingesting the item is relatively small. Therefore, it would seen unprofitable for woodcock to reject prey based on size, regardless of the density of prey in the environment.

Woodcock did concentrate searching in areas of higher relative density which suggests that they are able to evaluate prey density at a site. There is no evidence, however, to conclude that this is an a priori assessment made on the basis of exploratory probing. Rather, it seems to be a function of the success rate associated with the non-random foraging pattern following an initial prey capture. Probability theory would predict that probing in the vicinity of a previous capture would be more successful than completely random probing only when earthworms are aggregated. In this way birds can use the information from one successful capture to improve their chances of locating additional prey. On the other hand, when earthworms are randomly distributed there is no advantage in knowing the location of previous captures, and therefore a non-random search pattern would be less efficient than completely random searching. Even though prey were randomly placed in soil trays, the higher density trays more closely represent an aggregation of prey, whereas the lower density trays are more representative of a random distribution. Edwards and Lofty (1977) and Satchell (1955) found that earthworm reproduction, as well as local variations in moisture and food supply, frequently result in aggregations of earthworms even within relatively homogeneous soil types. Therefore, it appears that woodcock have evolved the non-random foraging strategy in response to a non-random distribution of prey.

THE EFFECT OF WEATHER ON THE BIOENERGETICS OF BREEDING WOODCOCK

Weather patterns and extremes are known to affect woodcock behavior and are a suspected cause of mortality. Studies have shown that cold spring temperatures cause a decline in singing male activity (Duke 1966) and that temperature and wind play an important role in the timing of spring and fall migrations (Sheldon 1971, Godfrey 1974, Coon 1977). Less is known about the affect of weather as a mortality factor. Mendall and Aldous (1943) observed nest losses and adult mortality on the breeding grounds following an extended period of inclement weather. Sheldon (1971) and Owen (1977) believe that adverse weather during the incubation and brood-rearing periods may cause significant chick mortality.

Earthworms, a major food source for woodcock, are also affected by weather conditions. Reproduction and growth rates of earthworms have been shown to decline when temperatures are either too hot or cold (Evans and Guild 1948, Satchell 1955). Activity of the animal and its distribution in the soil are also related to moisture and temperature conditions (Edwards and Lofty 1977).

The objective of this study was to evaluate both the direct and indirect effects weather can have on woodcock. Field studies in this area have had limited success because of difficulties in finding dead birds and determining cause of death. In order to overcome these limitations, simulation modelling was used to study the relationship between energy requirements of woodcock and food availability. By modelling each of these components as a function of temperature and precipitation, it should be possible to identify periods of weather-related stress.

LIFE HISTORY BACKGROUND

Woodcock migrate to their breeding grounds very early in the spring, at times arriving before all the accumulated snow has melted. In Michigan, the first birds generally arrive by the second week in March. The earliest arrival record for the state is 24 February 1976 (Whitcomb 1976). Males usually arrive before females in order to establish singing grounds. Females begin nesting very soon after arrival.

Female woodcock are reproductively active their first year after hatching, and nearly all females attempt to nest each year (Sheldon 1971). Eggs are laid directly on the ground and the nest bowl is lined only with leaf litter. Although a normal clutch size is four eggs, renesting or late nesting birds may lay only three eggs (Mendall and Aldous 1943). The best estimates are that it takes 4-6 days to lay a full clutch (Sheldon 1971). Incubation takes 19-22 days (Liscinsky 1972), and the precocial chicks leave the nest within hours after they have hatched.

The peak hatch varies considerably with latitude (Sheldon 1971), but for northern lower Michigan it generally occurs during the first week in May. The total hatch period for that region extends from late April to early June. Chicks are most dependent on the hen for brooding up until the time they lose their natal down and begin flying (12-14 days).

Newly hatched chicks weigh 10-15 g (Sheldon 1971). Growth for both sexes is equivalent during the first two weeks, increasing approximately 4 g/day (Ammann 1980). Less data are available for the period after the chicks learn to fly. As adults, however, females average 185 g while males average only 150 g (Liscinsky 1972). Broods remain together for 6-8 weeks (Sheldon 1971) with the chicks being most dependent on the hen during the first 2-3 weeks.

Both adults and juveniles molt during the summer. While adults undergo a complete molt which begins in June and lasts about 120 days, juveniles have only a partial molt that generally starts in July and lasts only about 90 days (Owen and Krohn 1973).

Earthworms are the single most important food in the woodcock's diet during the summer and fall (Aldous 1939, Sperry 1940, Glasgow 1958, Sheldon 1971), and it is generally believed that they are equally important during the breeding season as well. Whole and fragmented earthworms have been found in stomach analyses of young chicks (Rabe, unpublished). Earthworms usually comprise 60-90% of the adult diet. Insects and other soil invertebrates, plus a small amount of plant material, make up the balance.

THE MODEL

The simulation model (Appendix A) was written in the FORTRAN IV computer language. The function of the main program is to initialize program variables, read in weather data, call the appropriate subroutines to calculate energy requirements and earthworm availability, and increment time in the model. A list of subroutines and their specific function in the model is given in Table 9. Time is incremented on a daily basis. The simulation year begins prior to spring migration (the exact date is optional) and continues up to the fall migration. As currently written, the earthworm and woodcock sub-models can be run independently because sufficient data did not exist to evaluate the effects of resource depletion from woodcock feeding.

Inputs to the model include daily average temperature and precipitation values (in inches of rainfall). Weather data used in this study (1965-80) was obtained from the National Weather Service at Houghton Lake, Michigan. The model was also run using average values for daily temperature and precipitation for the same period. The

Table 9. A description of subroutines used in the simulation model.

Name	Description
WSTAT	Monitors and updates the timing of breeding and post-breeding events (eg. nesting,incubation, brooding, molting)
WORMS	Calculates the biomass of earthworms available to woodcock based on their distribution in the soil.
METAB	Calculates the daily maintenance energy requirements for the adult hen woodcock.
ACTIV	Calculates the daily energy requirements of movement activities for the hen.
NEST	Calculates the daily energy requirements of reproduction for the hen.
MOLT	Calculates the daily energy requirements of molt for the adult woodcock.
CHICK	Calculates the daily energy requirements for growth, activity, and maintenance for a chick during the first 30 days after hatching.
F	Performs linear interpolation from a series of table values. It is used in computing many of the functional relationships in the model.
GRAPHS	Transforms the simulation output into a graphic format.

arrival date of woodcock on the breeding grounds is the only other data needed to execute the model.

Outputs from the model consist of daily estimates of earthworm availability and woodcock energy requirements. The output data can be listed in tabular or graphic form.

Hen Energetics

Daily energy requirements of the hen (HENEN) were divided into four major components: maintenance (METEN), activity (ACTEN), nesting (NESTEN), and molting (MOLTEN). These components were assumed to be independent and additive so that total energy requirements were obtained by summation

$$\text{HENEN} = \text{NESTEN} + \text{MOLTEN} + \text{ACTEN} + \text{METEN}$$

As modelled, maintenance costs include both the basal metabolic rate (BMR) and thermoregulation. Since there were no data in the literature on woodcock metabolism, an estimate of 21.3 kcal/day for the BMR was derived from the Aschoff and Pohl equation (1970) for non-passerines using an average female weight of 185 g. Thermoregulation (THERMO) was estimated by the relationship

$$\begin{array}{ll} \text{THERMO} = 0.3*(10.0-\text{ATEMP}) & \text{ATEMP} < 10^{\circ}\ \text{C} \\ \text{THERMO} = 0.0 & \text{ATEMP} \geq 10^{\circ}\ \text{C} \end{array}$$

where ATEMP is the average daily air temperature. Modelling thermoregulatory costs for high temperatures was not considered necessary because woodcock generally spend days in cooler forested areas. The general inverse relationship between temperature and metabolism is discussed by Kendeigh (1969), King and Farner (1961), King (1974), and Ricklefs

(1974). Thermoregulatory adjustments due to acclimation at lower temperatures have been shown to be small relative to total energy requirements in Anatidae (Owen and Reinecke 1979) and therefore were not included in this model.

The total energy cost of activity (ACTEN) was expressed as the sum of products for the amount of time spent in each activity (resting, walking, feeding, and flying) multiplied by the energy cost for that activity (expressed as a multiple of BMR).

$$\text{ACTEN} = \sum_{i=1}^{n} \text{activity}_i * \text{cost}_i$$

Activity data (Table 10) was obtained from Wenstrom (1973). Estimates of energy costs were derived from studies by Prange and Schmidt-Nielson (1970), King (1974), and Prince (1979).

Nesting energetics includes both the costs of developing the reproductive system and the production of eggs (Fig. 6). An average daily reproductive tissue cost estimate of 2.0 kcal was based on the assumption that the rate of recrudescence is spread equally over a ten day period, and that the total energy content of the tissue is 20 kcal. Total tissue cost was based on a mature organ weight of 8 g (Rabe, unpublished), an energy density of 1.9 kcal/g, and a production efficiency of 75% (Ricklefs 1974).

Cost estimates for the eggs are based on a four egg clutch size, laid at a rate of 0.8 eggs/day. The rate of egg development was assumed to follow a bell shaped curve (King 1973) and the total energy content of an egg (34 kcal)

Table 10. Percent of time woodcock hen and chicks spend resting, walking, feeding, and flying during various periods. The basal metabolic rate conversion factor for converting activity to caloric equivalent is included.

	Hen [a]				Chicks		
Activity	Nesting	Incubation	Brooding	Post-brooding	Pre-flight	Post-flight	BMR multiple
Resting	75	83	56	67	57	56	1.3
Walking	16	10	9	13	9	9	2.0
Feeding	18	5	34	16	34	34	2.0
Flying	2	2	1	3	0	1	15.0

[a] Data from Wenstrom (1973).

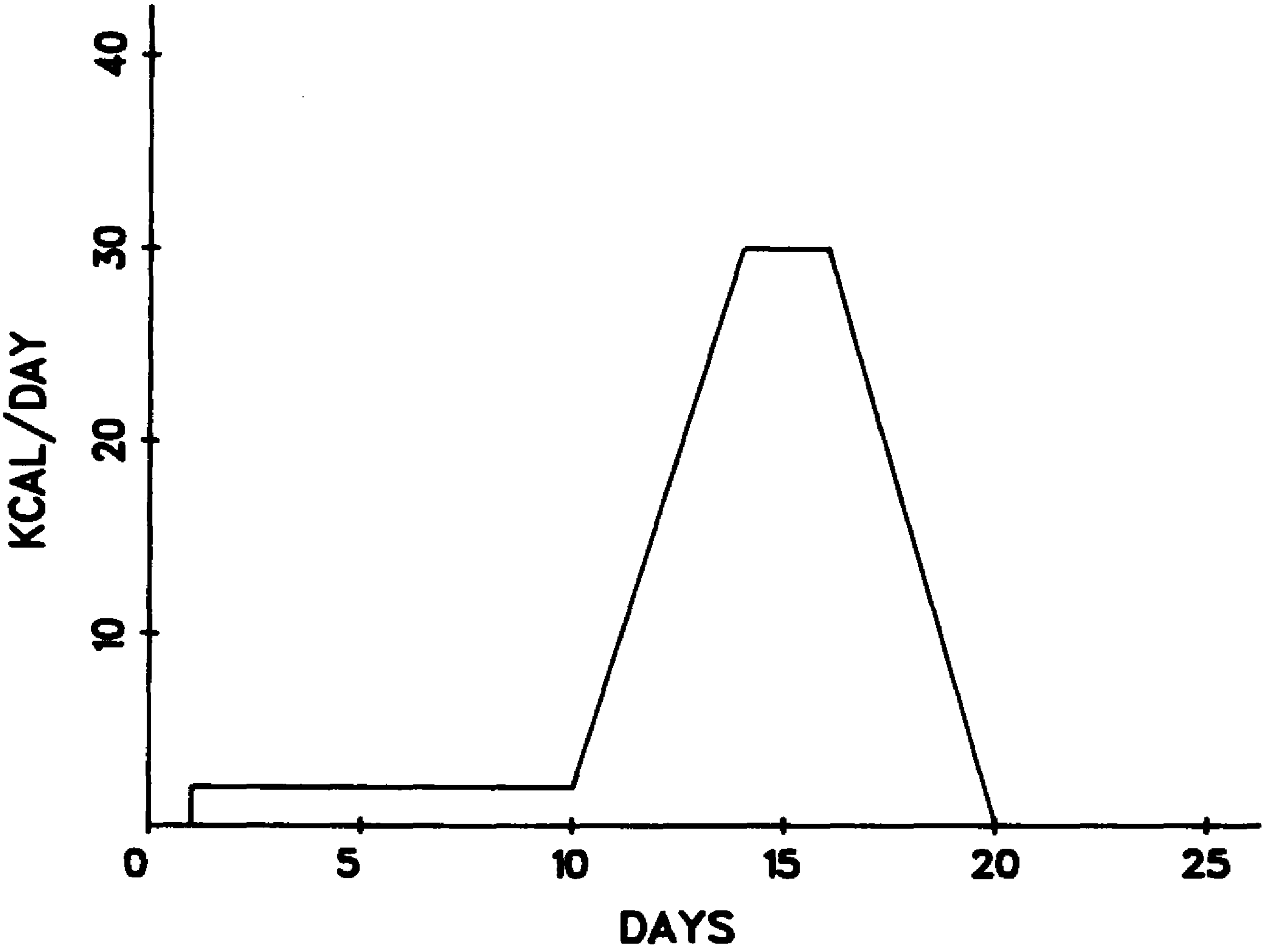

Figure 6. An estimate of daily nesting energy requirements including tissue recrudescence and egg production.

is based on an average weight of 16 g and an energy density of 1.7 kcal/g, again assuming a production efficiency of 75%.

Data from Owen and Krohn (1973) were used as the basis for modelling energy requirements of molt (Fig. 7). The estimate was made entirely on the energy content of the feathers plus an additional 25% for biosynthesis. Thermal conductive losses were considered minor because woodcock molt in the summer. Daily energy costs were then calculated according to the relationship

MOLT = (0.032*DAY - 0.000256*DAY**2)*MSF

where MSF is the molt scaling factor used to convert the molting costs into a kcal equivalent and DAY is the n-th day of the molt.

Chick Energetics

Major energy requirements for chicks during the brood-rearing period are maintenance (CMETEN), activity (CACTEN), and growth (CGROEN). Molt was not included because it does not begin until after broods disband. Total energy requirements for a chick (CHICEN) were computed by summation in the same manner as for the hen

CHICEN = CMETEN + CACTEN + CGROEN

Energetics data for woodcock chicks is very limited. In order to use information from other studies (Norton 1970, Ricklefs 1974) it was necessary to express growth rate as a percent of adult weight (PAW) using the formula

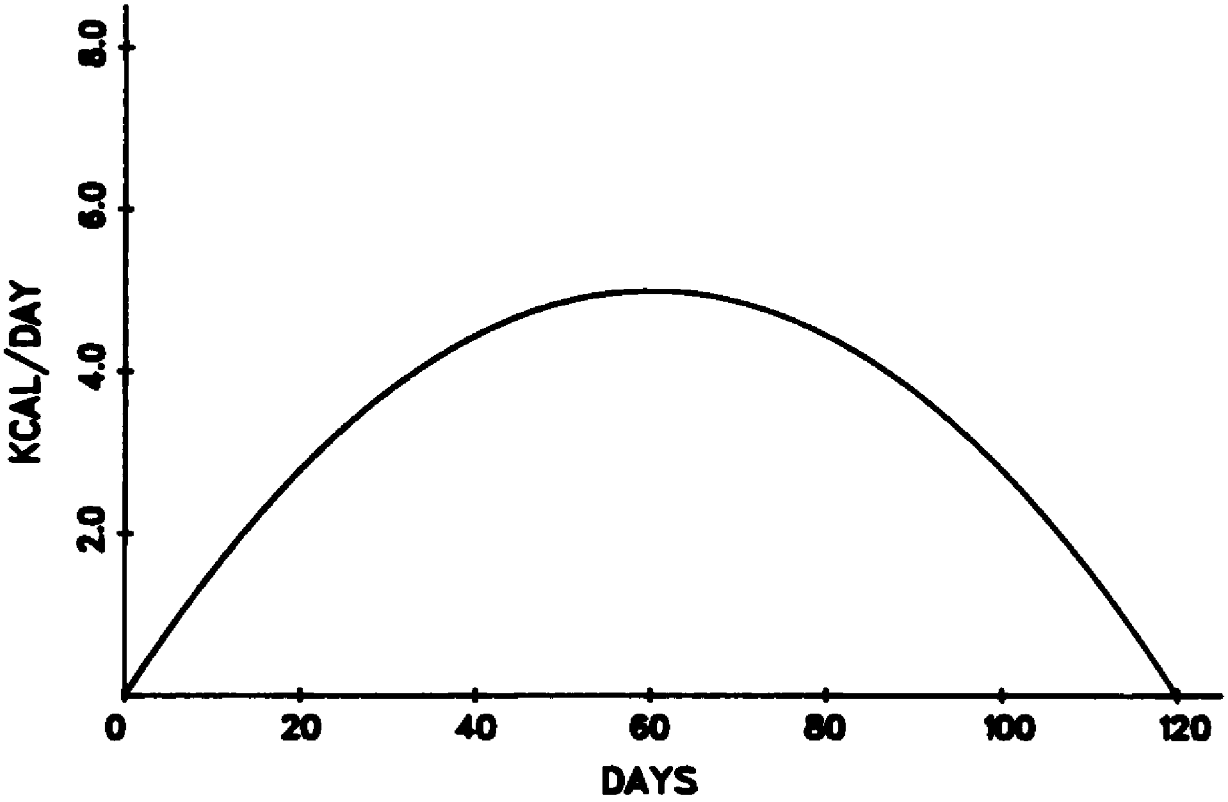

Figure 7. Energy requirements of molt for adult woodcock (data from Owen and Krohn 1973).

$$PAW = 0.085 + 0.027*AGE$$

where AGE is the number of days after hatching. To simplify the model an average adult weight of 175 g was used rather than including separate calculations for each sex. A single linear relationship to describe growth was used for the 30 day period being modelled.

Estimates of maintenance energy requirements for chicks was done by computing a BMR value (Aschoff and Pohl 1970) using current chick size and multiplying by a metabolic rate conversion factor (Fig. 8). The conversion factor was necessary to compensate for the relatively high metabolic rates of precocial chicks (Ricklefs 1974). Additional costs for thermoregulation were based on this estimate of BMR using the same temperature relationship that was used for the hen.

The energetic cost of growth was estimated from gross animal weight and its corresponding energy density (kcal/g) plus an additional 25% for biosynthesis. Energy density (EDEN) of chicks has been shown to change with maturity (Ricklefs 1974). The best estimate for changes in woodcock chicks was derived from data on dunlin (*Calidris alpina*) chicks (Norton 1970), expressed in the equation

$$EDEN = 1.5 + 0.3*PAW$$

Total energy content of the chick (ETISS) could then be computed by

$$ETISS = PAW*EDEN*175.0$$

and the daily growth increment (CGROEN) by

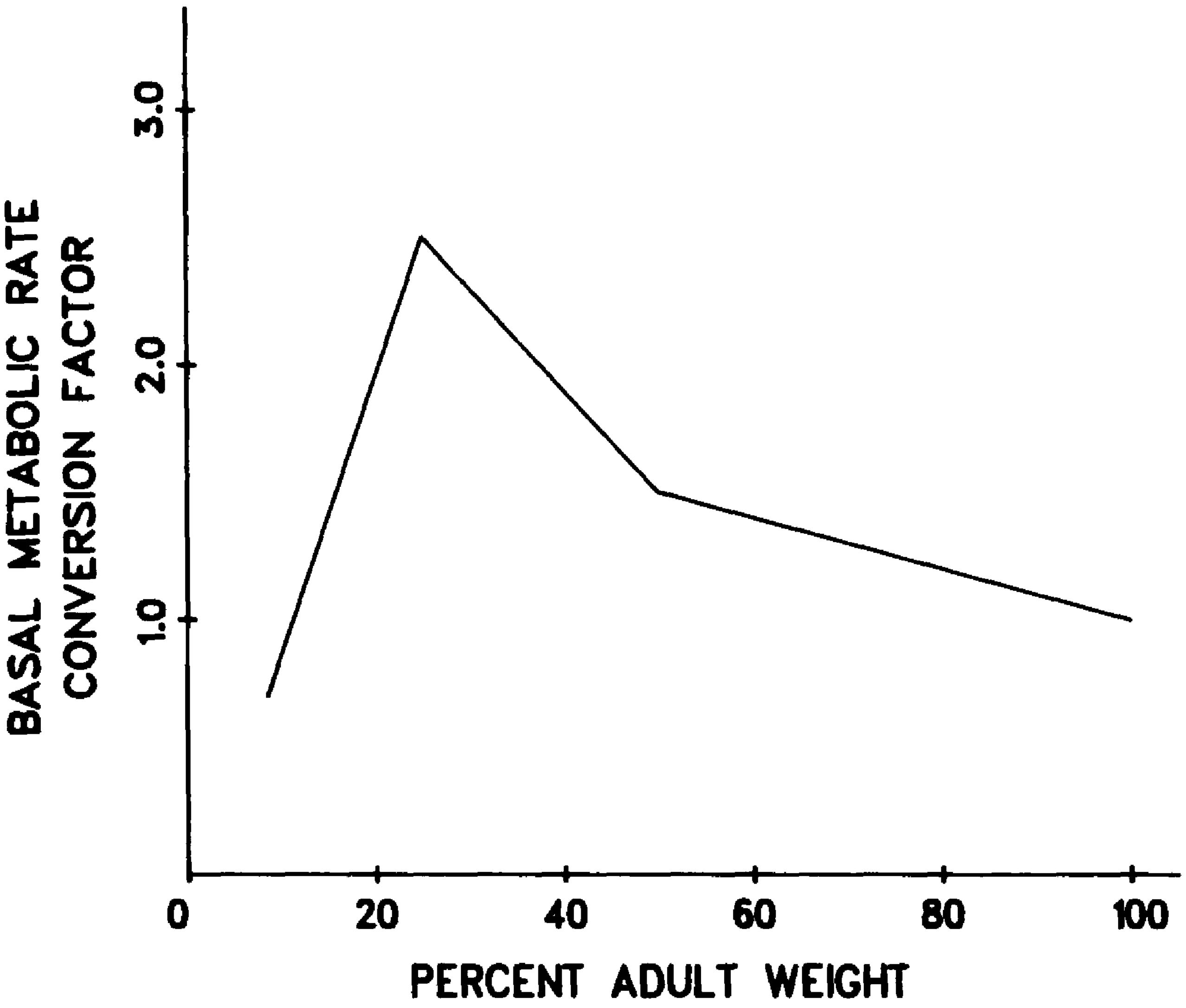

Figure 8. The basal metabolic rate conversion factor for chicks.

CGROEN = 1.25*(ETISS-ELAST)

where ELAST is the total energy content of the bird on the previous day.

Energy requirements for chick activity (kcal/day) were computed in the same manner as for the adult hen. Likewise, time allocations for the chicks were assumed to be the same as for the hen during the brood-rearing period. The only exception was that during the first 14 days flight activity was set to zero.

Earthworms

The biomass of earthworms that are available to woodcock (AVWORM) were modelled as a function of their vertical distribution in the soil. Soil temperature and moisture conditions play an important role in regulating the vertical distribution of earthworms (Guild 1948, Reynolds and Jordan 1975, Edwards and Lofty 1977). Because the model uses air temperature and precipitation data as inputs, the first step in modelling earthworm availability is to relate atmospheric weather to climatic conditions in the soil.

Soil moisture and temperature dynamics are affected by a number of factors including soil type, soil compaction, vegetative cover, slope, and air temperature differential (Hillel 1971, Baver et al. 1972). In general, soil temperature (STEMP) exhibits a delayed response to changes in air temperature (ATEMP) and was expressed in the model as

$$STEMP = 0.6*ATEMP + 0.4*STEMP$$

Simulating the effects of soil moisture (SMOIST) changes was somewhat more involved. Both moisture additions in the form of precipitation (PRECIP) and moisture losses from percolation, evaporation, and transpiration need to be included. Moisture additions were modelled by the linear relationship

$$SMOIST = 9.0*PRECIP$$

Two components were necessary to model the behavior of moisture loss from the soil. One is the effect of soil moisture content on the rate of percolation (Foth and Turk 1972). In general, as soil moisture content decreases, the bond between soil and water particles becomes stronger making further moisture loss more difficult. This relationship (MMLSF) was modelled as a linear scaling factor (Fig. 9).

The second component deals with the effect of evaporation and transpiration on the rate of water loss. Since both evaporation and transpiration rates are directly related to temperature, this relationship (TMSLF) was modelled as a function of soil temperature (Fig. 9). The combined interaction of the two components is represented in the equation

$$SMOIST(t+1) = SMOIST(t)*MMLSF*TMLSF$$

The distribution of earthworms, in turn, is based on computed soil moisture and temperature conditions. Their combined effects were modelled in the form

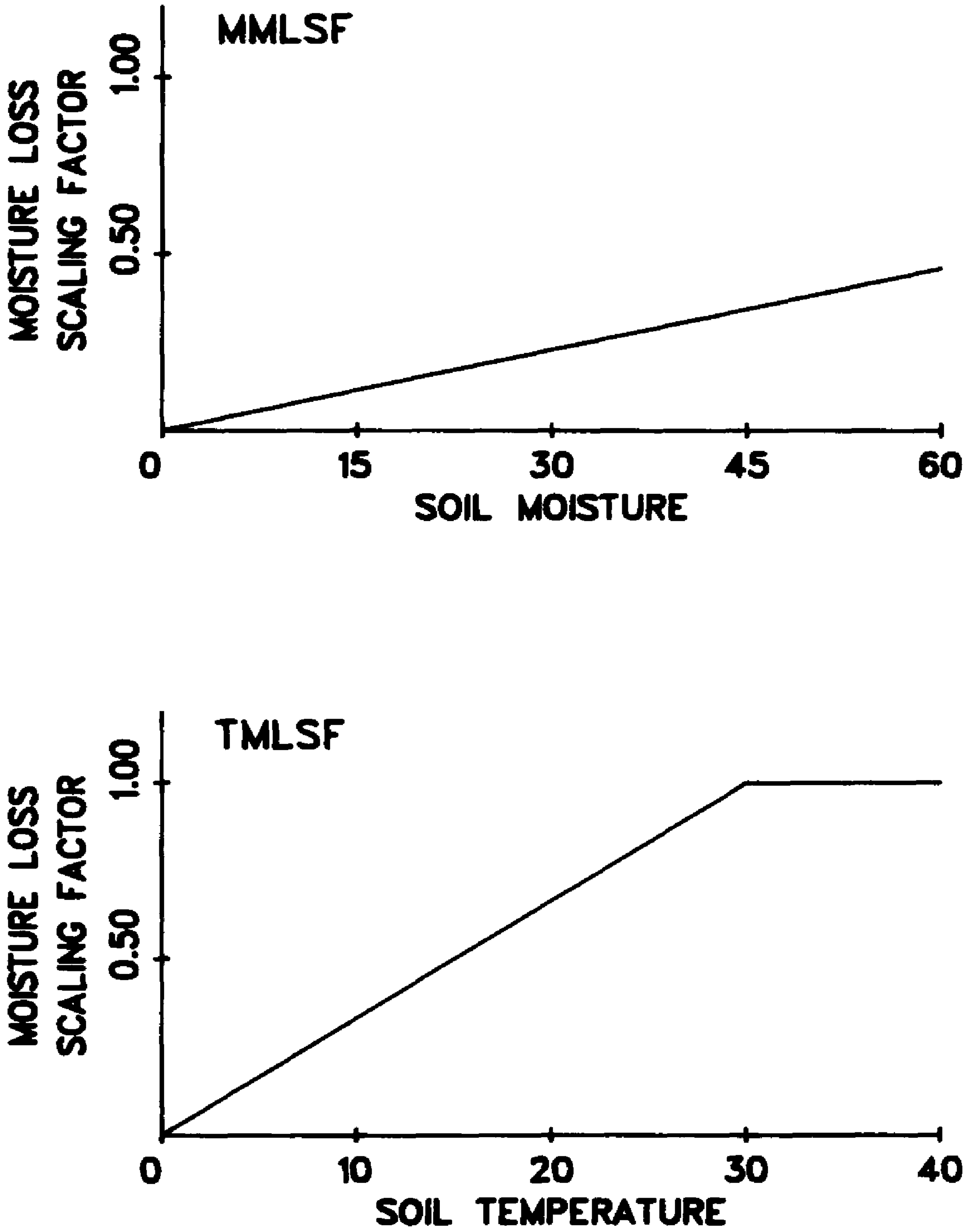

Figure 9. Scaling factors for soil moisture loss as affected by soil moisture and temperature conditions.

$$AVWORM = 27.0*MEASF*TEASF$$

where MEASF and TEASF are scaling factors which represent the functional relationship of earthworm tolerance to moisture and temperature, respectively (Fig. 10). Temperature effects are based on studies of lethal temperatures (Grant 1955, Reinecke 1974) and growth rate (Guild 1948, Satchell 1955). Information on earthworm response to various moisture conditions was assimilated from studies by Olson (1928), El-Duweini and Ghabbour (1965), and Gerard (1967). The value 27.0 in the equation represents the maximum observed biomass ($g/.25m^2$) of earthworms from field sampling (discussed below).

FIELD OBSERVATIONS OF EARTHWORM ABUNDANCE

Soil moisture and earthworm biomass data were collected weekly at three locations in Missaukee County, Michigan between 10 April and 17 August 1976. The collection sites were about 25 km from the National Weather Bureau at Houghton Lake. These data were used to test the fit of the earthworm simulation sub-model.

All three sites were in aspen dominated forest communities, and all were considered good woodcock habitat. Soil types ranged from loam to sandy loam. Earthworm abundance was sampled in two 0.25 m^2 plots at each site using a formalin extraction technique (Reynolds et al. 1977). Soil moisture determinations were made using a gravimetric method (percent moisture by weight). Both

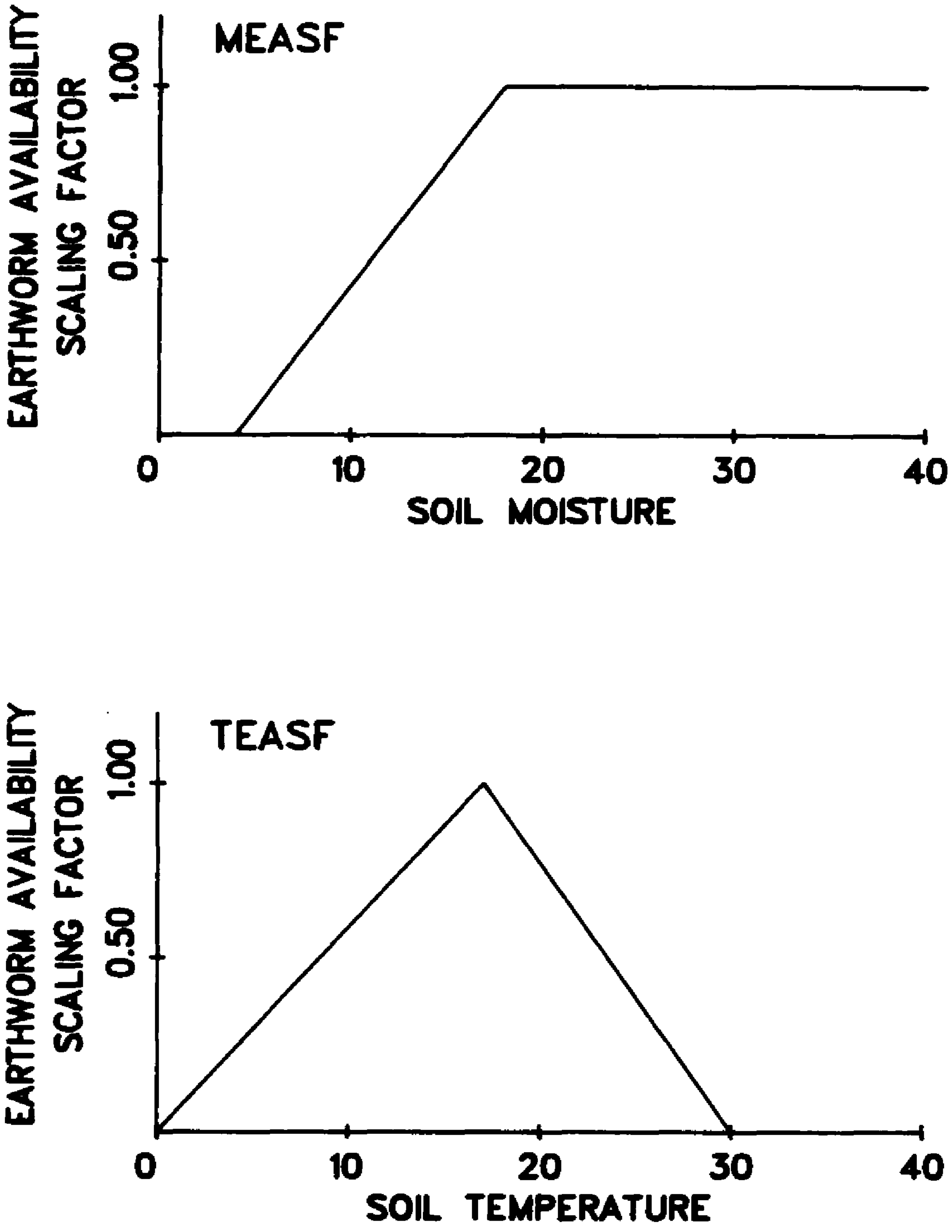

Figure 10. Scaling factors used to model the relationship between soil moisture and temperature, and the availability of earthworms to woodcock.

moisture and earthworm samples were averaged among sites for comparison with the simulation model.

RESULTS

The Earthworm Model

Figure 11 shows the relationship between simulated and actual soil moisture conditions. These comparisons indicate that the model did a reasonably good job of tracking observed field conditions. The worst discrepancies were a 5% underestimate of soil moisture in late May, and a 6% overestimate in August. The model responded well to rapid increases in moisture.

Earthworm abundance fluctuated considerably over relatively short periods (Fig. 12) and followed much the same pattern of changes as soil moisture. Here again, the correspondence between observed and simulated values is fairly good. During the spring period (April to June) the model tended to underestimate actual earthworm abundance, however, during the summer months it accurately tracked major changes in availability.

Woodcock Energetics

As a preliminary means of examining the impact of weather on the bioenergetic requirements of woodcock (both hen and chicks), the model was run using long-term averages of temperature and precipitation. In this way, it was possible to eliminate yearly variability and examine the

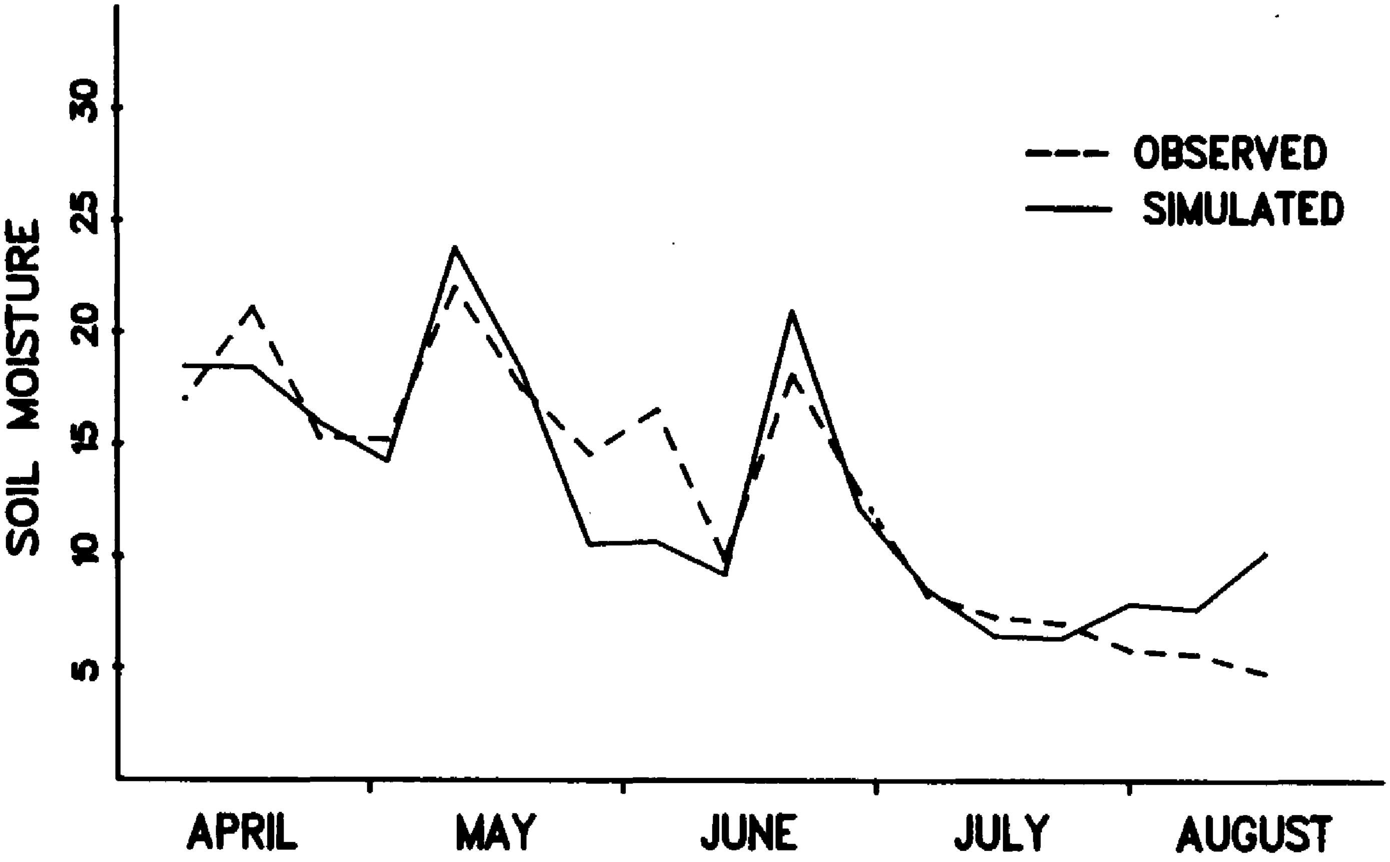

Figure 11. Comparison of simulated moisture changes with field observations.

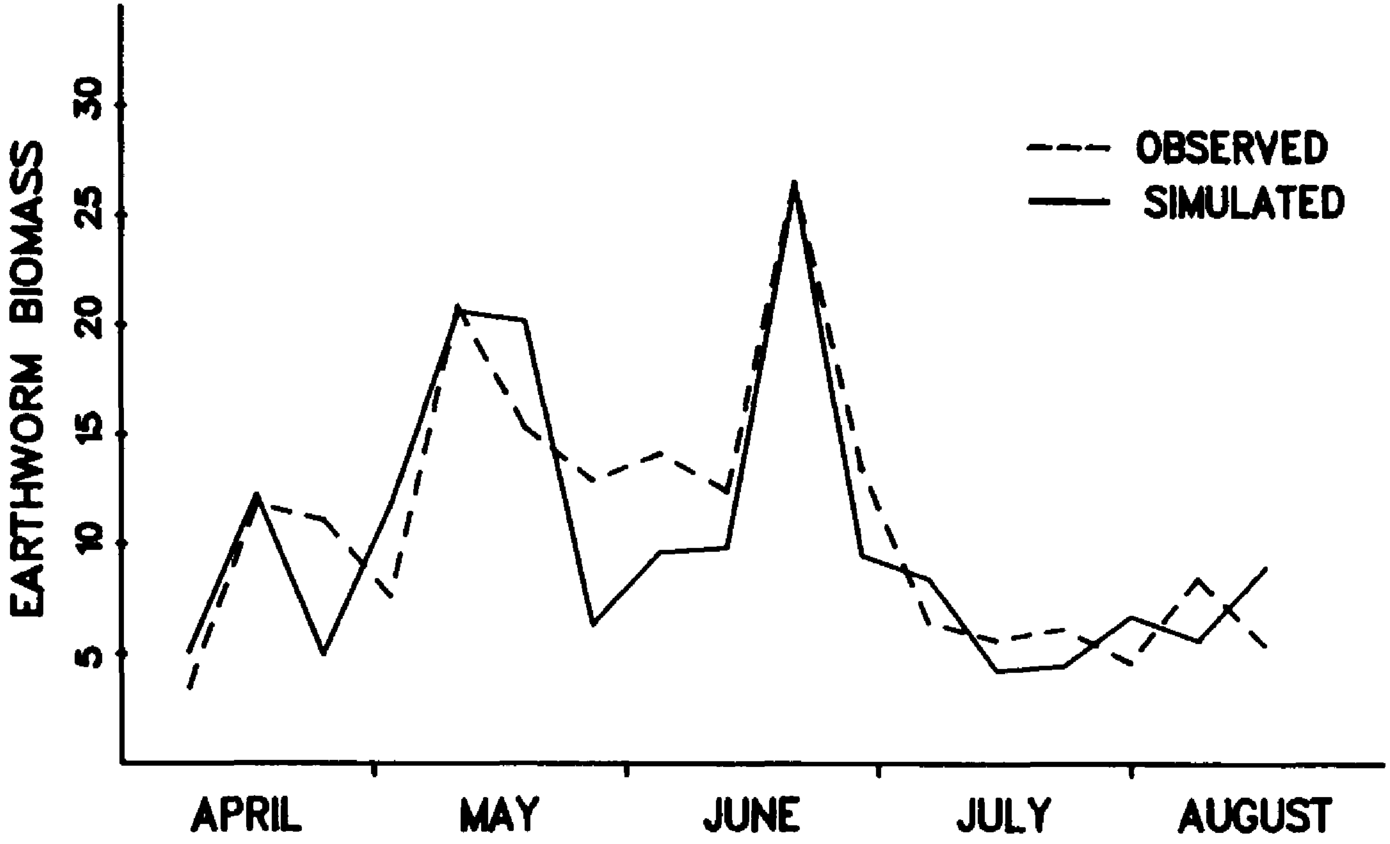

Figure 12. Comparison of observed and simulated earthworm biomass near the soil surface.

energy requirements under what might be considered normal weather conditions.

A partitioning of the energy requirements for the hen are illustrated in Figure 13. These calculations were based on an arrival date of 20 March, which is typical for northern Michigan. Assuming that the estimates for each component are reasonably accurate, results indicate that total daily energy requirements are relatively constant at about 60 kcal/day except during the nesting period when energy requirements increase to a peak of approximately 90 kcal/day. Maintenance accounts for about 30% of the annual energy requirements, while activity uses nearly 60% of the total. In contrast, nesting and molt account for a relatively small portion of total energy needs. At its peak, molt adds only 8% to total daily requirements. When the hen first arrives on the breeding ground, thermoregulation causes a 12% increase in energy requirements. This declines steadily until early May, when it is no longer a factor.

As with the adult, the energy requirements for activity of chicks are nearly twice that of maintenance (Fig 14). Growth, on the average, accounts for only 20% of daily energy requirements. It is interesting to note that daily energy requirements for the chicks are nearly equal to that of the hen after only 3-4 days. The energy demand on chicks increases very rapidly the first few days after hatch and then begins to stabilize for the remainder of the growth

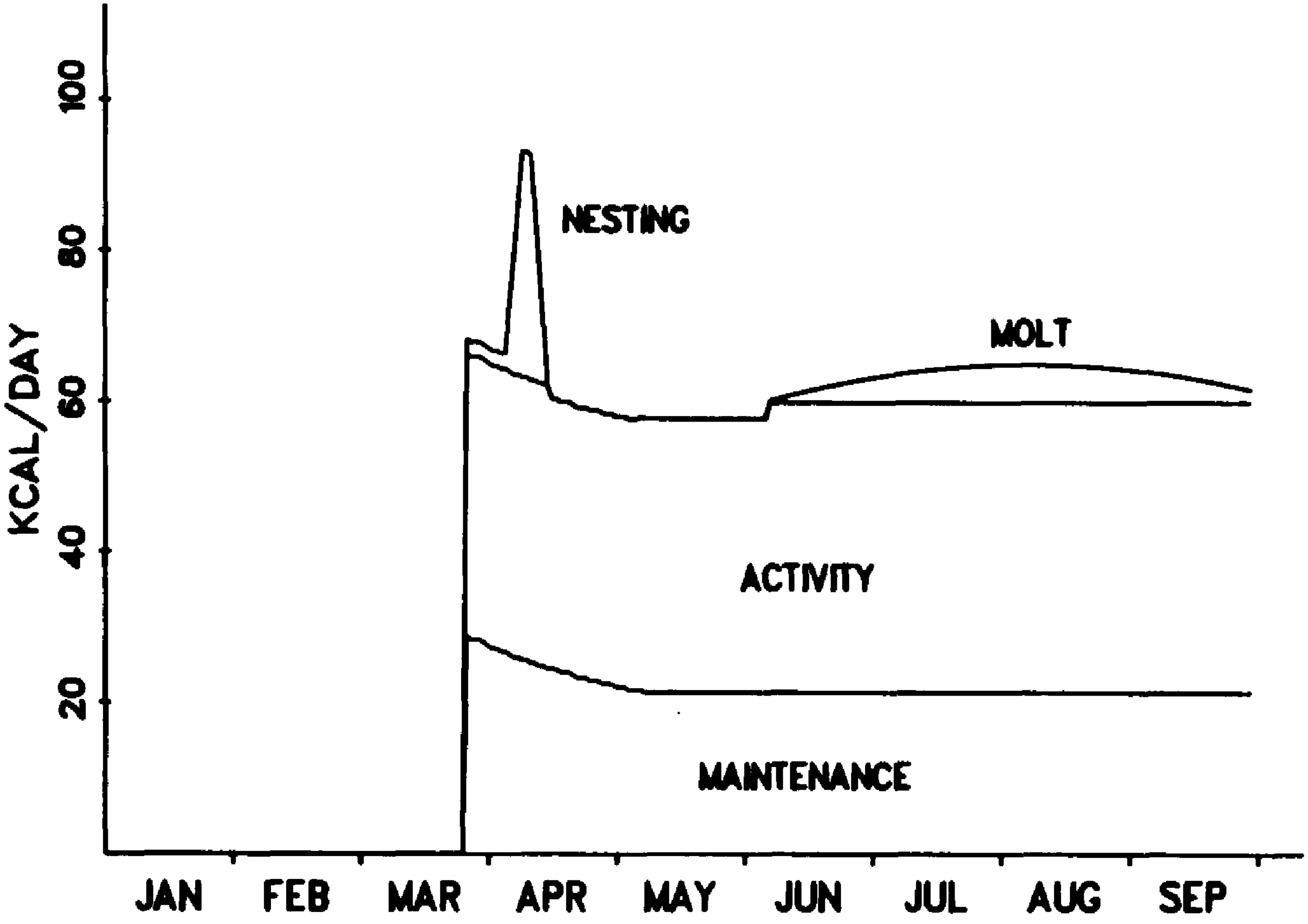

Figure 13. Simulated energy partitioning for the hen woodcock.

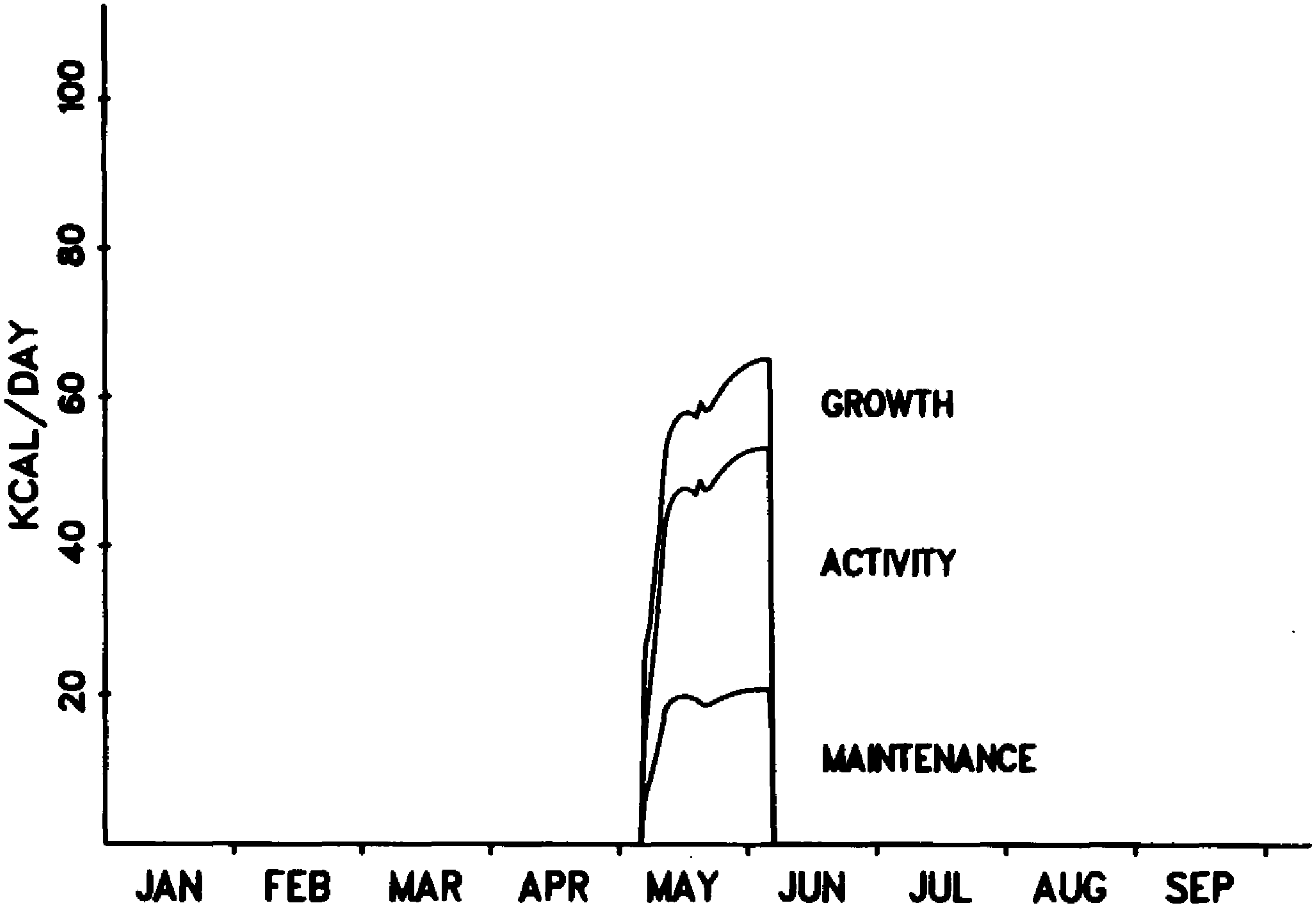

Figure 14. Simulated energy partitioning for the chicks.

period. Based on an average hatch date of 5 May, the model indicates that chicks do not incur extra costs for thermoregulation under average weather conditions.

Figure 15 shows the relationship between soil moisture, soil temperature, and earthworm availability under simulated normal weather conditions. Based on daily precipitation of 0.25 cm the model indicates that soil moisture content increases to its highest level in early April, reaching a value of nearly 60%. At that time, increasing temperatures cause the rate of water loss to exceed the rate of gain which accounts for the decline to 12% in August. Soil moisture begins to increase again in the fall as temperatures decline. Soil temperature response to average air temperature conditions follows a sine curve pattern with a low of -8° C in February and a high of 19° C in July. Low temperatures tend to limit earthworm activity near the soil surface before April. Earthworm numbers increase rapidly to a peak in June, decrease during the summer months, and begin to recover again in the fall. Temperature and moisture conditions are most ideal in late May and early June. During the summer, soils tend to be too hot and dry for earthworms to remain active near the surface.

Weather Related Energy Stress

In order to identify periods of potential energy stress, the combined energy requirements of the hen and brood (4 chicks) were plotted together with earthworm availability (Fig. 16). Because hen and chicks forage in

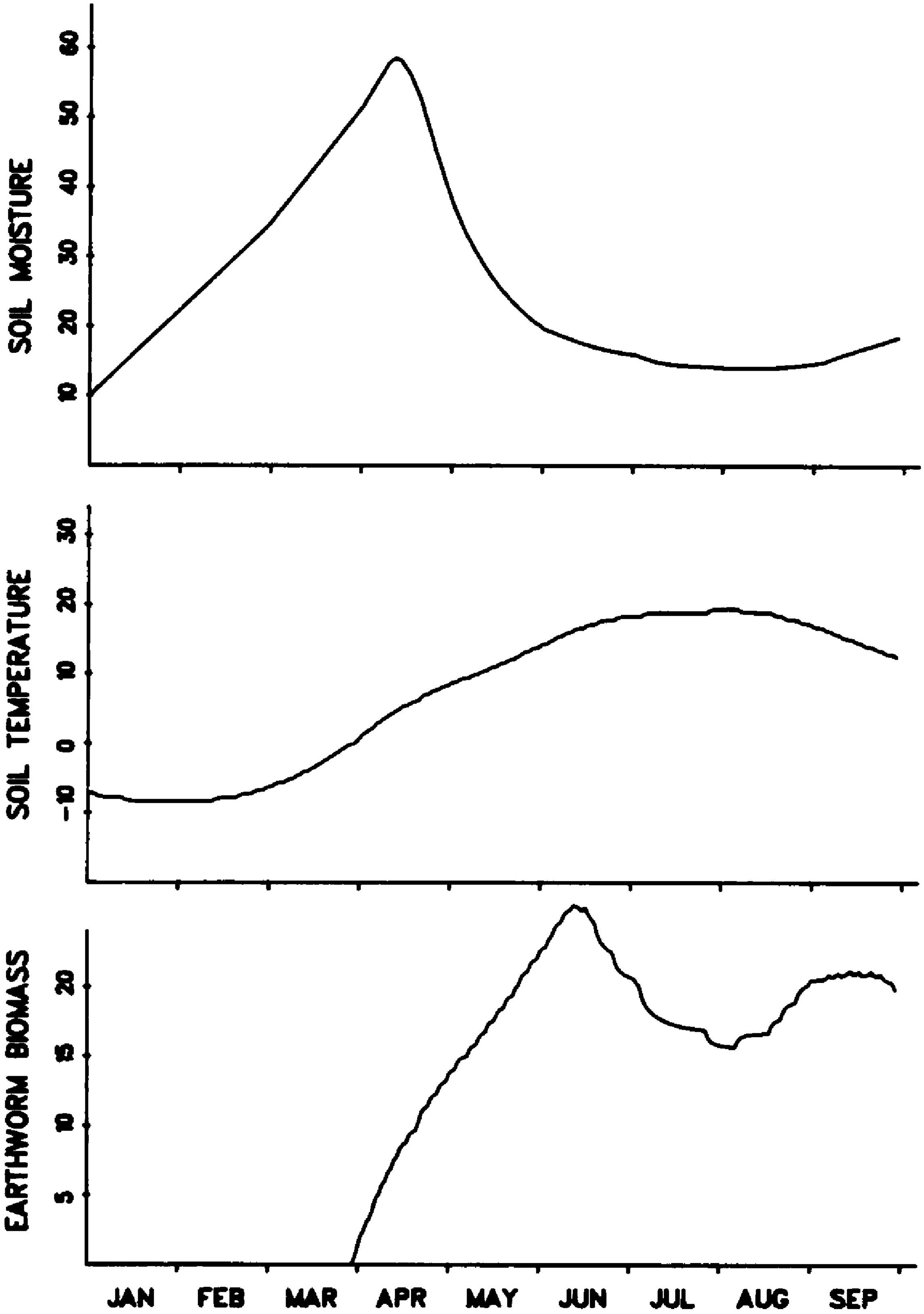

Figure 15. Simulated earthworm availability under average temperature and rainfall conditions.

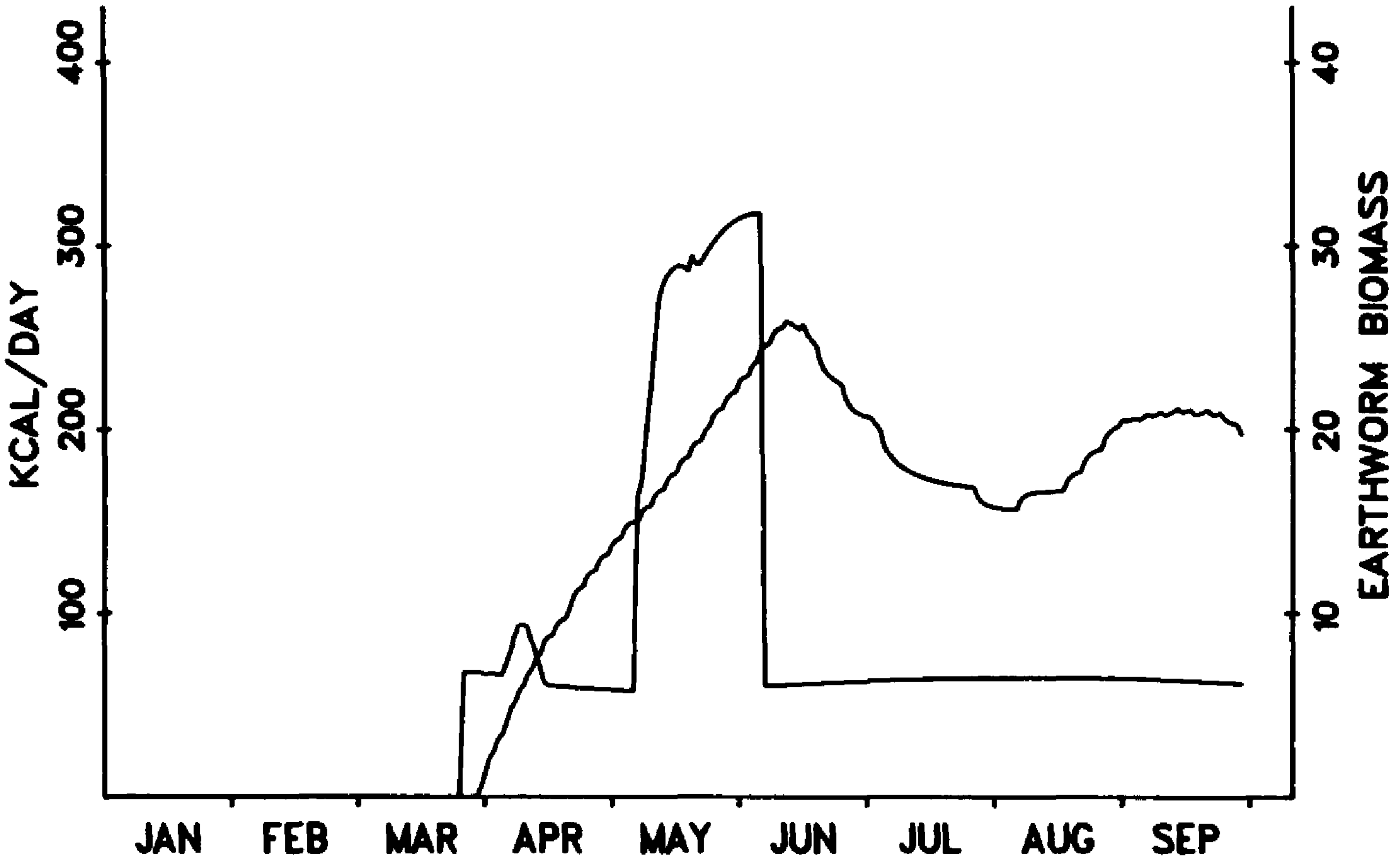

Figure 16. Relationship between simulated earthworm availability and energy requirements for woodcock (hen and chicks).

close proximity, particularly during the first 2-3 weeks, it seems reasonable to consider their exploitation of food resources on a combined basis. This comparison suggests that the greatest potential energy stress is likely to occur during the brood-rearing period. It is also possible that nesting can be stressful because of reduced food availability. Even though food abundance declines during the summer, earthworms appear to be sufficiently numerous relative to the energy needs of woodcock.

If earthworm availability during the brood period is a limiting factor, it is likely that it would cause higher juvenile mortality during years when earthworms are relatively scarce. To test this hypothesis, average earthworm abundance during the brood period (20 April to 1 June) was simulated for 1965 through 1980 (Appendix B). These data were then compared to reproductive success data for the state of Michigan. Reproductive success data (expressed as the number of chicks per adult hen in the fall harvest) were obtained from the U.S. Fish and Wildlife Service through their annual wing survey program. Each years estimate of reproductive success is based on at least 1100 wings, and generally more than 2000 wings.

Results of a regression analysis on these data (Fig. 17) show a significant linear relationship ($P<0.05$, $r=0.53$) between food availability and chick survival. Data best fit the line in years of low earthworm availability and tend to be more variable in years of abundant food.

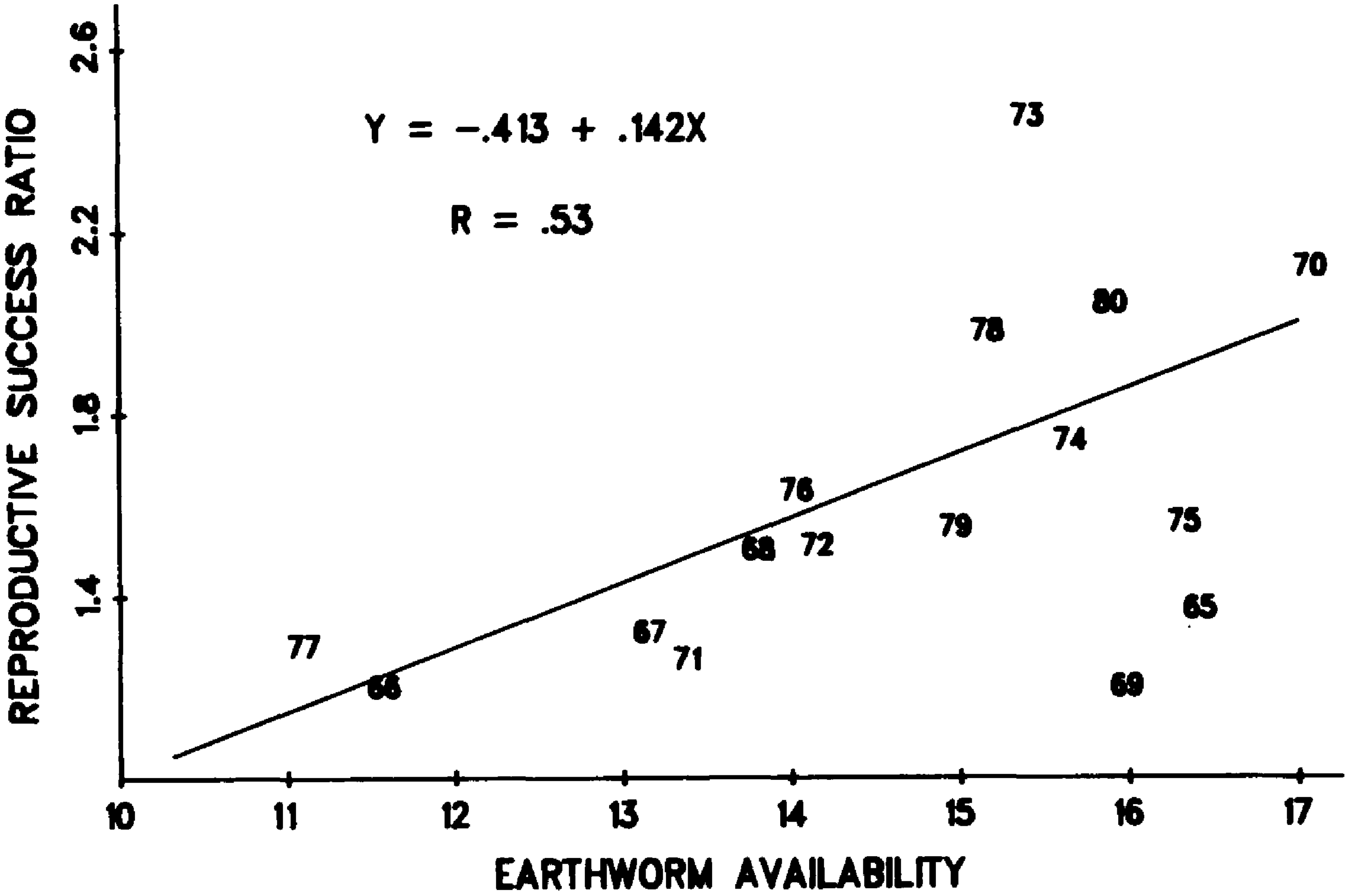

Figure 17. Regression analysis between average simulated earthworm availability (g/0.25 m^2) during the brood period (20 April to 1 June) and reproductive success ratios (numbers of chicks per adult hen) for the state of Michigan.

DISCUSSION

Since weather conditions are unpredictable, it is reasonable to expect that woodcock base their breeding strategies on the expectation of normal weather conditions. In that light, the results generated using average weather data suggest that bioenergetic relationships may explain much of observed woodcock breeding behavior.

The model indicates that woodcock arrival on the breeding grounds coincides closely with increased earthworm activity near the soil surface. If woodcock were to arrive much earlier, not only would food be less abundant, but thermoregulatory costs would likely be much greater as well. Pre-breeding weights (Owen and Krohn 1973) suggest that females arrive on the breeding grounds with a certain amount of energy reserve which can help them to endure short periods of inclement weather, however, nesting failure and adult mortality have been attributed to extended periods of cold weather (Mendall and Aldous 1943).

If, on the other hand, woodcock were to delay their migration to avoid potentially hazardous weather, the model suggests that they would be more likely to jeopardize their breeding success. When nesting takes place by the end of March, chicks hatch in early May when earthworm abundance would be expected to be near its maximum. If nesting were appreciably delayed, there is a greater likelihood that chicks would be confronted with declining food supplies at the time their energy requirements are increasing. The expectation of decreased earthworm numbers in summer may also account for the greater frequency of three egg clutches by late nesting birds. In this way, the total energy demand of the family unit would be proportionally less.

Although Rabe (1979) reported an instance of a possible second nesting attempt, it is likely that limited earthworm supplies in summer generally prevent woodcock from raising more than one brood in a year. Theoretically, there is enough time for a second brood to reach adult size before fall migration but chances of success are likely to be considerably reduced because of an unreliable food supply.

The model indicates that earthworm availability increases from summer to fall. Food habit studies for these periods suggest that woodcock supplement with insects and other foods during summer months when earthworms are less available. Sperry (1940) reported that the percentage of insects consumed was highest (38%) in August. Sheldon (1971) found that beetles were the most abundant food in birds collected during the summer in Massachusetts. In contrast, earthworms comprised 86% of the diet in Nova Scotia (Pettingill 1939) and Maine (Aldous 1939) during October. Many of the insects eaten by woodcock during the summer are not readily available in the spring which leads me to suspect that there is an even greater dependency on earthworms during the breeding season.

The relationship between earthworm availability and reproductive success (Fig. 17) implies that food availability during late April and May has a direct impact on chick survival. This assumes, of course, that an equal proportion of females nest each year. Even though there is a significant fit to a linear model, the pattern of data points suggests that food tends to limit the maximum potential for reproductive success, but that other mortality factors (eg. predation or disease) may prevent woodcock from reaching that level in years when food is abundant. This would account for the relatively low production ratios in 1965, 1969, and 1975, however, there is no readily apparent explanation for the unusually high success ratio in 1973.

MANAGEMENT CONSIDERATIONS

The popularity of woodcock as a game species has increased significantly in recent years. In 1975 it was estimated that 1.5 million birds were harvested nationwide, providing between 2.5 and 3.0 million man-days of hunting recreation (Artmann 1977). This represents a 79% increase in harvest from a decade earlier, and all indications are that this trend is likely to continue.

With greater demand, there is need for more accurate population data to insure that the species is not over harvested. Because of the seclusive nature of the bird, however, good populations estimates are difficult to obtain. Currently, the only population estimate made annually is a spring census of singing males. This alone is inadequate for estimating fall populations because it does not account for mortality from spring to fall.

While the use of field surveys to directly measure fall population levels would be time consuming and expensive, simulation models have the potential to provide a relatively inexpensive means of improving fall estimates in conjunction with spring survey estimates. If this, or a similar model, can be applied on a regional level, it would be possible to predict juvenile mortality during the spring and summer by monitoring weather conditions. It is possible that additional models can be developed to account for other mortality factors (ie. predation, habitat changes, etc.).

RESEARCH NEEDS

This modelling study has provided insight into the food-energy relationships of woodcock that would be difficult to study in other ways. Both the process of developing the model and the results it generated, suggested many areas that would benefit from addition research. Among these are:

1. Verifying the woodcock energy model. Most of the energetic relations used (for both hen and chick) were derived from studies of other species. This makes it difficult to evaluate the accuracy of the model and points to the need for specific research on woodcock energetics.

Every effort was made to include all the major energy components, however, lack of information prevented the inclusion of certain aspects, such as the possible energetic costs of incubation. Studies on these topics would provide data necessary to accurately determine their relevance to the model.

2. Improving the earthworm model. Even though the earthworm availability model did a good job of tracking field data, it used greatly oversimplified soil-weather and soil-earthworm relationships, and does not include estimates of earthworm reproduction or mortality. I expect that such additions could improve the predictive qualities of the model. It would also be useful to expand the model to describe earthworm dynamics in soils other than loam.

3. Testing the model in other geographic areas. If the model is to have large-scale management value it needs to be tested in other parts of the woodcock's breeding range. With modification, the model might also be useful for studying woodcock wintering ecology.

4. Studying food habits of woodcock during the breeding season. Most food habits studies have been done during summer, fall, and winter, with little focus on the spring breeding season. The model is based on the assumption that earthworms are the primary food source during breeding and post-breeding seasons. Research in this area is needed to substantiate this assumption.

5. Expanding the model to include other forms of weather related mortality. This study concentrated on weather as an indirect form of woodcock mortality, yet there are several accounts in the literature which suggest that

weather also affects survival directly. The model would be useful if it could be expanded to include these effects.

LITERATURE CITED

Aldous, C.M. 1939. Studies on woodcock management in Maine, 1938. Trans. N. Am. Wildl. Nat. Resour. Conf. 4: 437-441.

Ammann, G.A. 1980. Aging American woodcock chicks by bill length. Seventh Woodcock Symp. (in press).

Artmann, J.W. 1977. Woodcock status report, 1976. U.S. Fish and Wildl. Serv., Spec. Sci. Rep. Wildl. 209.

Aschoff, J. and H. Pohl. 1970. Rythmic variations in energy metabolism. Fed. Proc. 29: 1541-1552.

Baker, J.R. 1938. The evolution of breeding seasons. Pp. 161-177 in Evolution. Essays on aspects of evolutionary biology (B.R. De Beir, Ed.). Oxford.

Baver, L.D., W.H. Gardner, and W.R. Gardner. 1972. Soil Physics. John Wiley and Sons, New York.

Bennett, C.L., D.L. Rabe, and H.H. Prince. 1981. Response of several game species, with emphasis on woodcock, to extensive habitat manipulations. Seventh Woodcock Symp. (in press).

Bengston, S.A., S. Rundgren, A. Nilson, and S. Nordstrom. 1978. Selective predation to lumbricids by golden plovers. Oikos 31: 164-168.

Blankenship, L.H. 1957. Investigations of the American woodcock in Michigan. Ph.D. Thesis. Michigan State Univ., E. Lansing.

Bourgeois, A. 1977. Quantitative analysis of American woodcock nest and brood habitat. Proc. Woodcock Symp. 6: 109-118.

Coon, R.A. 1977. Nesting habitat, fall migration and harvest characteristics of the American woodcock in Pennsylvania. Ph.D. Thesis. Pennsylvania State Univ., State College.

Duke, G.E. 1966. Reliability of censuses of singing male woodcock. J. Wildl. Manage. 30: 697-707.

Dyer, J.M. 1976. An evaluation of diurnal habitat requirements for the American woodcock (Philohela minor, Gmelin) in southern Louisiana. Ph.D. Thesis. Louisiana State Univ., Baton Rouge.

Dyer, J.M. and R.B. Hamilton. 1977. Analyses of several site components of diurnal woodcock habitat in southern Louisiana. Proc. Woodcock Symp. 6: 51-62.

Edwards, C.A. and J.R. Lofty. 1977. Biology of earthworms. John Wiley and Sons, New York.

El-Duweini, A.K. and S.I. Ghabbour. 1965. Temperature relations of three Egyptian oligochaete species. Oikos 16: 9-15.

Evans, A.C. and W.J.Mc.L. Guild. 1948. Studies on the relationships between earthworms and soil fertility. V. Field observations. Ann. Appl. Biol. 34: 307-330.

Foth, H.D. and L.M. Turk. 1972. The fundamentals of soil science. John Wiley and Sons, New York.

Gerard, B.M. 1967. Factors affecting earthworms in pastures. J. Anim. Ecol. 36: 235-252.

Gill, J.L. 1978. Design and analysis of experiments in the animal and medical sciences, Volume 1. The Iowa State University Press, Ames, Iowa.

Glasgow, L.L. 1958. Contributions to the knowledge of the ecology of the American woodcock, Philohela minor (Gmelin), on the wintering range of Louisiana. Ph.D. Thesis. Texas A.& M. College, College Station.

Godfrey, G.A. 1974. Behavior and ecology of American woodcock on the breeding range in Minnesota. Ph.D. Thesis. Univ. Minnesota, Minneapolis.

Godfrey, G.A. 1975. A needed revision in the concept of surveying American woodcock populations. Biologist 57: 89-103.

Goss-Custard, J.D. 1977. Optimal foraging and size selection of worms by redshank (Tringa totanus). Anim. Behav. 25: 10-29.

Goudy, W.H. 1960. Factors affecting woodcock spring population indexes in southern Michigan. M.S. Thesis. Michigan State Univ., E. Lansing.

Grant, W.C. 1955. Studies on moisture relationships in earthworms. Ecology 36: 400-407.

Guild, W.F.Mc.L. 1948. The effect of soil type on the structure of earthworm populations. Ann. Appl. Biol. 35: 181-192.

Hillel, D. 1971. Soil and water, physical principles and processes. Academic Press, New York.

Kendeigh. S.C. 1969. Energy responses of birds to their thermal environments. Wilson Bull. 81: 441-449.

King, J.R. 1973. Energetics of reproduction in birds. Pp. 78-120. in Breeding Biology of birds (D.S. Farner, Ed.). National Acad. Sci., Washington, D.C.

King, J.R. 1974. Seasonal allocations of time and energy resources in birds. Pp. 4-70. in Avian energetics (R.A. Paynter, Jr., Ed.). Nuttall Ornithol. Club Publ. 15.

King, J.R. and D.S. Farner. 1961. Energy metabolism, thermoregulation and body temperatures. Pp. 215-288. in Biology and comparative physiology of birds. Vol. II. (A.J. Marshell, Ed.). Academic Press, New York.

Krebs, J.R., J.C. Ryan, and E.L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22: 953-964.

Krebs, J.R., J.T. Ericksen, M.I. Webber, and E.L. Charnov. 1977. Optimal prey selection in the great tit (Parus major). Anim. Behav. 25: 30-38.

Kroll, J.C. and R.M. Whiting. 1977. Discriminant function analysis of woodcock winter habitat in east Texas. Proc. Woodcock Symp. 6: 62-72.

Liscinsky, S.A. 1972. The Pennsylvania woodcock management study. Pennsylvania Game Comm. Res. Bull. No. 171.

Maxfield, H.K. 1961. A vegetational analysis of fifty woodcock singing grounds in central Massachusetts. M.S. Thesis. University of Mass., Amherst.

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

Miller, D.R. 1957. Soil types and earthworm abundance in woodcock habitat in central Pennsylvania. M.S. Thesis. Pennsylvania State Univ., University Park.

Murchie, W.R. 1958. Biology of the Oligochaete Eisenis rosea (Savigny) in an upland forest soil in southern Michigan. Am. Midl. Nat. 66(1): 113-131.

Nordstrom, S. and S. Rundgren. 1974. Environmental factors and lumbricid associations in southern Sweden. Pedobiologia. 14: 1-27.

Norton, D.W. 1970. Thermal regime of nests and bioenergetics of chick growth in the dunlin (Calidris alpina) at Barrow, Alaska. M.S. Thesis. Univ. of Alaska, Anchorage.

Olson, H.W. 1928. The earthworms of Ohio. Ohio Biol. Surv. Bull. 17: 47-90.

Owen, R.B., Jr. 1977. American woodcock (Philohela minor = Scolopax minor of Edwards 1974). Pp. 149-186 in Management of mirgatory shore and upland game birds of North America (G.C. Sanderson, Ed.). Int. Assoc. Fish. Wildl. Agencies, Washington, D.C.

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

Owen, R.B. Jr. and K.J. Reinecke. 1979. Bioenergetics of dabbling ducks. Pp. 71-93 in Waterfowl and wetlands - An integrated review (T.A. Bookhout, Ed.). La Crosse Pringing Co., Inc., La Crosse, Winconsin.

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

Pettingill, O.S. 1939. Additional information on the food of the American woodcock. Wilson Bull. 51: 78-82.

Prange, H.D. and K. Schmidt-Nielsen. 1970. The metabolic cost of swimming in ducks. J. Exp. Biol. 53: 763-777.

Prince, H.H. 1979. Bioenergetics of postbreeding dabbling ducks. Pp. 103-117 in Waterfowl and wetlands - An integrated review (T.A. Bookhout, Ed.). La Crosse Pringing Co., Inc., La Crosse, Winconsin.

Rabe, D.L. 1977. Strucutral analysis of woodcock diurnal habitat in northern Michigan. Proc. Woodcock Symp. 6: 125-134.

Rabe, D.L. 1979. A possible second nesting attempt by an American woodcock. Jack-Pine Warbler. 57: 166-167.

Reinecke, A.J. 1974. The upper lethal temperature of Eisenia rosia (Oligochaeta). Wetenskaplike Bydraes van die P.U. vir C.H.O. Reeks B: Natuurwetenskappe. 62: 1-14.

Reynolds, J.W. 1977. Earthworms utilized by the American woodcock. Proc. Woodcock Symp. 6: 161-169.

Reynolds, J.W. and G.A. Jordan. 1975. A preliminary conceptual model of Megadrile activity and abundance in the Haliburton Highlands. Megadrilogia 2: 1-9.

Reynolds, J.W., W.B. Krohn, and G.A. Jordan. 1977. Earthworm populations as related to woodcock habitat usage in central Maine. Proc. Woodcock Symp. 6: 135-146.

Ricklefs, R.E. 1974. Energetics of reproduction in birds. Pp. 152-292. in Avian energetics (R.A. Paynter, Jr., ed.). Nuttall Ornithol. Club Publ. 15.

Satchell, J.E. 1955. Some aspects of earthworm ecology. Pp. 180-201 in Soil Zoology, D.K.Mc.E. Kevan, ed. Butterworth, London.

Sheldon, W.G. 1971. The book of the American woodcock. University of Massachusetts Press, Amherst.

Simons, S. and J. Alcock. 1971. Learning and foraging persistence of white-crowned sparrows (Zonotrichia levcophrys). Ibis. 113: 447-482.

Smith, J.N.M. and R. Dawkins. 1971. The hunting behavior of individual great tits in relation to spatial variations of their food density. Anim. Behav. 19: 695-706.

Sperry, C.C. 1940. Food habits of a group of shorebirds: woodcock, snipe, knot and dowitcher. U.S. Biol. Surv. Wildl. Res. Bull. No. 1.

Stickel. W.H., W.G. Sheldon, and L.F. Stickel. 1965. Care of captive woodcocks. J. Wildl. Manage. 29: 161-172.

Wenstrom, W.P. 1973. Habitat utilization and activities of female American woodcock (Philohela minor, Gmelin) in northern Minnesota during spring and summer. Ph.D. Thesis. Univ. of Minnesota, Minneapolis.

Werner, E.E. and D.J. Hall. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (Leponmis macrochirus). Ecology 53: 1042-1052.

Westfall, C.Z. 1954. A study of woodcock behavior on their breeding grounds in central Maine. M.S. Thesis. Univ. of Maine, Orono.

Wetzel, R.G. 1975. Limnology. W.B. Saunders Co., Philadelphia.

Whitcomb, D.A. 1972. Nocturnal use of forest clearings during summer by an insular woodcock population. M.S. Thesis. Michigan State Univ., East Lansing.

Whitcomb, D.A. 1974. Characteristics of an insular woodcock population. Mich. Dept. Nat. Resour., Wildl. Div. Rep. No. 2720.

Whitcomb, D.A. 1976. Woodcock bander's news letter, No. 10. Mich Dep. Nat. Resour., Wildl. Div. Inf. Circ. 180.

Wishart, R.A., and J.R. Bider. 1976. Habitat preferences of woodcock in southwestern Quebec. J. Wildl. Manage. 40: 523-531.

APPENDICES

APPENDIX A

WOODCOCK SIMULATION PROGRAM

```
C     A SIMULATION PROGRAM WHICH RELATES WEATHER FACTORS TO
C     WOODCOCK ENERGETIC REQUIREMENTS AND FOOD AVAILABILITY
C
      REAL AVWORM(300),STEMP,ATEMP,PRECIP,WORM,ACTEN(300),
     *CGROEN(300),GROW,METEN(300),METAB,CHICEN(300),
     *CMETEN(300),NESTEN(300),NEST,MOLTEN(300),MOLT,
     *TOTEN(300),SM(300),ST(300),CEN2(300),DAT(300),SMOIST,
     *ACTIV,CACTEN(300),HENEN(300),ELAST
      INTEGER ARRIVE,CLUTCH,DATE,DAY,STATUS
      COMMON/WO/SMOIST,STEMP
      DATA STATUS,DATE,DAY,ELAST/1,0,0,21./
      DATA TOTEN,SM,ST,DAT,CEN2,HENEN,NESTEN,MOLTEN,ACTEN,
     *METEN,CHICEN,CGROEN,CACTEN,CMETEN,AVWORM/4500*0.0/
C
C     ********************VARIABLE NAMES********************
C
C     ACTEN        ENERGY REQUIREMENTS FOR HEN ACTIVITY
C     ARRIVE       DATE OF ARRIVAL ON BREEDING GROUNDS
C     ATEMP        AIR TEMPERATURE
C     AVWORM       BIOMASS OF AVAILABLE EARTHWORMS
C     CACTEN       ENERGY REQUIREMENTS FOR CHICK ACTIVITY
C     CEN2         TOTAL ENERGY REQUIREMENTS FOR ENTIRE
C                  BROOD
C     CGROEN       ENERGY REQUIREMENTS OF CHICK GROWTH
C     CHICEN       TOTAL ENERGY REQUIREMENTS FOR A CHICK
C     CLUTCH       CLUTCH SIZE
C     CMETEN       ENERGY REQUIREMENTS FOR CHICK MAINTENANCE
C     DATE,DAT     DAY COUNTERS
C     DAY          DAY COUNTER FOR VARIOUS ACTIVITIES
C     HENEN        TOTAL ENERGY REQUIREMENTS FOR HEN
C     METEN        ENERGY REQUIREMENTS FOR HEN MAINTENANCE
C     MOLTEN       ENERGY REQUIREMENTS FOR HEN MOLTING
C     NESTEN       ENERGY REQUIREMENTS FOR HEN NESTING
C     PRECIP       PRECIPITATION (INCHES OF RAIN)
C     STATUS       CHRONOLOGICAL STATUS OF WOODCOCK
C                            1 = NESTING
C                            2 = INCUBATING
C                            3 = BROODING
C                            4 = MOLTING
C                            5 = POST-MOLTING
C     TOTEN        TOTAL ENERGY REQUIREMENTS FOR BOTH
```

```
C                    HEN AND CHICKS
C     SMOIST,SM      SOIL MOISTURE
C     STEMP,ST       SOIL TEMPERATURE
C
C     ******************************************************
C
      SMOIST=10.0
      STEMP=-7.0
      READ(5,101) ARRIVE,CLUTCH
  101 FORMAT(2I3)
   10 READ(5,102,END=90)ATEMP,PRECIP
  102 FORMAT(2F10.5)
      ATEMP=(ATEMP-32.0)*5.0/9.0
      DATE=DATE+1
      DAT(DATE)=DATE
      CALL WORMS(ATEMP,PRECIP,AVWORM(DATE))
      SM(DATE)=SMOIST
      ST(DATE)=STEMP
      IF (DATE .LT. ARRIVE) GO TO 10
      DAY=DAY+1
      CALL WSTAT(STATUS,DAY)
      IF (STATUS-3) 2,1,2
    1 CALL CHICK(ATEMP,DAY,CACTEN(DATE),CGROEN(DATE),
     *CMETEN(DATE),ELAST)
      CACTEN(DATE)=CACTEN(DATE)+CMETEN(DATE)
      CHICEN(DATE)=CACTEN(DATE)+CGROEN(DATE)
      CEN2(DATE)=CHICEN(DATE)*CLUTCH
    2 NESTEN(DATE)=NEST(STATUS,CLUTCH,DAY)
      METEN(DATE)=METAB(ATEMP,DAY,2)
      MOLTEN(DATE)=MOLT(STATUS,DAY)
      ACTEN(DATE)=ACTIV(STATUS)+METEN(DATE)
      HENEN(DATE)=NESTEN(DATE)+ACTEN(DATE)+MOLTEN(DATE)
      TOTEN(DATE)=HENEN(DATE)+CEN2(DATE)
      GO TO 10
   90 CONTINUE
      CALL GRAPHS(DAT,METEN,ACTEN,HENEN,CHICEN,
     *CACTEN,CMETEN,TOTEN,AVWORM,SM,ST)
      END
```

```
      SUBROUTINE WSTAT (STATUS,DAY)
C
C     WSTAT MONITORS AND UPDATES THE STATUS OF WOODCOCK
C     ACTIVITIES FROM NESTING THROUGH MOLTING
C
      INTEGER STATUS,DAY
C
C     ********************VARIABLE NAMES********************
C
C     DAY          DAY COUNTER FOR VARIOUS ACTIVITIES
C     STATUS       CHRONOLOGICAL STATUS OF WOODCOCK
C                            1 = NESTING
C                            2 = INCUBATING
C                            3 = BROODING
C                            4 = MOLTING
C                            5 = POST-MOLTING
C
C     ******************************************************
C
      IF (STATUS .EQ. 5) RETURN
      IF (STATUS-1) 2,1,2
    1 IF (DAY .LE. 20) RETURN
      STATUS=2
      DAY=1
      RETURN
    2 IF (STATUS-2) 4,3,4
    3 IF (DAY .LE. 21) RETURN
      STATUS=3
      DAY=1
      RETURN
    4 IF (STATUS-3) 6,5,6
    5 IF (DAY .LE. 30) RETURN
      STATUS=4
      DAY=1
      RETURN
    6 IF (DAY .LE. 120) RETURN
      STATUS=5
      DAY=1
      RETURN
      END
```

```
      SUBROUTINE WORMS (ATEMP,PRECIP,AVWORM)
C
C     WORMS CALCULATES THE BIOMASS OF EARTHWORMS AVAILABLE
C     TO WOODCOCK BASED ON THEIR DISTRIBUTION IN THE SOIL
C
      REAL MEASF,MX(2),MY(2),TX(3),TY(3),TLX(2),TLY(2),
     *TMLSF,MMLSF,SMOIST,STEMP,MEASF,TEASF,AVWORM,
     *MLX(2),MLY(2),ATEMP,PRECIP
      COMMON/WO/SMOIST,STEMP
      DATA MX,MY/4.,18.,0.,1./
      DATA TX,TY/0.,17.,30.,0.,1.,0./
      DATA TLX,TLY/4.,30.,0.,1./
      DATA MLX,MLY/0.,100.,.0,.7/
C
C     *********************VARIABLE NAMES********************
C
C     ATEMP        AIR TEMPERATURE
C     AVWORM       BIOMASS OF AVAILABLE EARTHWORMS
C     MEASF        MOISTURE-ACTIVITY SCALING FACTOR
C     MMLSF        MOISTURE LOSS CONVERTION FACTOR
C     PRECIP       PRECIPITATION IN INCHES OF RAIN
C     SMOIST       SOIL MOISTURE (PERCENT)
C     STEMP        SOIL TEMPERATURE
C     TEASF        TEMPERATURE-ACTIVITY SCALING FACTOR
C     TMLSF        TEMPERATURE LOSS CONVERSION FACTOR--
C                  RATE OF SOIL MOISTURE LOSS RESULTING
C                  FROM AMBIENT TEMPERATURE
C
C     ******************************************************
C
      TMLSF=F(ATEMP,TLX,TLY,2)
      MMLSF=F(SMOIST,MLX,MLY,2)
      SMOIST=SMOIST+PRECIP*9.0-SMOIST*MMLSF*TMLSF
      STEMP=.6*ATEMP+.4*STEMP
      MEASF=F(SMOIST,MX,MY,2)
      TEASF=F(STEMP,TX,TY,3)
      AVWORM=27.0*TEASF*MEASF
      RETURN
      END
```

```
      FUNCTION METAB (ATEMP)
C
C     METAB CALCULATES THE DAILY MAINTENANCE ENERGY
C     REQUIREMENTS FOR ADULT WOODCOCK INCLUDING
C     THERMOREGULATION
C
      REAL BMR,XMR(2),YMR(2),TCF,ATEMP,METAB
      DATA XMR,YMR/-20.,10.,2.0,1.0/
C
C     ********************VARIABLE NAMES********************
C
C     ATEMP         AIR TEMPERATURE
C     BMR           BASAL METALBOLIC RATE
C     METAB         ENERGY COST OF METABOLISM
C     TCF           METABOLIC TEMPERATURE CORRECTION FACTOR
C     XMR,YMR       TABLE CONVERSIONS FOR METABOLIC RATE
C                   AS A FUNCTION OF TEMPERATURE
C
C     ******************************************************
C
      BMR=21.3
      TCF=F(ATEMP,XMR,YMR,2)
      METAB=TCF*BMR
      RETURN
      END
```

```
      FUNCTION ACTIV (STATUS)
C
C     ACTIV CALCULATES THE TOTAL ENERGY REQUIREMENTS OF
C     DAILY MOVEMENT ACTIVITIES FOR HEN WOODCOCK
C
      REAL ACTIV,FLIGHT,REST,WALK,FEED
      INTEGER STATUS
C
C     ********************VARIABLE NAMES********************
C
C     ACTIV        TOTAL DAILY ENERGY COST OF ACTIVITY
C     BMR          BASAL METABOLIC RATE (KCAL/DAY)
C     FEED         PERCENTAGE OF TIME SPENT FEEDING
C     FLIGHT       PERCENTAGE OF TIME SPENT FLYING
C     REST         PERCENTAGE OF TIME SPENT RESTING
C     STATUS       CHRONOLOGICAL STATUS OF WOODCOCK
C     WALK         PERCENTAGE OF TIME SPENT WALKING
C
C     ******************************************************
C
      BMR=21.3
      IF (STATUS-1) 2,1,2
    1 FLIGHT=.02
      REST=.75
      WALK=.16
      FEED=.08
      GO TO 10
    2 IF (STATUS-2) 4,3,4
    3 FLIGHT=.02
      REST=.83
      WALK=.10
      FEED=.05
      GO TO 10
    4 IF (STATUS-3) 6,5,6
    5 FLIGHT=.01
      REST=.61
      WALK=.14
      FEED=.24
      GO TO 10
    6 IF (STATUS-4) 8,7,8
    7 FLIGHT=.015
      REST=.555
      WALK=.09
      FEED=.34
      GO TO 10
    8 FLIGHT=.03
      REST=.67
      WALK=.13
      FEED=.16
   10 ACTIV=(FLIGHT*15.2+REST*1.3+WALK*2.0+FEED*2.0)*BMR
      RETURN
      END
```

```
      FUNCTION NEST(STATUS,EGGS,DAY)
C
C     NEST CALCULATES THE ENERGY REQUIREMENTS ASSOCIATED
C     WITH NESTING HEN WOODCOCK
C
      INTEGER STATUS,EGGS,INIT,DAY
      REAL NEST,DA,XEGG4(5),YEGG4(5),XEGG3(5),YEGG3(5)
      DATA XEGG4,YEGG4/0.,10.,14.,16.,20.,2.,2.,
     *30.,30.,0./
      DATA XEGG3,YEGG3/0.,10.,14.,15.,19.,2.,2.,
     *27.,27.,0./
C
C     ********************VARIABLE NAMES********************
C
C     DAY,DA        DAY COUNTER FOR NESTING EFFORT
C     EGGS          NUMBER OF EGGS IN THE CLUTCH
C     NEST          ENERGY COST OF LAYING EGGS AND
C                   REPRODUCTIVE TISSUEDEVELOPMENT
C     STATUS        CHRONOLOGICAL STATUS OF WOODCOCK
C     XEGG3,YEGG3   ENERGETIC COST OF LAYING A 3 EGG CLUTCH
C     XEGG4,YEGG4   ENERGETIC COST OF LAYING A 4 EGG CLUTCH
C
C     ****************************************************
C
      IF (STATUS-1) 1,6,1
    1 NEST=0
      RETURN
    6 DA=DAY
      IF (EGGS-4) 4,3,4
    3 NEST=F(DA,XEGG4,YEGG4,5)
      RETURN
    4 NEST=F(DA,XEGG3,YEGG3,5)
    5 RETURN
      END
```

```
      FUNCTION MOLT (STATUS,DAY)
C
C     MOLT CALCULATES THE DAILY ENERGY REQUIREMENTS FOR
C     MOLTING HEN WOODCOCK
C
      INTEGER STATUS,DAY
      REAL MOLT,MSF
C
C     ********************VARIABLE NAMES********************
C
C     DAY          DAY COUNTER FOR THE DURATION OF THE MOLT
C     MSF          MOLT ENERGY SCALING FACTOR
C     MOLT         ENERGY COST OF MOLTING
C     STATUS       CHRONOLOGICAL STATUS OF WOODCOCK
C
C     ******************************************************
C
      MSF=5.0
      IF (STATUS-4) 1,2,1
    1 MOLT=0.0
      RETURN
    2 MOLT=(.032*DAY-.000256*DAY*DAY)*MSF
      RETURN
      END
```

```
      SUBROUTINE CHICK (ATEMP,DAY,CACT,CGROW,CMETAB,ELAST)
C
C     SUBROUTINE CHICK CALCULATES THE ENERGY REQUIREMENTS
C     FOR GROWTH, ACTIVITY, AND MAINTENANCE FOR WOODCOCK
C     CHICKS IN BROODS
C
      REAL XCBMR(4),YCBMR(4),ELAST,PAW,TCF,ATEMP,CACT,CGROW,
     *CMETAB,BMR,EDEN,TISS,ETISS,FLIGHT,REST,WALK,FEED,
     *XMR(2),YMR(2)
      INTEGER DAY
      DATA XMR,YMR/-20.,10.,2.0,1.0/
      DATA YCBMR,XCBMR/.7,2.5,1.5,1.0,0.,.25,.50,1.0/
C
C     ********************VARIABLE NAMES********************
C
C     ATEMP         AIR TEMPERATURE
C     BMR           BASAL METABOLIC RATE OF CHICKS
C     CACT          ENERGY REQUIREMENT FOR CHICK ACTIVITY
C     CGROW         ENERGY REQUIREMENT FOR CHICKGROWTH
C                   (TISSURE AND BIOSYNTHESIS)
C     CMETAB        ENERGY REQUIREMENT FOR CHICK MAINTENANCE
C     DAY           AGE OF CHICKS (DAYS)
C     EDEN          ENERGY DENSITY OF TISSUE
C     ELAST         ACCUMULATED TISSUE ENERGY FOR PREVIOUS
C                   DAY
C     ETISS         ACCUMULATED TISSUE ENERGY TO PRESENT DAY
C     FEED          PERCENTAGE OF TIME SPENT FEEDING
C     FLIGHT        PERCENTAGE OF TIME SPENT FLIGHTING
C     GROWTH        ENERGY COST FOR TISSUE GROWTH FOR CURRENT
C                   DAY
C     PAW           PERCENT OF ADULT WEIGHT
C     REST          PERCENTAGE OF TIME SPENT RESTING
C     TCF           TEMPERATURE CONVERSION FACTOR FOR
C                   METABOLISM
C     WALK          PERCENTAGE OF TIME SPENT WALKING
C     XMR,YMR       TABLE CONVERSIONS FOR METABOLIC RATE AS
C                   FUNCTION OF TEMPERATURE
C     XCBMR,YCBMR   TABLE CONVERSIONS FOR CHICK BMR AS A
C                   FUNCTION OF ADULT SIZE
C
C     ******************************************************
C
      PAW=.085+.027*DAY
      TCF=F(ATEMP,XMR,YMR,2)
      BMR=.463*(175.*PAW)**.732*F(PAW,XCBMR,YCBMR,4)
      CMETAB=BMR*TCF
      EDEN=1.5+(.3*PAW)
      ETISS=PAW*EDEN*175.0
      CGROW=1.25*(ETISS-ELAST)
      ELAST=ETISS
      IF (DAY-14) 1,2,2
    1 FLIGHT=0.0
      GO TO 5
```

```
2 FLIGHT=.01
5 REST=.50
  WALK=.14
  FEED=.24
  CACT=(FLIGHT*15.2+REST*1.3+WALK*2.0+FEED*2.0)*BMR
  RETURN
  END
```

```
      FUNCTION F(X,XTAB,FTAB,NTAB)
C
C     FUNCTION F DOES LINEAR INTERPOLATION OF X FROM
C     TABLE VALUES XTAB AND FTAB
C
C     IF X IS OUTSIDE THE RANGE OF XTAB, THE APPROPRIATE
C     ENDPOINT OF THE FTAB TABLE IS RETURNED
C
      REAL XTAB(NTAB),FTAB(NTAB),F,X
C
C     CHECK IF X IS OUTSIDE THE RANGE OF XTAB
C
      IF (X-XTAB(1)) 1,1,2
    1 F=FTAB(1)
      RETURN
    2 IF (X-XTAB(NTAB)) 3,4,4
    4 F=FTAB(NTAB)
      RETURN
C
C     LOCATION OF X WITHIN TABLE VALUES
C
    3 DO 10 I=1,NTAB
      IF (X-XTAB(I)) 5,10,10
   10 CONTINUE
C
C     LINEAR INTERPOLATION OF F FROM TABLE VALUES ON EITHER
C     SIDE OF X
C
    5 F=(X-XTAB(I-1))*(FTAB(I)-FTAB(I-1))/
     *(XTAB(I)-XTAB(I-1))+FTAB(I-1)
      RETURN
      END
```

```
      SUBROUTINE GRAPHS(DAT,METEN,ACTEN,HENEN,CHICEN,
     *CACTEN,CMETEN,TOTEN,AVWORM,SM,ST)
      REAL DAT(300),METEN(300),ACTEN(300),HENEN(300),
     *CHICEN(300),CMETEN(300),CACTEN(300),TOTEN(300),
     *AVWORM(300),SM(300),ST(300)
C
C     PLOTTED OUTPUT
C
C     HEN
C
      CALL PLTSIZ(.85)
      CALL PLTOFS(0.0,40.,0.0,25.,4.,4.)
      CALL XAXIS
      CALL PAXIS(4.,-4.8,' ',0,3.7,90.,20.,25.,.8)
      CL=PSMLEN('KCAL/DAY',8,.15)
      CALL PSYM(3.6,4.+(4.5-CL)/2.,.15,'KCAL/DAY',90.,8,0)
      CALL PSYM(7.5,4.35,.13,'MAINTENANCE',0.,11,0)
      CALL PSYM(7.75,5.4,.13,'ACTIVITY',0.,8,0)
      CALL PSYM(9.2,6.7,.13,'MOLT',0.,4,0)
      CALL PSYM(6.7,7.3,.13,'NESTING',0.,7,0)
      CALL PLINE(DAT,METEN,268,1,0,0,1)
      CALL PLINE(DAT,ACTEN,268,1,0,0,1)
      CALL PLINE(DAT,HENEN,268,1,0,0,1)
      CALL PLTEND
C
C     CHICKS
C
      CALL PLTSIZ(.85)
      CALL PLTOFS(0.0,40.,0.0,25.,4.,4.)
      CALL XAXIS
      CALL PAXIS(4.,-4.8,' ',0,3.7,90.,20.,25.,.8)
      CL=PSMLEN('KCAL/DAY',8,.15)
      CALL PSYM(3.6,4.+(4.5-CL)/2.,.15,'KCAL/DAY',90.,8,0)
      CALL PSYM(8.2,4.4,.13,'MAINTENANCE',0.,11,0)
      CALL PSYM(8.2,5.45,.13,'ACTIVITY',0.,8,0)
      CALL PSYM(8.2,6.3,.13,'GROWTH',0.,6,0)
      CALL PLINE(DAT,CHICEN,268,1,0,0,1)
      CALL PLINE(DAT,CACTEN,268,1,0,0,1)
      CALL PLINE(DAT,CMETEN,268,1,0,0,1)
      CALL PLTEND
C
C     COMBINED ENERGY AND AVAILABLE WORMS
C
      CALL PLTSIZ(.85)
      CALL PLTOFS(0.0,40.,0.,100.,4.,4.)
      CALL XAXIS
      CALL PAXIS(4.,-5.,' ',0,3.3,90.,100.,100.,1.0)
      CL=PSMLEN('KCAL/DAY',8,.15)
      CALL PSYM(3.6,4.+(4.5-CL)/2.,.15,'KCAL/DAY',90.,8,0)
      CALL PLINE(DAT,TOTEN,268,1,0,0,1)
      CALL PLTOFS(0.0,40.,0.,10.,4.,4.)
      CALL PENUP(11.,4.)
      CALL PENDN(11.,5.)
```

```
      CALL PAXIS(11.,-5.,' ',-0.0,3.3,90.,10.,10.,1.0)
      CL=PSMLEN('EARTHWORM BIOMASS',17,.15)
      CALL PSYM(11.55,4.+(4.5-CL)/2.,.15,'EARTHWORM BIOMASS'
     *,90.,17,0)
      CALL PLINE(DAT,AVWORM,268,1,0,0,1)
      CALL PLTEND
C
C     MOISTURE-TEMPERATURE-EARTHWORM ABUNDANCE
C
      CALL PLTSIZ(.85)
      CALL PLTOFS(0.,50.,0.,10.,3.,3.)
      CALL PAXFRM('MF3.0*')
      CALL PALPHA('SANSERIF.2 ',0)
      CALL PAXTTL(.12)
      CALL PAXTIC(1)
      CALL PAXVAL(.10)
      CALL PENUP(8.5,3.)
      CALL PENDN(3.,3.)
      CALL PENDN(3.,4.)
      X=3.0
      DO 95 I=1,9
      X=X+.6
      CALL PENUP(X,3.0)
      CALL PENDN(X,2.95)
   95 CONTINUE
      CLEN=PSMLEN('JAN',3,.12)
      CALL PSYM(3.0+(.6-CLEN)/2.0,2.7,.12,'JAN',0.,3,0)
      CLEN=PSMLEN('FEB',3,.12)
      CALL PSYM(3.6+(.6-CLEN)/2.0,2.7,.12,'FEB',0.,3,0)
      CLEN=PSMLEN('MAR',3,.12)
      CALL PSYM(4.2+(.6-CLEN)/2.0,2.7,.12,'MAR',0.,3,0)
      CLEN=PSMLEN('APR',3,.12)
      CALL PSYM(4.8+(.6-CLEN)/2.0,2.7,.12,'APR',0.,3,0)
      CLEN=PSMLEN('MAY',3,.12)
      CALL PSYM(5.4+(.6-CLEN)/2.0,2.7,.12,'MAY',0.,3,0)
      CLEN=PSMLEN('JUN',3,.12)
      CALL PSYM(6.0+(.6-CLEN)/2.0,2.7,.12,'JUN',0.,3,0)
      CLEN=PSMLEN('JUL',3,.12)
      CALL PSYM(6.6+(.6-CLEN)/2.0,2.7,.12,'JUL',0.,3,0)
      CLEN=PSMLEN('AUG',3,.12)
      CALL PSYM(7.2+(.6-CLEN)/2.0,2.7,.12,'AUG',0.,3,0)
      CLEN=PSMLEN('SEP',3,.12)
      CALL PSYM(7.8+(.6-CLEN)/2.0,2.7,.12,'SEP',0.,3,0)
      CALL PAXIS(3.,-3.5,' ',0,1.9,90.,5.,10.,.5)
      CL=PSMLEN('EARTHWORM BIOMASS',17,.13)
      CALL PSYM(2.6,3.+(2.5-CL)/2.,.13,'EARTHWORM BIOMASS',
     *90.,17,0)
      CALL PLINE(DAT,AVWORM,268,1,0,0,1)
C
      CALL PLTOFS(0.,50.,-20.,20.,3.,5.75)
      X=3.0
      DO 108 J=1,9
      X=X+.6
      CALL PENUP(X,5.75)
```

```
      CALL PENDN(X,5.70)
  108 CONTINUE
      CALL PENUP(8.5,5.75)
      CALL PENDN(3.,5.75)
      CALL PENDN(3.,6.4)
      CALL PAXIS(3.,-6.25,' ',0,2.2,90.,-10.,20.,.5)
      CL=PSMLEN('SOIL TEMPERATURE',16,.13)
      CALL PSYM(2.6,5.75+(2.7-CL)/2.,.13,'SOIL TEMPERATURE',
     *90.,16,0)
      CALL PLINE(DAT,ST,268,1,0,0,1)
C
      CALL PLTOFS(0.,50.,0.,20.,3.,8.75)
      CALL PAXIS(3.,-9.25,' ',0,2.8,90.,10.,20.,.5)
      CL=PSMLEN('SOIL MOISTURE',13,.13)
      CALL PSYM(2.6,8.75+(3.-CL)/2.,.13,'SOIL MOISTURE',
     *90.,13,0)
      X=3.0
      DO 105 I=1,9
      X=X+.6
      CALL PENUP(X,8.75)
      CALL PENDN(X,8.70)
  105 CONTINUE
      CALL PENUP(8.5,8.75)
      CALL PENDN(3.,8.75)
      CALL PENDN(3.,9.4)
      CALL PLINE(DAT,SM,268,1,0,0,1)
      CALL PLTEND
      RETURN
      END
```

```
      SUBROUTINE XAXIS
      CALL PAXVAL(.13)
      CALL PAXFRM('MF3.0*')
      CALL PAXTTL(.15)
      CALL PALPHA('SANSERIF.2 ',0)
      CALL PENUP(11.,4.)
      CALL PENDN(4.,4.)
      CALL PENDN(4.,5.)
      X=4.0
      DO 110 I=1,9
      X=X+.75
      CALL PENUP(X,4.0)
      CALL PENDN(X,3.95)
  110 CONTINUE
      CLEN=PSMLEN('JAN',3,.15)
      CALL PSYM(4.0+(.75-CLEN)/2.0,3.7,.15,'JAN',0.,3,0)
      CLEN=PSMLEN('FEB',3,.15)
      CALL PSYM(4.75+(.75-CLEN)/2.0,3.7,.15,'FEB',0.,3,0)
      CLEN=PSMLEN('MAR',3,.15)
      CALL PSYM(5.5+(.75-CLEN)/2.0,3.7,.15,'MAR',0.,3,0)
      CLEN=PSMLEN('APR',3,.15)
      CALL PSYM(6.25+(.75-CLEN)/2.0,3.7,.15,'APR',0.,3,0)
      CLEN=PSMLEN('MAY',3,.15)
      CALL PSYM(7.0+(.75-CLEN)/2.0,3.7,.15,'MAY',0.,3,0)
      CLEN=PSMLEN('JUN',3,.15)
      CALL PSYM(7.75+(.75-CLEN)/2.0,3.7,.15,'JUN',0.,3,0)
      CLEN=PSMLEN('JUL',3,.15)
      CALL PSYM(8.5+(.75-CLEN)/2.0,3.7,.15,'JUL',0.,3,0)
      CLEN=PSMLEN('AUG',3,.15)
      CALL PSYM(9.25+(.75-CLEN)/2.0,3.7,.15,'AUG',0.,3,0)
      CLEN=PSMLEN('SEP',3,.15)
      CALL PSYM(10.0+(.75-CLEN)/2.0,3.7,.15,'SEP',0.,3,0)
      RETURN
      END
```

APPENDIX B

Simulated Earthworm Abundance for 1965-80

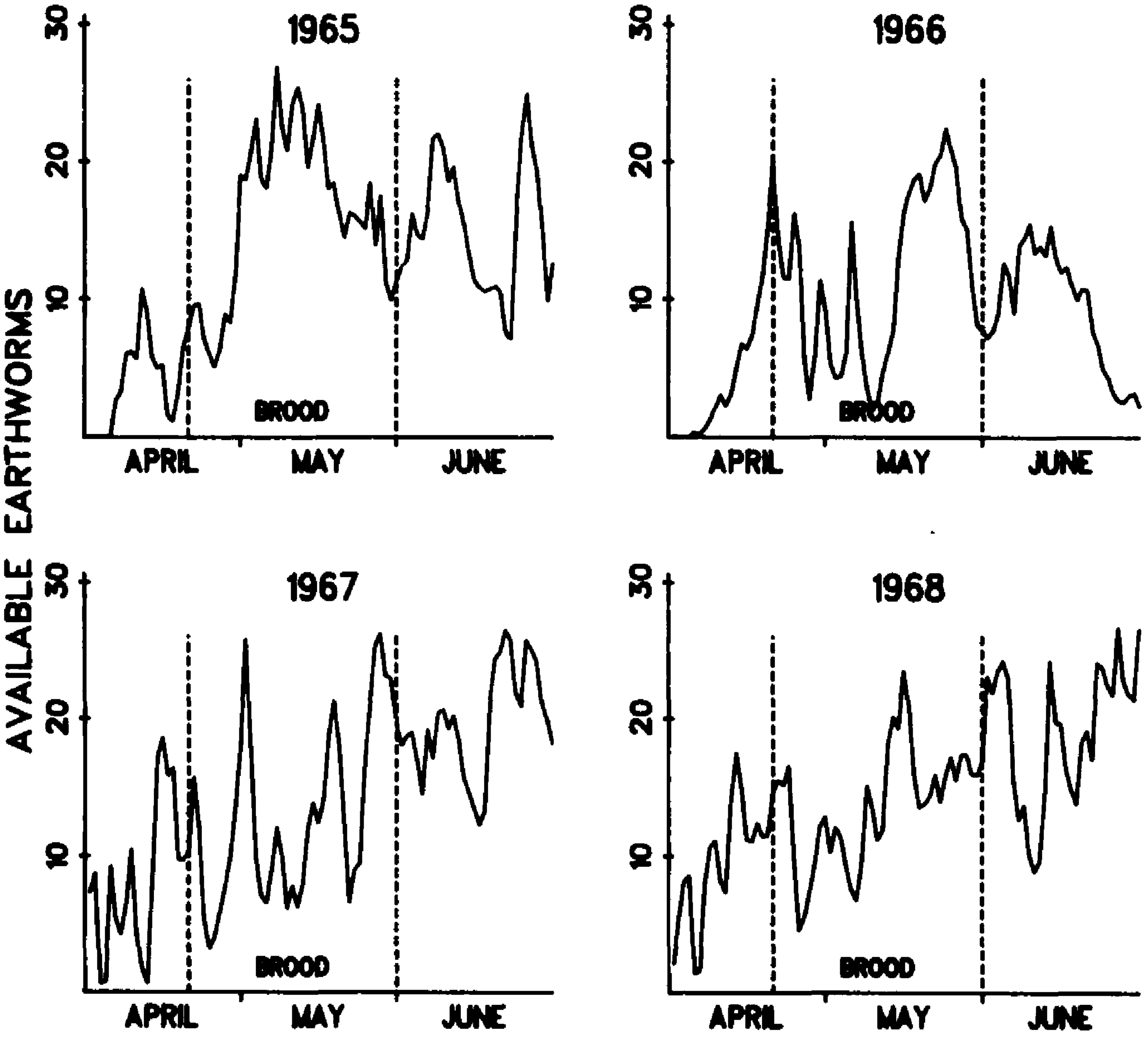

Figure 18. Simulated earthworm abundance during the spring period for 1965-80.

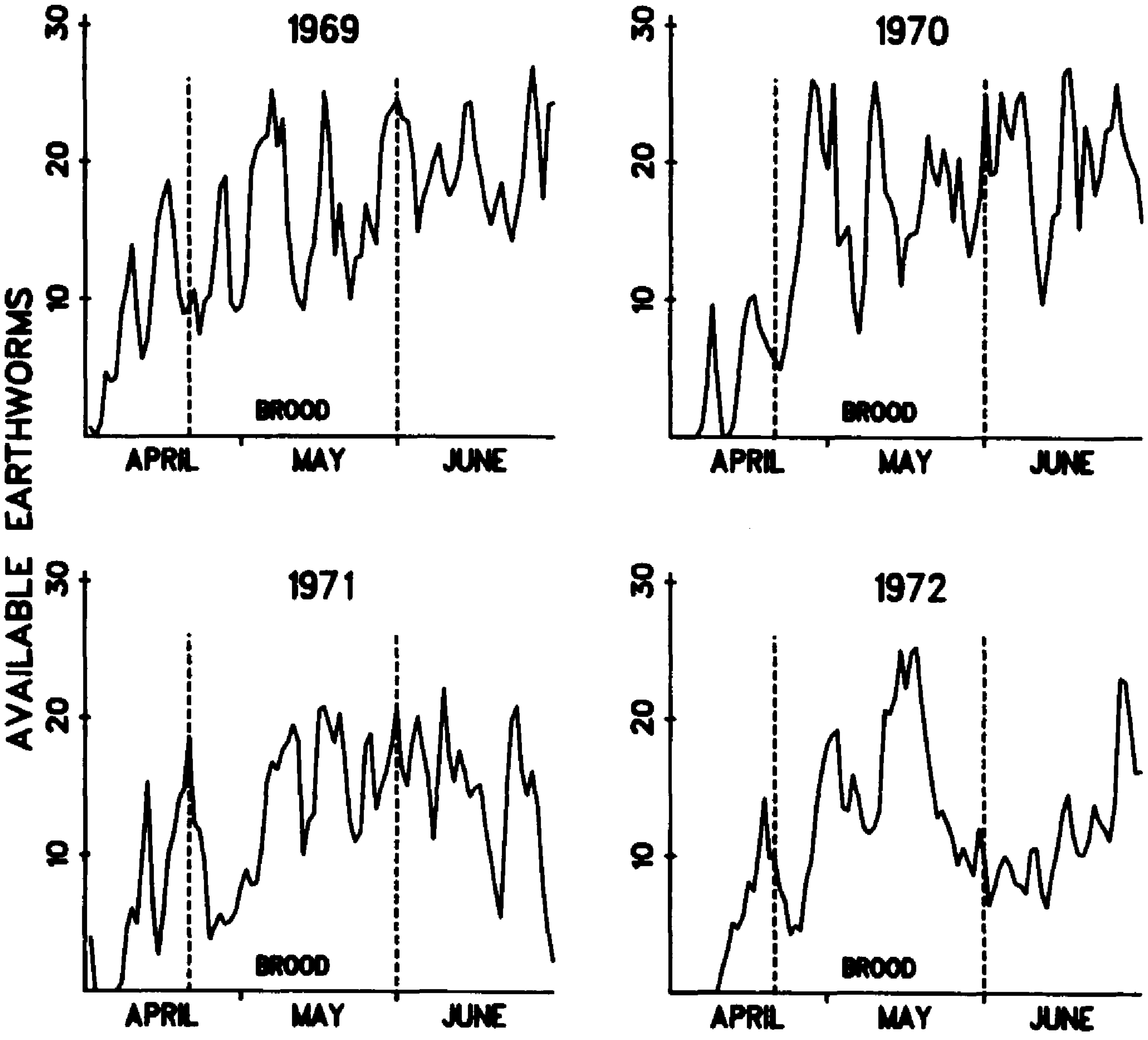

Figure 18. continued.

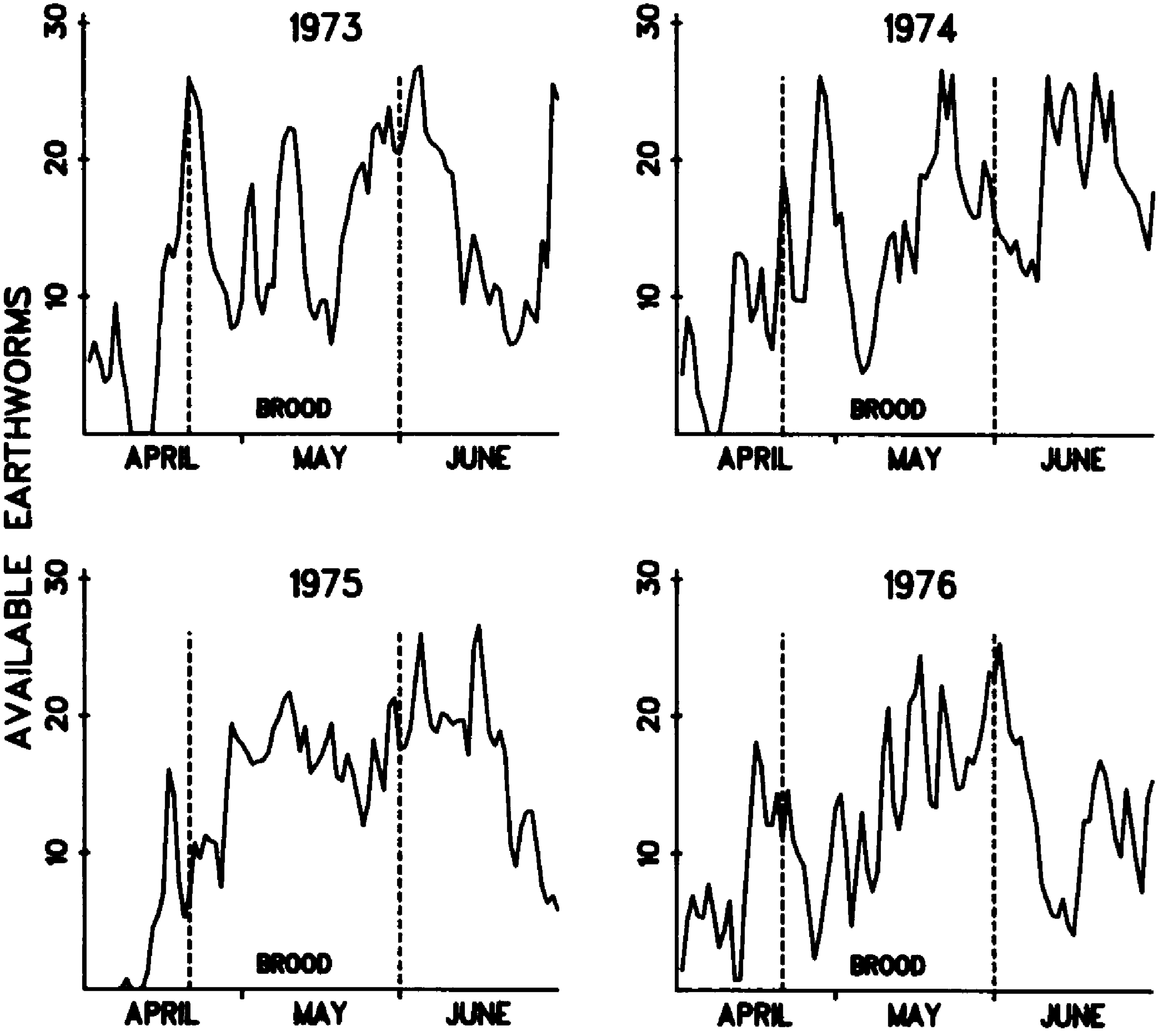

Figure 18. continued.

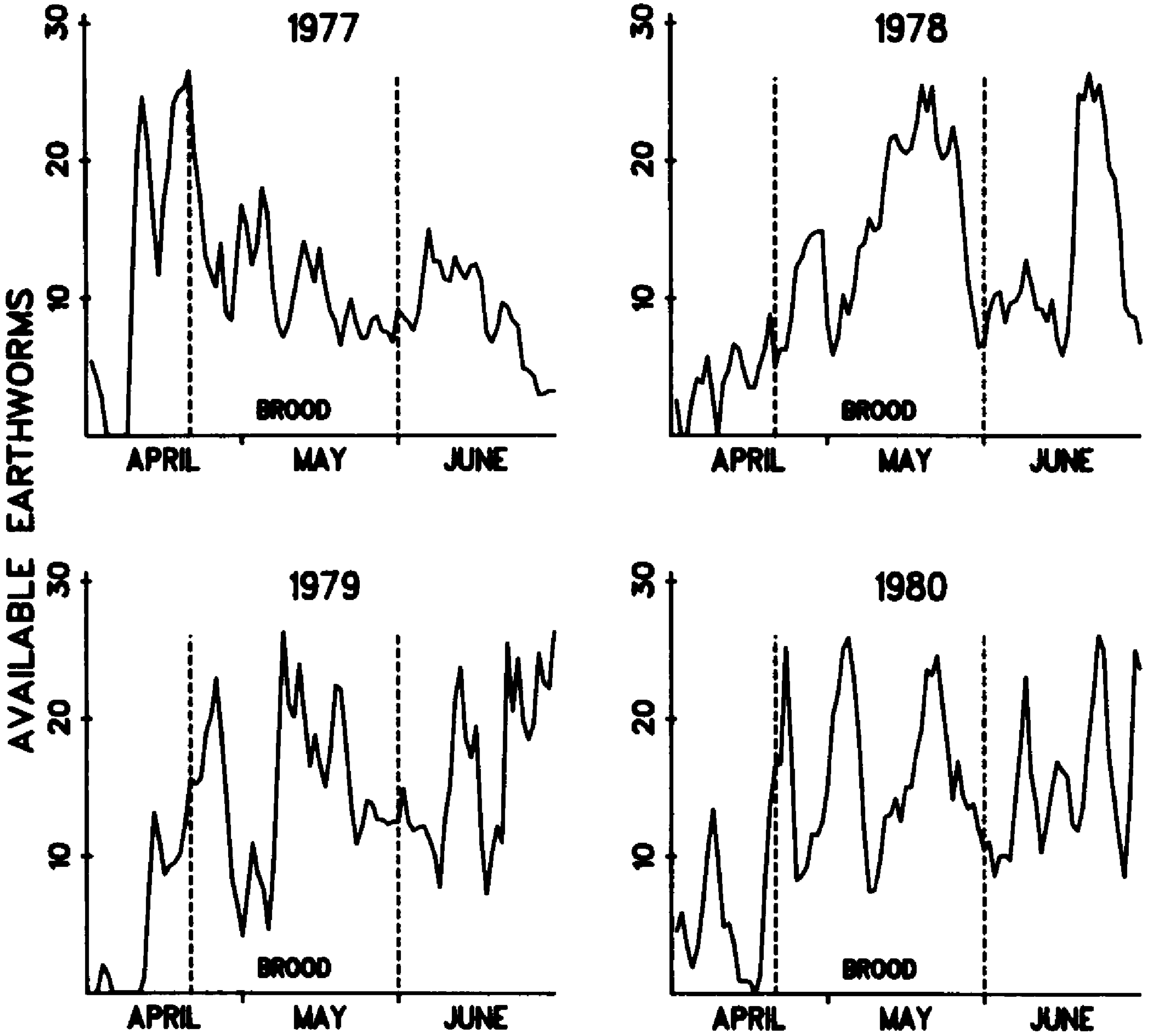

Figure 18. continued.