BIOENERGETICS OF AMERICAN WOODCOCK DURING THE BREEDING SEASON ON MOOSEHORN NATIONAL WILDLIFE REFUGE, MAINE

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By

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Bioenergetics of female American woodcock (Scolopax minor) was studied from 1987-1989 at Moosehorn National Wildlife Refuge, Maine. A model of daily energy expenditure was developed from laboratory-derived data on metabolic rates; from data on activity and microclimates collected in the field; and from body component analysis of collected birds.

Energy demands incurred by female woodcock on the breeding grounds were highest during the Pre-nesting (60.3 kcal/day) and Laying (89.1 kcal/day) periods. Availability of food (earthworms [Lumbricidae]) is normally sufficient during these periods, but shortages such as the one caused by persistent soil frost in spring of 1989 can delay nesting and affect productivity. Female woodcock feed throughout the diel period prior to incubation, obtaining nutrients for reproductive tissues and to store fat for use during incubation. Incubating females spend only 8% of the day active and used endogenous reserves to supplement energy derived by feeding, losing about 75%

of their body fat over incubation. In March and April 1989, energy intake was too low to initiate egg production as nesting did not occur until the frost melted and earthworm availability returned to normal, 3-4 weeks later than the typical nesting date in Maine.

Woodcock chicks are not homeothermic until 15-20 days old, and there is an inverse relationship between air temperature and brooding requirements. At air temperatures typical of the brood period, a drop in mean air temperature of 5 ^{o}C can result in a 40% decrease in time spent active, with a concomitant loss of foraging time. Rainfall also increases the brooding requirements of chicks, reducing by 30% the time spent active by chicks < 10 days old. Reduced foraging time lowers both energy intake by the female and her ability to feed the chicks.

Lack of snow cover, and freezing temperatures, influence the depth of soil frost and can reduce both food availability in spring and woodcock productivity. In addition, weather during the brood period and condition of the female at the end of incubation play important roles in determining the number of offspring produced. Thus, habitat management should strive to provide high earthworm biomass in a variety of suitable feeding sites to ameliorate the effects of weather.

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INTRODUCTION

The importance of energy allocation in a species' life history strategy has become increasingly evident to biologists. Research on nutrient allocation during the breeding season has provided useful information on reproductive strategies and possible limitations on egg production and incubation constraints in birds (Korschgen 1977, Alisaukus and Ankney 1985, Barzen and Serie 1990). Studies of energy expenditure by both modeling time-energy budgets and direct measurement via doubly-labeled water have provided insights into the seasonal demands on individuals (Mugaas and King 1981, Obst et al. 1987, Masman et al. 1988) and on populations (Wiens and Innis 1974, Holmes et al. 1979, Rotenberry 1980).

The American woodcock (Scolopax minor) is an upland shorebird that breeds in early successional forests of eastern North America (Sheldon 1967). It shares many characteristics with other Charadriiforms including migration to a northern breeding grounds, a clutch of 4 relatively large eggs, single-parent incubation and care of young, and a carnivorous diet (Sheldon 1967). Although some reproduction occurs on the wintering grounds in the southeastern United States, primary breeding occurs following a migration to northeastern and northcentral United States and Canada (Sheldon 1967). Unlike many shorebirds, the American woodcock inhabits sheltered, forested habitats, does not migrate extensive latitudinal distances, and spends a very small proportion of its day in flight (exceptions occur during migration and during the courtship flights of males).

The eastern population of American woodcock has been declining for at least the past decade (Bortner 1990), raising concern for the future of the population. Unfortunately, there are no comprehensive data available on how environmental and behavioral components affect woodcock survival and recruitment. In 1987, Patuxent Wildlife Research Center and Moosehorn National Wildlife Refuge began a 3-year study to examine reproductive success, survival rates, and habitat use within the expanding woodcock population on the refuge. A detailed study of the reproductive energetics of a population with concurrent survival and productivity data was initiated to provide a more complete appraisal of the factors impinging on the population.

Several characteristics of American woodcock make it suitable for study via energetics modeling. First, it subsists primarily on one prey species (Sheldon 1967), simplifying analysis of energy intake. Second, the female spends little time in flight during the breeding season, making assignment of flight costs of much less importance than in more aerial species. Third, the female alone is responsible for rearing the young, making partitioning of parental investments in care unnecessary. And fourth, woodcock are suitable for laboratory work (Stickel et al. 1967).

This dissertation is presented in three discrete sections, each dealing with a different aspect of woodcock energetics. Chapter 1 begins with the basic metabolic costs as measured through indirect calorimetry on captive birds. These species-specific metabolic costs are critical to accurate modeling (Weathers et al. 1984, Buttemer et al. 1986) and form the basis for the model developed in Chapter 3. A detailed analysis of woodcock time budgets is presented in Chapter 2. These activity data were collected on radio-tagged birds and are compared with concurrent weather data to assess the effects of air temperature and rainfall on activity of brood-rearing females. Chapter 3 incorporates the data from chapters 1 and 2 along with microclimate data collected in woodcock habitats, body composition of breeding females, costs and composition of reproductive tissues, and assimilation efficiencies into a detailed energy budget for the breeding season.

LITERATURE CITED

Alisauskas, R. T., and C. D. Ankney. 1985. Nutrient reserves and the energetics of reproduction in American coots. Auk 102:133-144 .

Barzen, J. A., and J. R. Serie. 1990. Nutrient reserve dynamics of breeding canvasbacks . Auk 107:75-85 .

Bortner, J. B. 1990. American woodcock harvest and population status, 1990. U.S. Fish and Wildl. Serv., Washington, D.C. 12pp.

Buttemer, W. A., A. M. Hayworth, W. W. Weathers, and K. A. Nagy. 1986. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. Physiol. Zool. 59:131-149.

Holmes, R. T., C. P. Black and T. W. Sherry. 1979. Comparative population bioenergetics of three insectivorous passerines in a deciduous forest. Condor 81:9-20 .

Korschgen, C. E. 1977. Breeding stress of female eiders in Maine. J. Wildl. Manage. 41:360-373.

Masman, D., S. Daan and G. J. A. Beldhuis. 1988. Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. Ardea 76:64-81.

Mugaas, J. N., and J. R. King. 1981. Annual variation of daily energy expenditure by the black-billed magpie: a study of thermal and behavioral energetics. Studies in avian biology No. 5, Cooper Ornithological Society, 78pp.

Obst, B. S., K. A. Nagy, and R. E. Ricklefs. 1987. Energy utilization by Wilson's storm-petrel (Oceanites oceanicus). Physiol. Zool. 60:200-210.

Rotenberry, J. T. 1980. Bioenergetics and diet in a simple community of shrubsteppe birds. Oecologia 46:7-12.

Sheldon, W. G. 1967. The book of the American woodcock. Univ. Massachusetts Press, Amherst, 227pp.

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

Weathers, W. W., W. A. Buttermer, A. M. Hayworth, and K. A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. Auk 101:459-472.

Wiens, J. A., and G. S. Innis. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. Ecology 55:730-746.

CHAPTER 1

METABOLIC RATES AND COST OF ACTIVITY IN THE AMERICAN WOODCOCK

The American woodcock (Scolopax minor) is an upland shorebird that breeds primarily in the northeast and northcentral United States and eastern Canada (Sheldon 1967). A decline in its eastern breeding population over the past decade has prompted concern about the welfare of the population (Bortner 1990). As one of the earliest nesting migrants in this region, the woodcock often encounters weather conditions that are potentially stressful. Research on the energy constraints acting on woodcock during the breeding season could help interpret reproductive strategies and explain yearly variations in reproductive success. In the absence of empirical data for woodcock, a previous attempt to model woodcock energetics used metabolic parameters derived for other species (Rabe et al. 1983).

Most energetics studies incorporate metabolic parameters as an integral part of the analysis. However, since metabolic rates have been measured only on a limited number of species, many such studies have depended upon predictive equations from the literature or estimates based on data from similar species for such basic parameters as standard metabolic rate (SMR) and lower critical temperature (LCT). Research has shown that use of species-specific metabolic parameters can have a pronounced effect on the outcome of energetic modeling (Weathers et al. 1984, Buttemer et al. 1986).

Metabolism data are generally lacking for shorebirds. Kersten and Piersma (1987) measured several metabolic parameters of turnstones (Arenaria interpres), grey plovers (Pluvialis squatarola), and oystercatchers (Haematopus ostralegus). Standard metabolic rate has been reported for sanderlings (Calidris alba) (Castro 1987) and Pacific golden plovers (Pluvialis fulva) (Mathiu et al. 1989). Standard metabolic rates measured in these studies were consistently above those predicted by published allometric equations, leading Kersten and Perisma (1987) to develop a separate equation specific to shorebirds. Because the woodcock has many life history characteristics different from most other shorebirds, it is not clear which, if any, allometric equation would adequately predict SMR or other metabolic parameters. Without these data accurate modeling of woodcock energetics is impossible.

As part of a larger study on woodcock reproductive energetics I determined the metabolic rates of American woodcock that would be of most use in modeling ecological energetics.

METHODS

American woodcock (3 M, 3 F) were reared from eggs collected on the Moosehorn National Wildlife Refuge, Calais, Maine. From July through mid-September 1988, birds were housed in outside pens at ambient temperature and photoperiod at Orono, Maine. From mid-September 1988 through March 1989, birds were housed in an environmental chamber and maintained at constant 19 ^{O}C air temperature. Photoperiod in the chamber was maintained at September levels (13:11, L:D) through December, and then advanced to normal levels over a period of several weeks. From April-June 1989, woodcock were housed in sheltered pens at ambient temperature and photoperiod in Calais. In late June, birds were moved into the environmental chamber in Orono 2 weeks prior to the experiments. All birds used in the analysis had completed their post-juvenile molts. The same birds were used in both phases of the study, advancing in age-class from hatch-year (n = 6) in 1988 to second-year (n= 4) in 1989. Birds were fed earthworms (Lumbricus terrestris) ad libitum and were handled daily and habituated to captivity (Vander Haegen et al. in press a).

Thermoregulatory experiments were conducted during December 1988. Standard metabolism was measured in a plexiglass metabolism chamber (22 x 21 x 10 cm) on post-absorptive birds during the resting phase of their daily cycle and in complete darkness. Flow rate through the chamber ranged from 2.5 to 3.0 l/min. Concentrations of O_2 and CO_2 were measured in an open circuit system using a Beckman 755 Oxygen analyzer and a Beckman 864 infrared CO_2 analyzer. Temperature in the metabolism chamber and in the air stream at the entrance to the flow meter was measured with 28 ga thermocouples. Gas concentrations and temperatures were sampled every second by a CR21X micrologger (Campbell Scientific, Logan, UT), averaged every 60 seconds, and output to a microcomputer. Metabolism was measured at 2-3 temperatures per run, always proceeding from higher to lower temperature (Pohl 1969). Following a 1 hour adjustment period at each temperature, O_2 and CO_2 concentrations were monitored for 30 minutes. Values reported represent the lower of two $\geq$ 4-minute constant rates obtained at each temperature during each run. All gas volumes were corrected to standard temperature and pressure. Metabolism was calculated using the appropriate equation in Withers (1977). Standard metabolic rate for each bird was determined by averaging all values obtained from 23 to 30 ^{o}C. I estimated LCT as the point where the line representing SMR intersected the regression line for all points $\leq$ 20 ^{o}C. The slope of the regression line was assumed to represent the temperature coefficient.

During the second set of experiments, birds were maintained at normal photoperiod (15:9) and at 25 ^{o}C. To check for changes between years, SMR was determined as in 1988. Metabolic cost of walking (active metabolic rate: AMR) was measured in thermoneutrality (25 ^{o}C) while birds walked on a treadmill contained within the plexiglass metabolism chamber described above. Experiments were conducted on fed birds, under artificial light during the birds normal active period. Birds were conditioned on the treadmill for 2 weeks prior to data collection. At the beginning of each run a bird was placed in the chamber and allowed to reach constant "resting" O_2 consumption. This value (resting metabolic rate: RMR) was derived from $\geq$4 minutes of constant O_2 consumption and represents the metabolic rate of a resting bird during the active phase of its diel cycle. The treadmill was then activated at slow speed (1.2 m/minute) for 2-3 minutes, then advanced to walking speed (2.2 m/minute) for a minimum of 15 minutes or until a plateau in O_2 consumption was reached. Walking speed was determined by observing captive woodcock during foraging trials in natural feeding covers and represents the typical speed of a woodcock walking and probing in the soil for food. Values for AMR and RMR represent the mean of 3 values obtained for each bird.

Differences between sexes and years for SMR were tested using t-tests. Least-squares regression was used to evaluate the effect of temperature on metabolic rate below the thermoneutral zone (TNZ). Differences in regression equations between sexes were tested using analysis of covarience. Means are reported ± 1 SE.

RESULTS

Standard metabolic rate for male (0.0187 ± 0.00007 ml O_2/g/minute; n = 2) and female (0.0207 ± 0.0041 ml O_2/g/minute; n = 3) woodcock were not significantly different ($t = 0.675$, $df = 3$, $P = 0.548$) (1 male woodcock had not completed molting and was excluded from the analysis). Similarly, the equations for the regression lines representing metabolic rate vs temperature below the TNZ did not differ significantly ($F = 1.455$, $df = 1$, $P = 0.239$) between male and female woodcock. Standard metabolic rate for 5 birds measured in December 1988 (0.0202 ± 0.0028 ml O_2/g/minute) did not differ significantly from values obtained for 4 birds in July 1989 (0.0185 ± 0.0019 ml O_2/g/min)(t = 1.033, df = 7, P = 0.388). Therefore, data for all birds were combined (Table 1.1)[1]. Estimated LCT was 21 °C; below the TNZ metabolic rate increased linearly as temperature decreased (Fig. 1.1). Temperature coefficients for 5 birds measured in 1988 averaged -0.000579 ±0.000139 ml O_2/g/minute/C.

Metabolic rates for active (AMR) and resting (RMR) woodcock during the active phase of the daily cycle are presented in Table 1.1. Oxygen consumption by a woodcock walking on a treadmill at 2.2 m/minute (AMR) was 42% greater than that of a bird at rest (RMR).

Mean weights for male and female woodcock during the 1988 experiments were 139.0 ± 2.5 g (n = 3) and 168.1 ± 3.8 g (n = 3), respectively. Mean weights for male and female woodcock during the 1989 experiments were 130.9 ± 8.9 g (n = 3) and 162.6 g (n = 1), respectively. Average weight for captive woodcock over all metabolic experiments was 156.7 ± 16.0 g.

DISCUSSION

Standard metabolic rate for American woodcock raised in captivity was greater than that predicted from the allometric equation (Aschoff and Pohl 1970) used by Rabe et al. (1983) in their model of woodcock energetics (Table 1.2). More significantly, the LCT of captive-reared woodcock (21 °C) was 11 °C higher than that assumed by Rabe et al. (1983). This combination of greater SMR and

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[1] Data for individual birds are in Appendix A.

Table 1.1. Metabolic rates of captive-reared American woodcock while active (walking at 2.2 m/minute) and resting (during the active phase of the diel cycle), as compared to Standard Metabolic Rate (SMR).

			ml/O_2/g/minute		Multiple of SMR[c]	
	N[a]	n[b]	$\bar{x}$	SE	$\bar{x}$	SE
Active	3	9	0.0322	0.0013	1.77	0.17
Resting	3	9	0.0227	0.0006	1.25	0.16
SMR	5	18	0.0199	0.0031	1.00	-

[a] Number of birds.
[b] Number of measurements.
[c] Calculated using individual SMR for each bird.

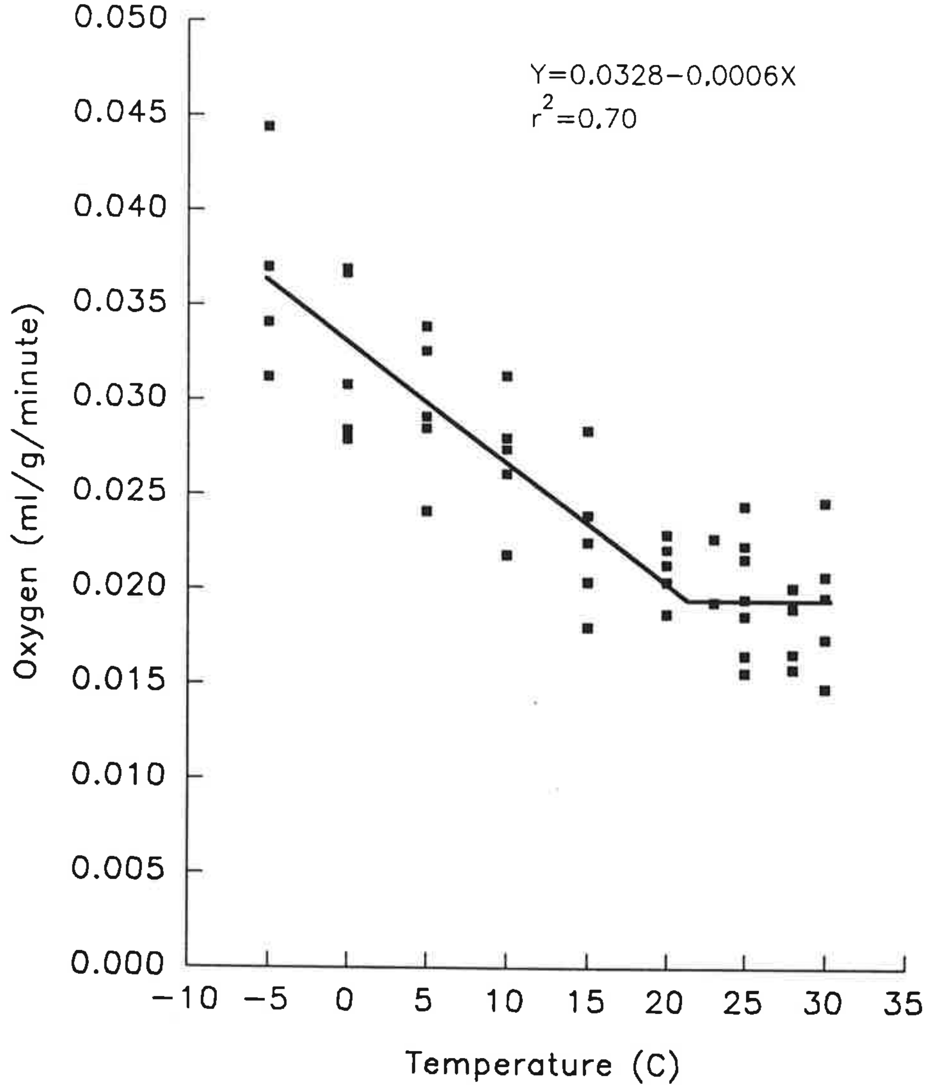

Figure 1.1. Effect of ambient temperature on oxygen consumption by captive-reared American woodcock (n = 2 males, 3 females).

Table 1.2. Comparison of measured and predicted Standard Metabolic Rate (SMR) in the American woodcock.

	SMR (W)[a]	Measured relative to predicted (%)
Measured SMR (this study)	1.02	
Predictive Equations		
Aschoff and Pohl (1970)[b,c]	0.92	+11
Lasiewski and Dawson (1967)[c]	0.88	+16
Kendeigh et al. (1977)[c]	1.09	- 7
Kersten and Piersma (1987)[d]	1.31	- 22

[a] SMR in watts; calculations based on 157g body weight.
[b] Equation used by Rabe et al. (1983).
[c] Equations for non-passerines.
[d] Equation for shorebirds.

higher LCT would result in maintenance and thermoregulatory costs substantially above those used in Rabe et al.'s (1983) model. Such disparities between predicted and measured values illustrate the value of using species-specific metabolic rates when modeling animal energetics.

Although SMR for the woodcock is greater than that predicted by some generalized equations for non-passerines (Table 1.2), it does not follow the elevated pattern for shorebirds predicted by the equation of Kersten and Piersma (1987). However, other shorebirds have been found to exhibit the high metabolic rates predicted by Kersten and Piersma's equation. Recent studies of sanderlings (Castro 1987) and Pacific golden plovers (Mathiu et al. 1989) have recorded high values for SMR. Several behavioral and physiological differences between woodcock and other studied shorebirds may explain these differences in metabolic rate.

Kersten and Piersma (1987) suggested that high SMR in shorebirds is caused by increased use of skeletal muscles to support a high daily energy expenditure (DEE) at some point in their yearly cycle (e.g., premigratory hyperphasia, migration, or winter cold periods). If this hypothesis is valid, woodcock should not encounter periods of energetic stress of the same magnitude as do other shorebirds. Environmental conditions experienced by woodcock on the northern breeding grounds can be severe, with prolonged cold temperatures and periods of reduced food availability (Sheldon 1967, Vander Haegen et al. in press b). Also, female woodcock preparing to nest are active both day and night as they increase stored energy reserves prior to laying a clutch (Chapter 2). Thus, DEE during the breeding season is likely to be high, although perhaps not equal to that experienced by arctic nesting shorebirds. A greater potential for difference in DEE between American woodcock and other shorebirds may exist during migration. American woodcock migrate considerably shorter daily and total distances than do most shorebirds, and perhaps do not incur as high an energetic cost during the pre-migratory and migration periods. If SMR is related to maximal DEE, these differences may explain the lower metabolic rates of woodcock.

Temperature coefficients describe the increase in metabolic rate with decreasing ambient temperature and are influenced by the insulative qualities of plumage (Kendeigh et al. 1977). Temperature coefficients measured for 3 species of shorebirds (Kersten and Piersma 1987) ranged from 14 to 47% above those obtained using a predictive equation (Kendeigh et al. 1977). A possible relationship between these high values and the windy environment common to most shorebird species is discussed by Kersten and Pierisma (1987). The temperature coefficient for woodcock is 20% below that predicted from the equation of Kendeigh et al. (1977). This discrepancy suggests that, under forested conditions with low convection, woodcock are better insulated than are some other species of shorebirds.

The measured value for LCT is above the ambient temperatures often encountered by woodcock on the northern breeding grounds, indicating a frequent metabolic cost for thermoregulation. The woodcock's LCT is within the range of values reported for 2 northern-breeding shorebird species (15-23 ^{O}C) of similar weight (Kersten and Piersma 1987) and is also close to the value of 19 ^{O}C predicted from the equation of Kendeigh et al. (1977) for non-passerines. At temperatures below the LCT, thermoregulatory costs will be lower for woodcock compared to other measured shorebirds because of the lower temperature coefficient.

Metabolic rates measured during the active phase of a bird's daily cycle are typically higher than values obtained during the resting phase (Aschoff and Pohl 1970). As a multiple of SMR, RMR of woodcock is slightly greater than the value of 1.1 reported for American black ducks (Anas rubripes) (Wooley and Owen 1978). Kendeigh et al. (1977) reported daytime values for avian SMR ranging from 1.1 to 1.4 times greater than nighttime values. Daytime metabolic rate for fed desert quail (Callipepla gambelii) in their TNZ was 1.1 times greater than nighttime values (Goldstein and Nagy 1985). Birds used in my experiments were conditioned to the metabolism chamber and displayed no signs of stress during the measurements. The only activity engaged by the birds was an occasional probe with their bills.

A number of studies have measured energetic costs of terrestrial locomotion in birds (e.g., Fedek et al. 1974), but few report data on walking specifically. As a multiple of SMR, the cost of walking for American black ducks was 1.7 (Wooley and Owen 1978), and the cost of hopping for loggerheaded shrikes (*Lanius ludoricianus*) was 2.3 (Weathers et al. 1984). Fedak et al. (1974) measured the cost of running for 7 species of ground-dwelling birds. Their data show that energy cost increases linearly with running speed, and increases on a per-gram basis as body size decreases. My measured cost for woodcock walking at 2.2 m/minute fits between the regression lines presented in Fedak et al. (1974) for running painted quail (*Excalfactoria chinensis*) (49g) and bobwhite quail (*Colinus virginianus*) (194g) when these lines are extrapolated through walking speed to zero. I conclude that the cost of walking for woodcock is typical of that of other ground-dwelling birds.

In conclusion, American woodcock differ from other studied shorebirds in having lower weight-specific SMR and better thermal insulation under conditions of low convection. These differences may be related to the more sheltered habitats and shorter migration typical of American woodcock. Although metabolic measurements on other species of upland shorebirds are generally lacking, SMR of one European woodcock (*Scolopax rusticola*) measured by Gavrilov and Dol'nik (Kendiegh et al. 1977) was 26% below the rate predicted by the equation of Kersten and Pierisma (1987), a value similar to the 22% differential reported here for American woodcock (Table 2.1). Like its North American congener, the European woodcock inhabits forested habitats and migrates relatively short distances (Sheldon 1967). Whether this pattern of lower SMR holds for other species of upland shorebirds is unknown. Additional work with upland shorebirds and species exhibiting short-distance migration is needed to elucidate the influence of habitat use and migration on metabolism within the Charadriiformes and within birds in general.

LITERATURE CITED

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

Bortner, J. B. 1990. American woodcock harvest and population status, 1990. U.S. Fish and Wildl. Serv., Washington, D.C. 12pp.

Buttemer, W. A., A. M. Hayworth, W. W. Weathers, and K. A. Nagy. 1986. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. Physiol. Zool. 59:131-149.

Castro, G. 1987. High basal metabolic rate in sanderlings (Calidris alba). Wilson Bull. 99:267-268.

Fedak, M. A., B. Pinshow, and K. Schmidt-Nielsen. 1974. Energy cost of bipedal running. Am. J. Physiol. 227:1038-1044.

Goldstein, D. L., and K. A. Nagy. 1985. Resource utilization by desert quail: time and energy, food and water. Ecology 66:378-387.

Kendeigh, S. C., V. R. Dol'nik, and V. M. Gavrilov. 1977. Avian energetics. Pages 127-204 in J. Pinowski and S. C. Kendeigh, eds. Granivorous birds in ecosystems. Cambridge Univ. Press.

Kersten, M., and T. Piersma. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. Ardea 75:175-187.

Lasiewski, R. C., and W. R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69:13-23.

Mathiu, P. M., O. W. Johnson, and P. M. Johnson. 1989. Basal metabolic rate of Pacific Golden-Plovers. Wilson Bull. 101:652-654.

Pohl, H. 1969. Some factors influencing the metabolic response to cold in birds. Fed. Proc. 28:1059-1064.

Rabe, D. L., H. H. Prince, and E. D. Goodman. 1983. The effect of weather on bioenergetics of breeding American woodcock. J. Wildl. Manage. 47:762-771.

Sheldon, W. G. 1967. The book of the American woodcock. Univ. Massachusetts Press, Amherst. 227pp.

Vander Haegen, W. M., W. B. Krohn, and R. B. Owen, Jr. In press a. Care, behavior, and growth of captive American woodcock. Proc. 8th Woodcock Symp.

Vander Haegen, W. M., R. B. Owen, Jr., and W. B. Krohn. In press b. Effects of weather on earthworm availability and spring food habits of American woodcock. Proc. 8th Woodcock Symp.

Weathers, W. W., W. A. Buttermer, A. M. Hayworth, and K. A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. Auk 101:459-472.

Withers, P. C. 1977. Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. J. Appl. Physiol. 42:120-123.

Wooley, J. B., and R. B. Owen, Jr. 1978. Energy costs of activity and daily energy expenditure in the black duck. J. Wildl. Manage. 42:739-745.

CHAPTER 2

ACTIVITY BUDGETS OF FEMALE AMERICAN WOODCOCK DURING THE BREEDING SEASON

The pattern of activity exhibited by an animal is important in determining its daily energy expenditure and, hence, the energy available for reproduction. Basal metabolic and thermoregulatory costs are largely beyond the control of the individual, but the degree of physical activity and its apportionment throughout the day and over the breeding season depend on the organism's strategy for foraging, courtship, and rearing of young. Time budget analyses based on visual observations have been conducted on numerous species (e.g., Ettinger and King 1980, Biedenweg 1983, Masman et al. 1988), but there have been few attempts at quantifying the activity of less visible birds.

The American woodcock (Scolopax minor) is an upland shorebird that breeds in the forested regions of eastern North America (Sheldon 1967). Its secretive nature in densely-vegetated habitats make it an impractical subject for visual time-budget analysis, yet its unique lifestyle for a shorebird and its declining population status (Bortner 1990) make investigations into its energetics of potential importance. This study examined the activity budget of female American woodcock, from their arrival on the breeding grounds in Maine through the fledging of young, and examined the influence of weather on activity of brood-rearing females and time available for feeding by chicks.

STUDY AREA AND METHODS

The study was conducted on the 6,580 ha Baring unit of Moosehorn National Wildlife Refuge, Washington County, Maine (45° 5' N, 67° 15' W). The refuge is located in the spruce-fir (Picea-Abies) forest type. Farm abandonment, wildfire, and clearcutting during the early 1900's produced stands of birch (Betula spp.), red maple (Acer rubrum), and aspen (Populus spp.), while alder (Alnus rugosa) occurs on the wetter sites (Dwyer et al. 1988). Extensive patch-type clearcutting for woodcock management has taken place on the Baring Unit since 1976 (Derleth and Sepik 1990). Regional mean air temperatures for April, May, and June are 5, 11.4, and 16.7 °C, respectively. Mean rainfall amounts for the region for the same months are 9.5, 9.2, and 8.3 cm, respectively (Dept. Commerce 1990).

Activity data were obtained from woodcock captured and radio-tagged on the refuge from March-May, 1987-89. Birds were captured in mist nets and ground traps and were equipped with back-mounted radios (ca. 3.5 g) attached with cattle-tag cement and a single-loop wire harness (McAuley et al. in press). Diel activity data were obtained during 4 distinct periods of the reproductive cycle: Pre-nesting (arrival to initiation of laying), Laying (the 4 days preceding continuous incubation), Incubation, and Brood-rearing (hatching to fledging).

Activity data were recorded by remote-monitoring units comprised of a 4-element yagi directional antenna (or an omni-directional whip antenna), a Telonics TR-2 receiver, a Telonics TDP-2 digital signal processor, and a Rustrak chart recorder operating at a chart speed of 15 cm/hr. Each unit recorded signal amplitude and signal presence or absence. Monitoring units were placed in or immediately adjacent to the cover being used by the target bird and had an effective range of about 200 m. Other than during crepuscular periods, birds generally restricted their activities to small areas for several consecutive days and were monitored until they switched locations.

I interpreted the activity data recorded on Rustrak charts and entered them on computer, assigning the signals to 1 of 4 classes: active, inactive, not present, or uninterpretable (those that could not be assigned to another class due to signal interference). Bouts of activity or inactivity were defined as continuous periods of the appropriate signal uninterrupted by contrasting signals $\geq$ 2.5 minutes in duration (0.65 cm on the recording tape--the minimum time period used in data interpretation). Computer programs written in BASIC were used to derive hourly, daily, and seasonal values for percent of the diel period spend active, mean length of activity bouts, and to plot daily activity for each bird. Data from days with >5% of the signal assigned to "not present" or "uninterpretable" categories were not used in calculation of means.

Accuracy of the monitoring system for detecting changes in behavior was determined in a double-blind test using 2 radio-tagged, captive birds housed in a 3 x 3 m pen. During each test an observer recorded the behavior of a radio-tagged woodcock in the pen, while 2 monitoring units (1 each with a yagi and whip antenna) recorded signal amplitude from distances typical of those encountered in the field (50-150 m). Percent activity for each 8-hour test was then calculated from the observers notes and (independently) from the monitor tapes, and compared. Observed behaviors defined as activity were limited to walking, running, foraging, and flying.

General weather data for the refuge were collected during 1988 and 1989 from a monitoring station located in a 20 ha field. Temperature data were obtained from 3 shielded thermocouple probes 10 cm above the ground. Wind speed and shortwave solar radiation were measured by a cup anemometer and a pyranometer positioned at a height of 1 m. Rainfall was measured with a tipping-bucket rain gauge. All probes were sampled every minute and averaged every 15 minutes by a Campbell Scientific CR21X micrologger (totalled for the rain gauge). Comparisons of brood-female activity with weather variables were limited to daylight hours (0400 - 2100 EST) because activity was negligible during darkness.

RESULTS

System Accuracy

In each of 4 tests, activity of the captive woodcock as interpreted from the monitor tapes was representative of the values recorded by the observer (Table 2.1). There was no consistent bias in the direction of error, and antenna type did

Table 2.1. Results of accuracy test on monitoring systems comparing activity of radio-tagged woodcock as determined by visual observer and by automatic recording systems using a directional (yagi) or omnidirectional (omni) antenna. Duration of each test was 8 hours.

	Percent active[a]			
Source	Test 1	Test 2	Test 3	Test4
Observed	58	52	28	7
Yagi	58	53	23	8
Omni	-[b]	54	29	11

[a] Activity defined as walking, running, foraging, or flying

[b] Omni antenna not used in test 1.

not affect results. Although the conditions where actual data were collected in the field were more variable than those in the tests, I believe the accuracy achieved in the tests to be representative of that attained in the field. Activity implies that the bird was walking, running, foraging, or flying: low effort activities such as preening were generally recorded as inactivity by the monitoring units.

Activity Patterns

Results of the activity analyses were based on 5,064 hours of time-budget data collected on 35 birds by radio-telemetry. Pre-nesting females were active 34-57% of the diel period during 1988 and 1989 (Table 2.2; no females were captured prior to nesting in 1987). However, the pattern of activity over the 24 hour period differed markedly between years. In 1988, woodcock were active throughout the day and night with minor peaks at mid-day and during crepuscular periods (Fig. 2.1A). In contrast, activity during 1989 was skewed toward mid to late afternoon hours, decreased markedly after dark and occurred only at low levels during the early morning hours (Fig. 2.1B). Activity levels during afternoon hours in 1989 regularly exceeded 60%--levels rarely displayed by Pre-nesting females during 1988. Mean duration of activity bouts in 1989 was significantly higher (ANOVA, $F = 18.6$, $df = 1,5$, $\underline{P} = 0.019$) than in 1988 (Table 2.2).

During Laying, females were active 27-39% of the diel period (Table 2.2) with no difference between years (ANOVA, $F = 0.032$, $df = 1,6$, $\underline{P} = 0.864$).

Table 2.2. Length of activity periods (minutes) and percent of the diel period spent active for female American woodcock during each phase of the breeding season, Moosehorn National Wildlife Refuge, Maine, 1987-1989.

		Period Length		Percent Active			
Period	Year	$\bar{x}$	SE	$\bar{x}$	SE	N[a]	n[b]
Pre-nest[c]	1988	12.5	1.50	37.0	2.00	2	6
	1989	23.2	2.24	40.8	4.22	5	21
	All years	20.1	2.53	39.7	3.03	7	27
Laying	1987	12.0	--	34.0	--	1	1
	1988	13.0	1.47	32.3	1.31	4	10
	1989	19.3	2.46	32.8	2.46	4	11
	All years	16.1	1.78	32.5	1.30	9	22
Incubation	1987	22.0	3.49	7.8	0.75	4	16
	1988	20.2	1.33	8.0	1.65	6	45
	1989	22.6	2.14	8.6	1.25	7	29
	All years	21.6	1.27	8.2	0.78	17	90
Brood	1987	15.4	1.27	35.3	1.52	3	7
(≤15 days)	1988	12.7	0.69	32.8	1.32	6	28
	1989	11.0	1.78	27.0	4.30	1	4
	All years	13.0	0.60	32.7	1.10	10	39
Brood	1987	22.0	1.06	43.9	1.67	4	10
(>15 days)	1988	17.8	0.56	43.5	1.39	4	22
	All years	19.3	0.62	44.0	1.01	8	32

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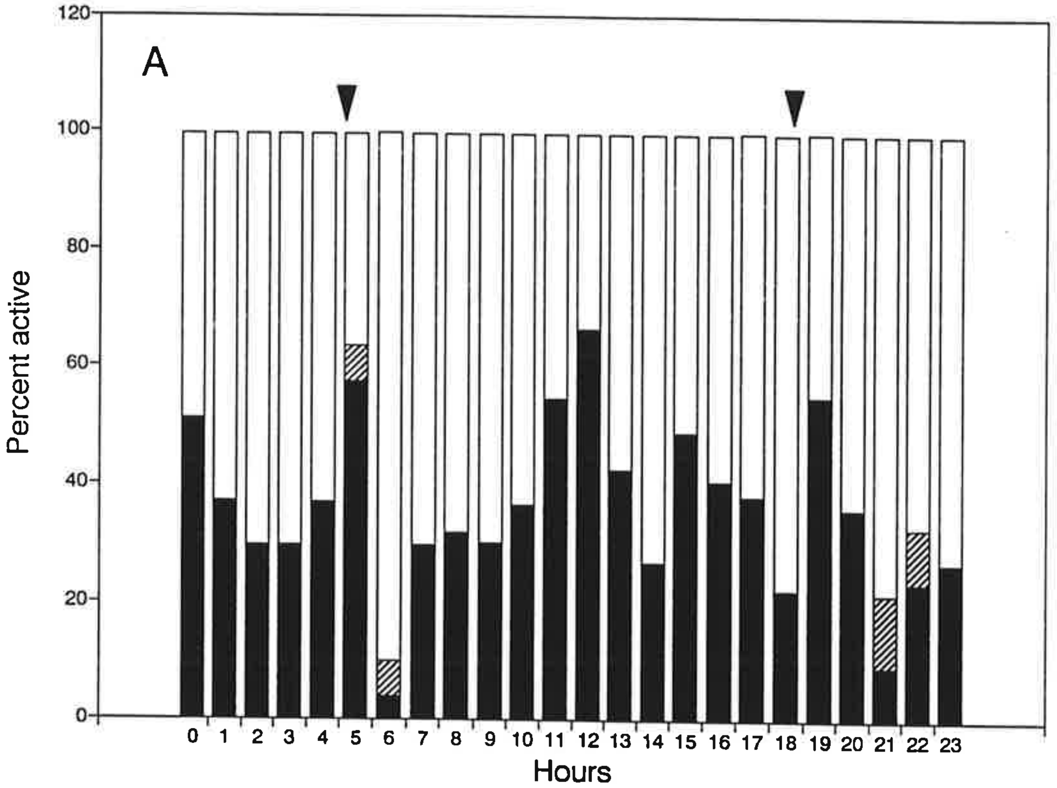
[a] Number of birds.
[b] Number of days.
[c] No females monitored prior to nesting in 1987.

Figure 2.1. Diel activity of female American woodcock during the Pre-laying period in (A) 1988 (2 birds, 6 days total) and (B) 1989 (5 birds, 21 days total). Black bars represent mean percentage of each hour spent active; hatched bars indicate mean percentage of uninterpretable data. Arrows above bars indicate approximate sunrise and sunset (EST).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Percent active
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Hours
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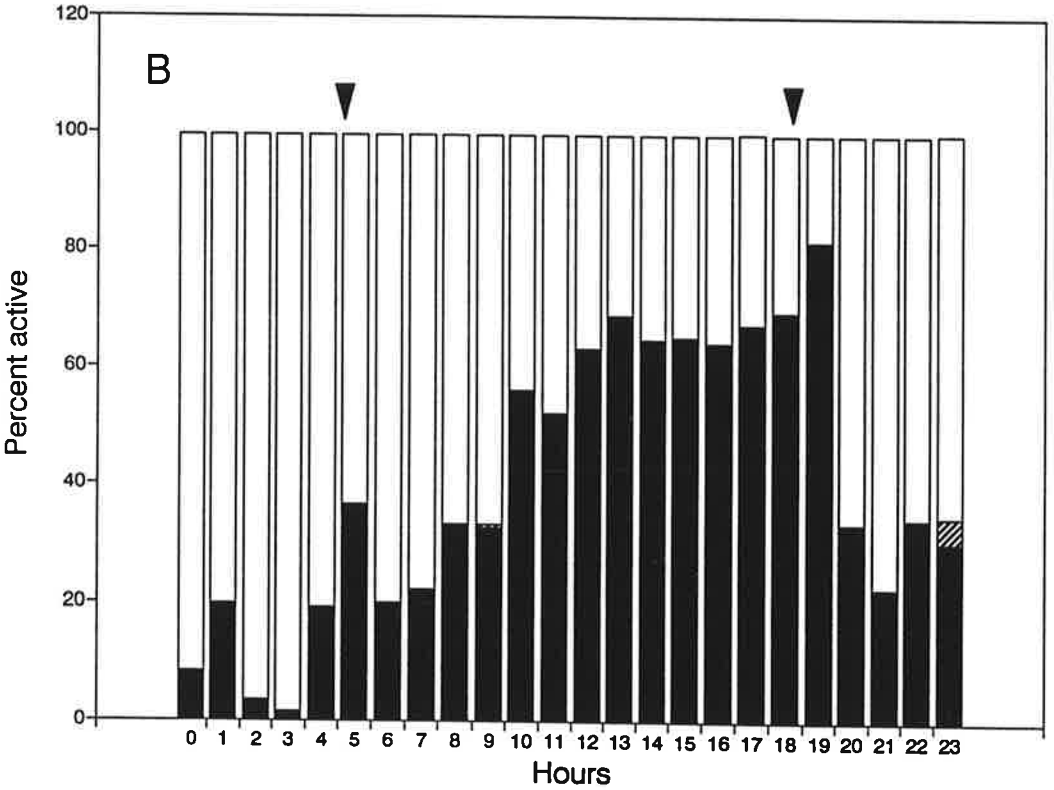
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Percent active
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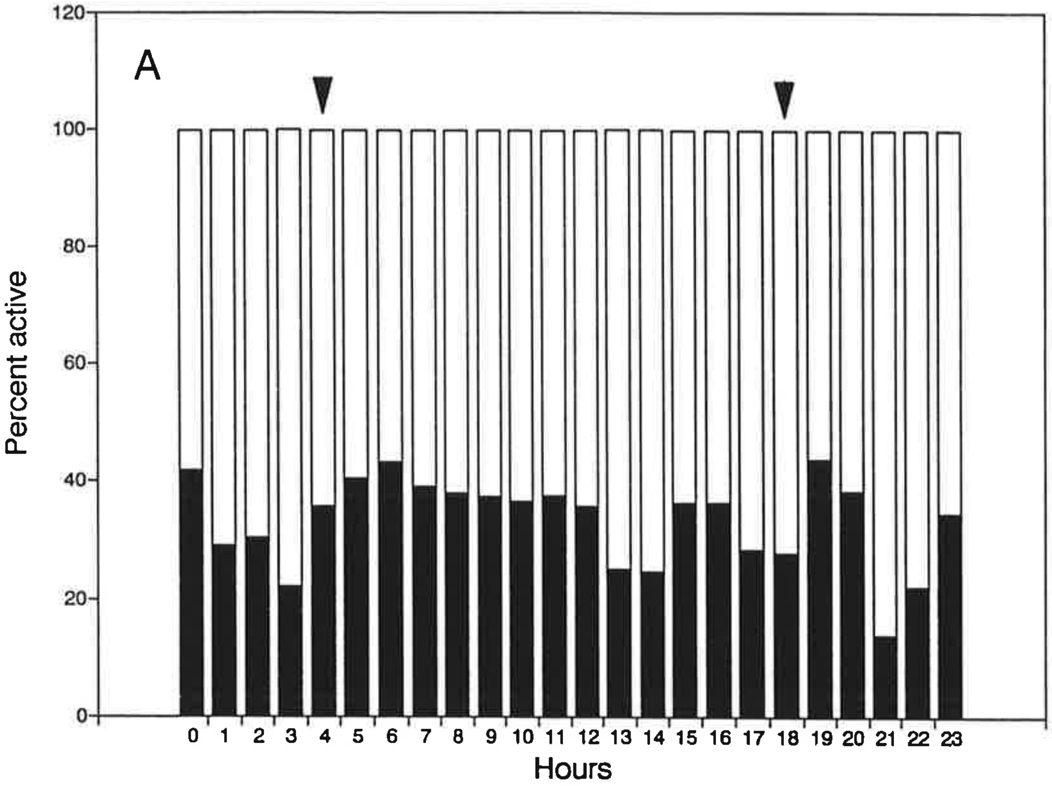
Pattern between years was similar, with females active throughout the day and night at somewhat constant levels (Fig. 2.2A). Mean length of activity bouts was higher in 1989 than in 1988, although the difference was not significant (ANOVA, F = 4.74, df = 1,6, P = 0.072)(Table 2.2). Extended periods of inactivity were apparent in some females, suggesting that they spent time incubating the eggs prior to completion of the clutch (Fig. 2.3).

Activity level (ANOVA, F = 0.091, df = 2,14, P = 0.914) and length of activity bouts (F = 0.351, df = 2,14, P = 0.710) of incubating females were very consistent among years (Table 2.2). Females were active 5-16% of the diel period, mainly during daylight (Fig. 2.2B). Females left the nest a mean of 4.8 times/day, for periods averaging 21.6 minutes. Five females were followed on a total of 14 crepuscular incubation recesses, and from their location and activity levels were believed to be feeding. On 3 occasions I was able to observe females during their crepuscular activities away from the nest. In each case the bird foraged during the entire period, probing more vigorously than birds observed foraging at other times during the breeding season. Activity peaked during the crepuscular periods and also occurred at somewhat unpredictable times throughout the day (Fig. 2.3).

During Brood-rearing, females exhibited distinctive activity patterns with activity limited to daylight hours (Fig. 2.3). Brood females increased their diel activity as the age of their chicks increased (Fig. 2.4A). Similarly, length of activity bouts increased with brood age (Fig. 2.4B). Slopes of the regression lines for

Figure 2.2. Diel activity of female American woodcock during the (A) Laying period (8 birds, 21 days total) and (B) Incubation period (17 birds, 90 days total), 1987-89. Black bars represent mean percentage of each hour spent active. Arrows above bars indicate approximate sunrise and sunset (EST).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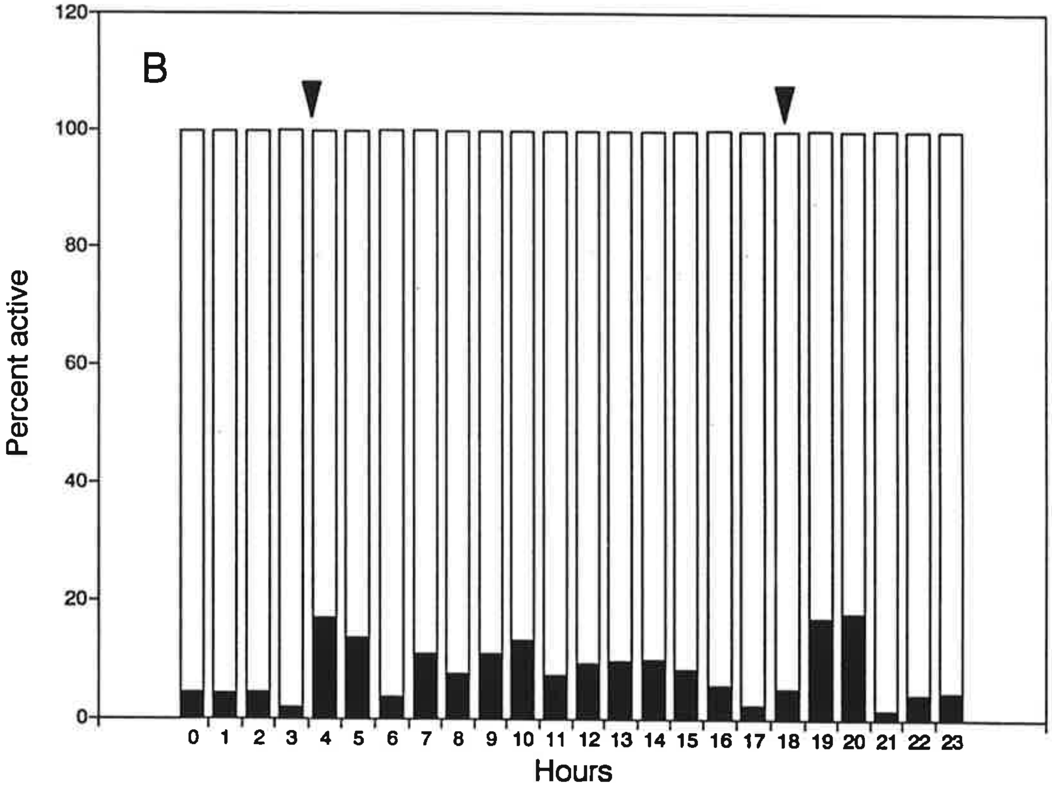
Hours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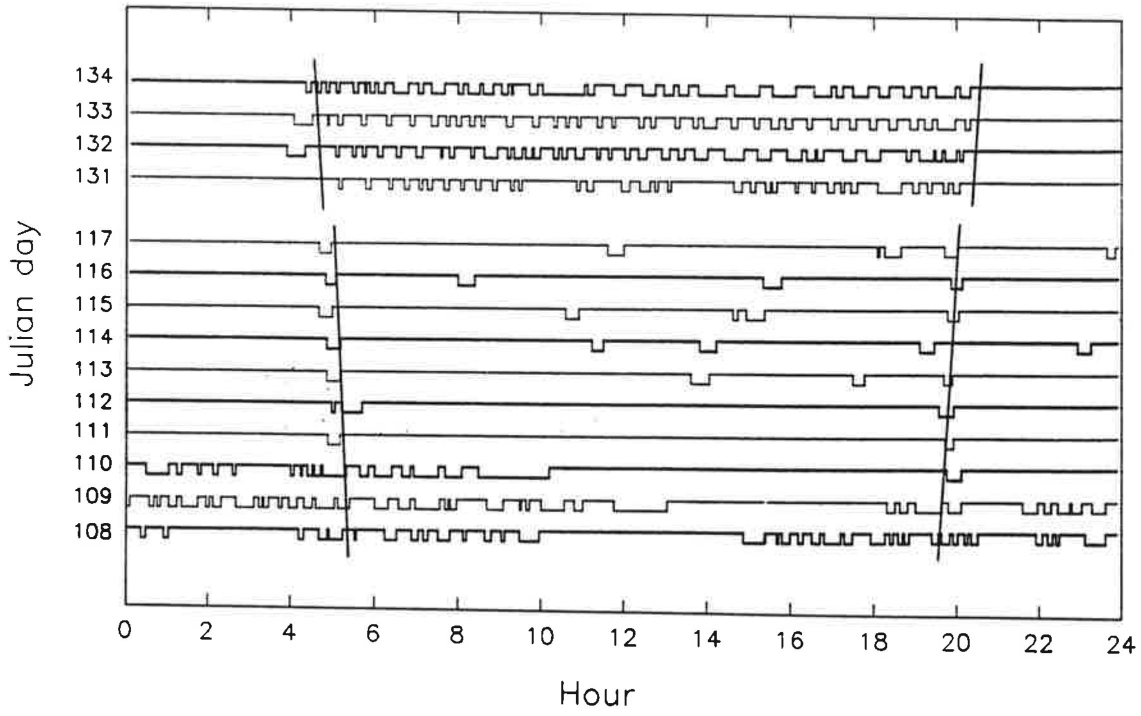
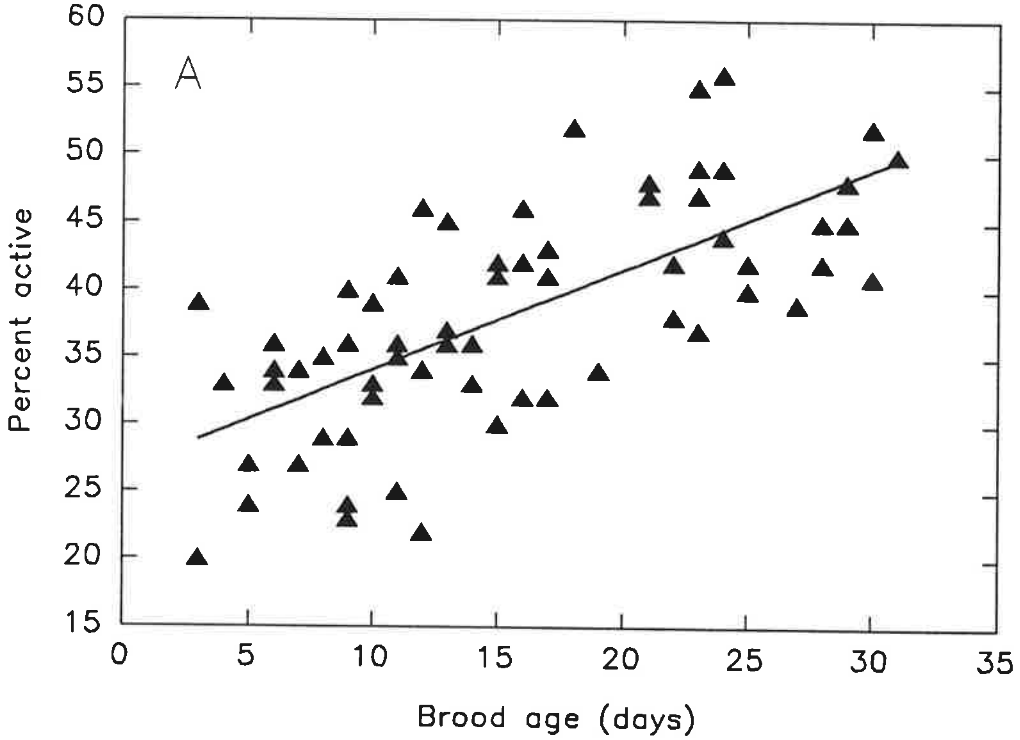


Figure 2.3. Diel activity of a female American woodcock during Laying (Julian days 108-110), Incubation (Julian days 111-117), and Brood-rearing (Julian days 131-134, chicks age 3-6 days). Julian days 131 and 133 were classified as "wet", with ≥5 cm of rainfall during the daylight period. Lines on the upper level for each day indicate inactivity; lines on the lower level indicate activity. Vertical lines represent sunrise and sunset (EST).

Figure 2.4. Mean percent of the diel period spent active (A) and mean length of activity periods (B) for female American woodcock (n = 14) as a function of age of their broods. Regression equations for A: $Y = 26.643 + 0.742X$, $r^2 = 0.49$, $n = 67$, $F = 63.14$, $\underline{P} < 0.001$, and B: $Y = 9.502 + 0.422X$, $r^2 = 0.47$, $n = 67$, $F = 56.55$, $\underline{P} < 0.001$.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Percent active
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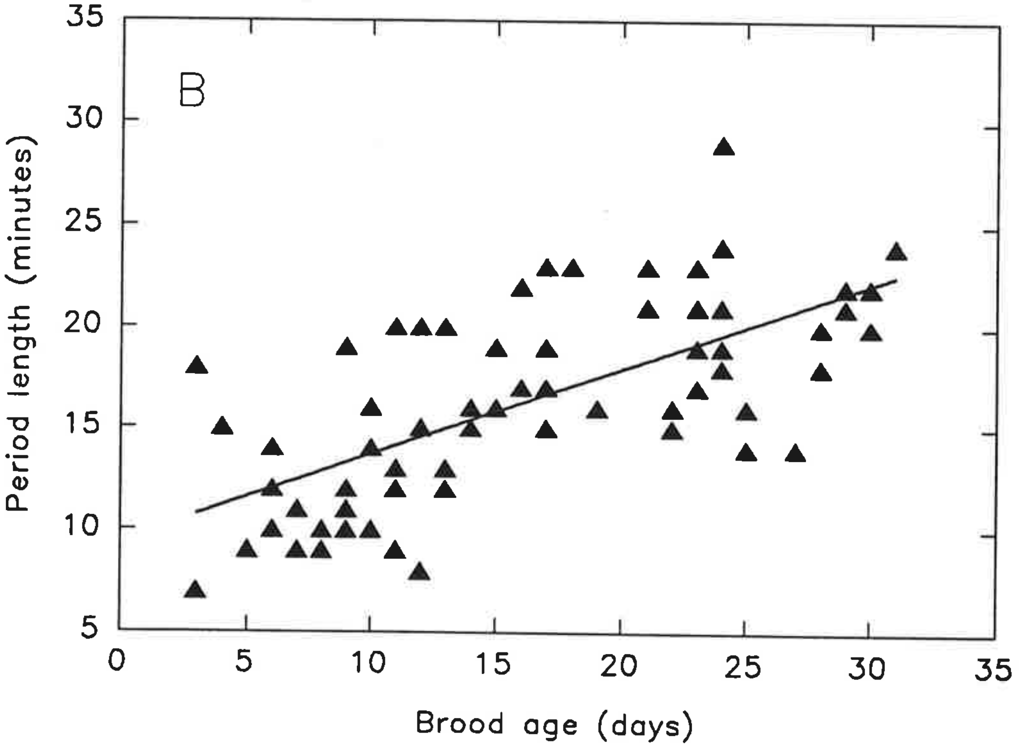
35
Brood age (days)


B
Period length (minutes)
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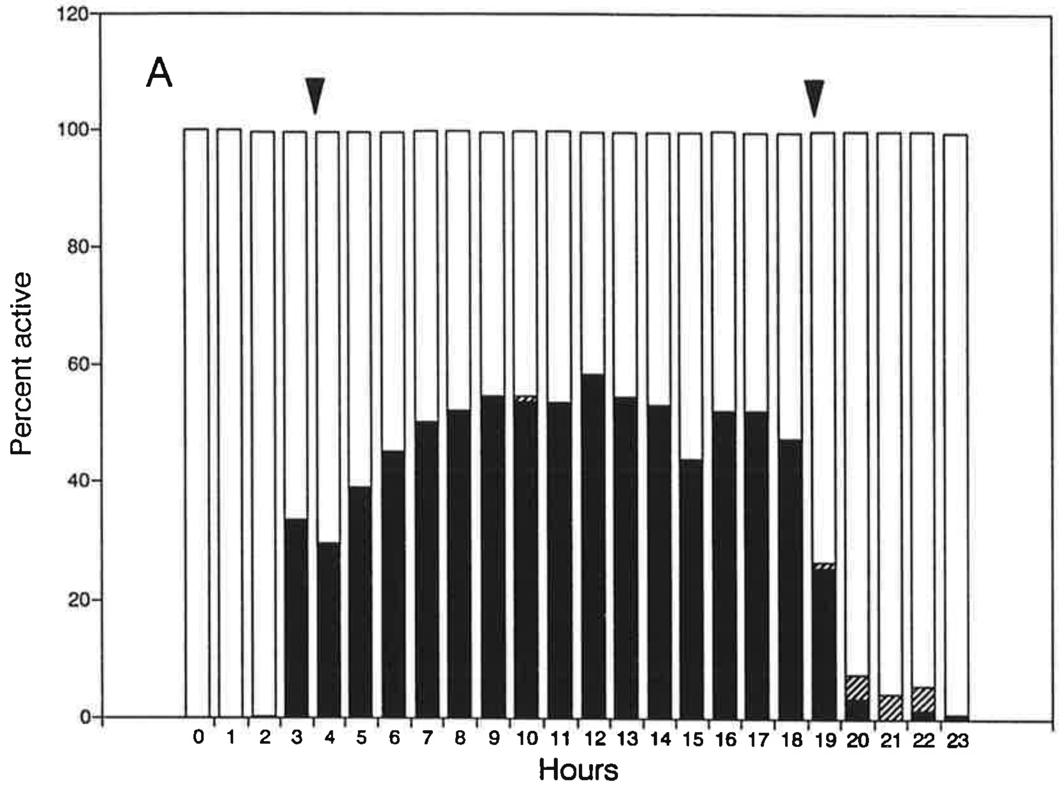
35
Brood age (days)

percent active (ANCOVA, $F = 3.59$, $df = 1$, $\underline{P} = 0.063$) and period length ($F = 0.22$, $df = 1$, $\underline{P} = 0.640$) did not differ between 1987 and 1988, and, therefor, data for both years were combined. Females with young chicks ($\leq$15 days) were active 20-46% of the diel period, with mean length of activity bouts ranging from 7-20 minutes; females with older chicks ($>$15 days) were active 32-56% of the time, with bout lengths averaging 14-29 minutes (Table 2.2). Percent of the diel period spent active did not differ between years for females with broods $\leq$ 15 days old (ANOVA, $F = 0.475$, $df = 1,7$, $\underline{P} = 0.510$) or for females with older broods ($F = 0.423$, $df = 1,6$, $\underline{P} = 0.540$). Mean length of activity bouts was similar between years for females with broods $\leq$ 15 days old ($F = 2.772$, $df = 1,7$, $\underline{P} = 0.134$), and for females with older broods ($F = 3.545$, $df = 1,6$, $\underline{P} = 0.109$).

Diel activity patterns of brood females changed with growth of the chicks. Females with young chicks ($\leq$ 15 days) were active almost exclusively during daylight, with lowest activity levels during the crepuscular periods and peak activity occurring during the midday hours (Fig. 2.5A). Females with broods $>$15 days old also were active primarily during daylight, but activity peaked during crepuscular periods and declined gradually toward midday (Fig. 2.5B). Brood females began exhibiting nocturnal activity only after chicks were 23 days old, but the behavior was not consistent. Two females began substantial nocturnal activity when their chicks reached age 23 days; 3 females, monitored through days 25, 30, and 31, remained inactive at night.

Figure 2.5. Diel activity of female American woodcock during the Brood-rearing period with broods (A) ≤15 days old (10 birds, 39 days total) and (B) >15 days old (8 birds, 32 days total), 1987-88. Black bars represent mean percentage of each hour spent active; hatched bars indicate mean percentage of uninterpretable data. Arrows above bars indicate approximate sunrise and sunset (EST).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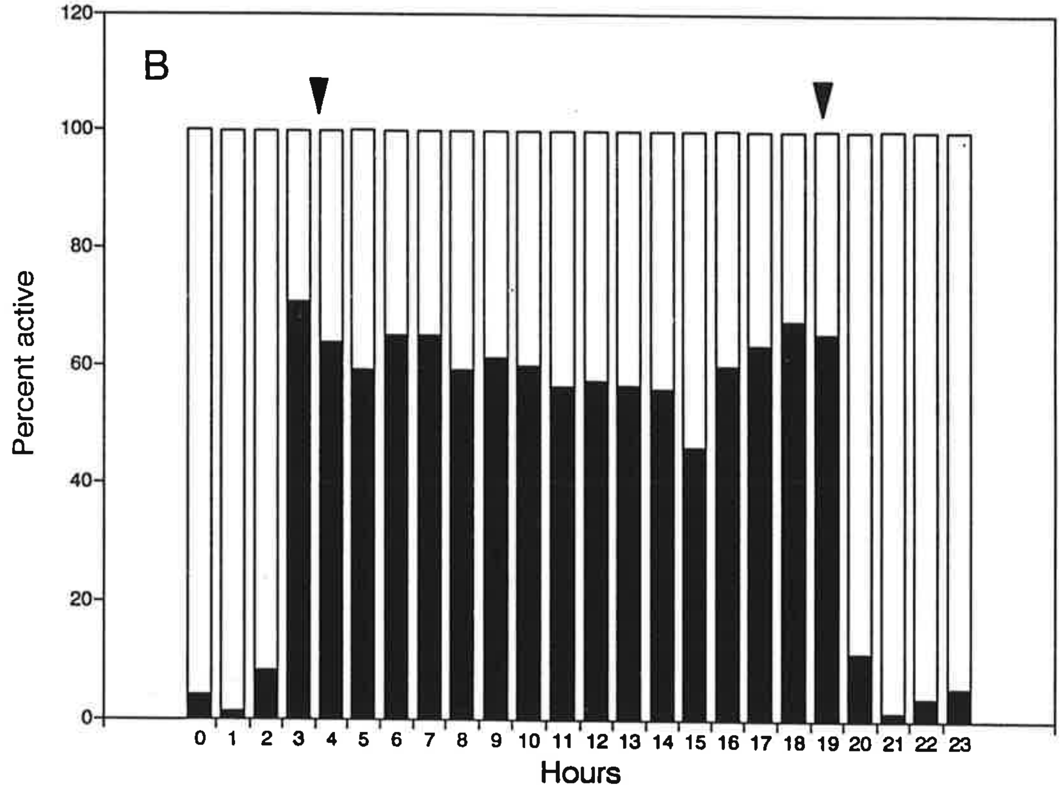
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Hours

Two females lost broods while being monitored; 1 lost a 14-day old brood on 12 May 1988 and immediately assumed a pattern of 24-hour activity similar to that of pre-nesting females, whereas a second female lost a 6-day old brood on 10 June 1989 and did not commence nocturnal activity in the ensuing 4 days.

Effects of Weather

Effect of rainfall on activity of brood females was examined by comparing activity levels on "wet" ($\geq$0.5 cm rainfall during daylight hours) vs "dry" (<0.5 cm) days. Availability of matching rainfall and activity data limited the analysis to broods 3-9 days old. Activity of brood females on 5 "wet" days was 34% lower than that recorded on 13 "dry" days (Fig. 2.6) (linear regression, ANOVA, $F = 19.42$, $df = 1$, $\underline{P} = 0.001$). Multiple regression analyses revealed that mean air temperature and age of the brood were not confounding factors in either the "dry" (ANOVA, $F = 0.317$, $df = 3$, $\underline{P} = 0.813$) or "wet" ($F = 0.538$, $df = 3$, $\underline{P} = 0.734$) data sets. Activity data collected on the 5 "wet" days were not used in subsequent analyses of activity/temperature relationships.

There was a positive relationship between ambient air temperature and activity rate of females with young broods (Table 2.3). Slopes of the relationship between hourly air temperature and hourly activity were highest for females with very young broods, and declined to zero or negative values after age 20 days (Fig. 2.7). Wind speed and solar radiation may also have influenced activity of brood females, but were found to be intercorrelated with air temperature. In a

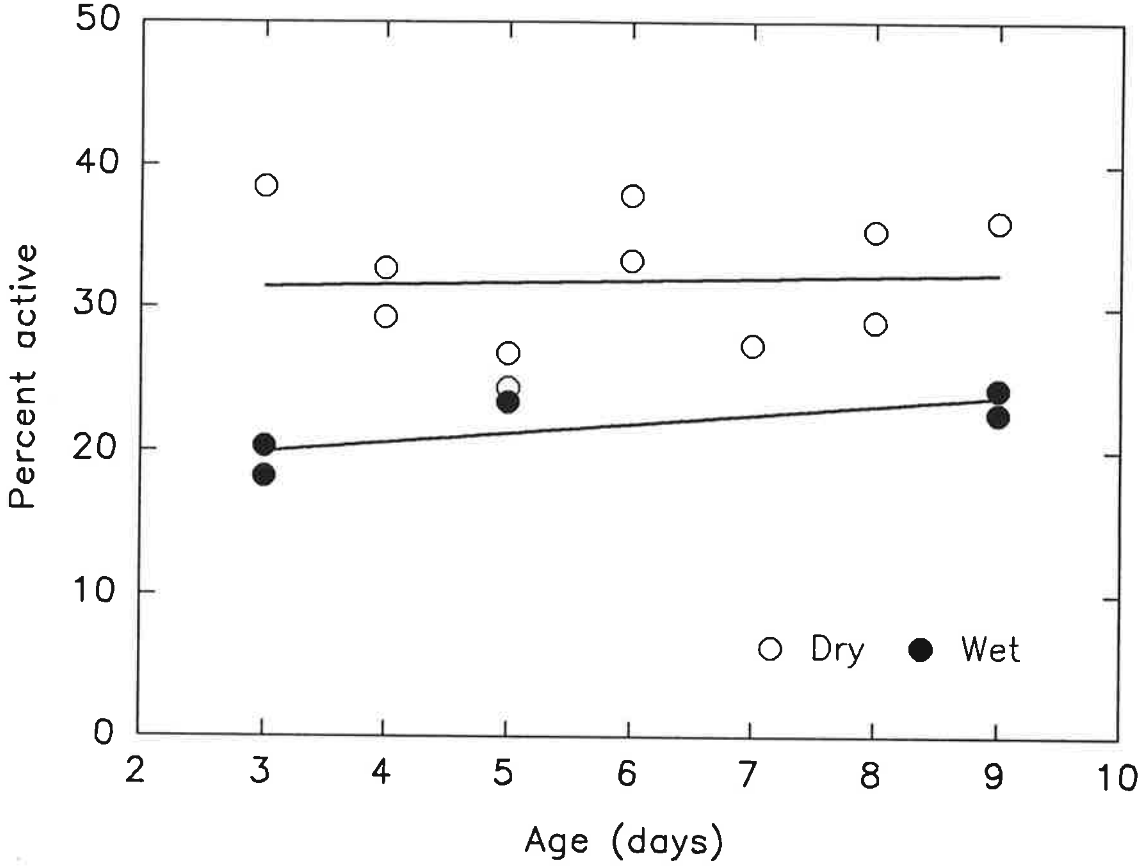

Figure 2.6. Diel activity of female American woodcock with broods of varing ages on days with ≥5 cm rainfall (open symbols, n = 11 days) and days with <5 cm rainfall (closed symbols, n = 5 days).

Table 2.3. Regression statistics for analysis of age-specific effects of air temperature on activity of American woodcock females with broods of different ages.

Age (days)	Constant	Slope	SE	r^2	P	n^a
3	0.088	0.028	0.006	0.539	0.001	1
4	-0.011	0.024	0.004	0.436	0.001	2
5	0.256	0.012	0.006	0.070	0.060	2
6	0.157	0.019	0.004	0.320	0.001	2
7	0.280	0.005	0.004	0.004	0.317	1
8	0.215	0.011	0.005	0.103	0.028	2
9	0.126	0.020	0.006	0.370	0.003	1
10	0.284	0.009	0.005	0.069	0.061	2
11	0.194	0.009	0.004	0.093	0.035	2
12	0.322	0.004	0.006	0.000	0.458	1
13	0.196	0.016	0.005	0.215	0.002	2
14	0.278	0.009	0.006	0.035	0.136	2
15	0.343	0.009	0.004	0.102	0.029	2
16	0.336	0.007	0.005	0.025	0.171	2
17	0.429	0.004	0.005	0.000	0.354	2
21	0.572	0.001	0.006	0.000	0.821	1
22	0.563	-0.003	0.004	0.000	0.421	2
23	0.565	0.002	0.004	0.000	0.657	3
24	0.605	-0.003	0.004	0.000	0.488	3
25	0.480	0.003	0.009	0.000	0.766	1
27	0.645	-0.007	0.006	0.023	0.248	1
28	0.718	-0.007	0.008	0.000	0.431	1
29	0.671	-0.005	0.008	0.000	0.529	1

[a] Number of brood-rearing females.

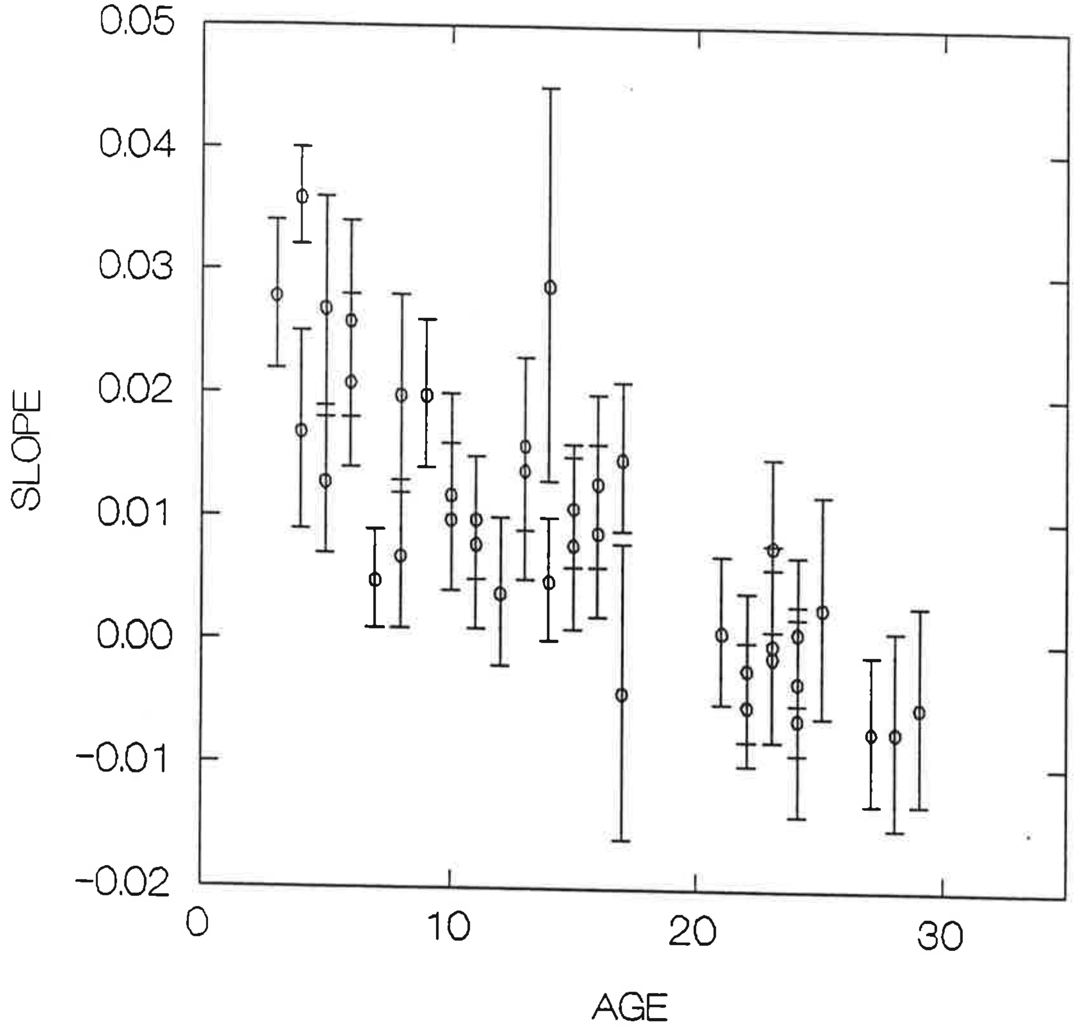

Figure 2.7. Slope of the regression of percent hourly activity on hourly mean air temperature for female American woodcock as a function of age of their brood (n = 39 days), Moosehorn National Wildlife Refuge, Maine, 1987-88. Symbol and error bar represent slope ± 1 SE.

principle component analyses of air temperature, wind speed, and solar radiation, the first component accounted for 75% of the variation. I selected air temperature as the comparison variable because it has a demonstrated influence on metabolic rate (Calder and King 1974).

DISCUSSION

The extensive activity of female woodcock during Pre-nesting and Laying likely was related to the acquisition of nutrients for reproduction and replacement of energy reserves used during migration. The majority of the time reported here as activity was probably spent foraging, as female woodcock do not establish territories or construct elaborate nests, and probably limit courtship activities to crepuscular periods (Sheldon 1967). By feeding throughout the night, woodcock gained needed energy reserves rather than roosting and incurring a negative energy balance. By feeding during the coldest part of the diel period they might also have taken advantage of heat liberated during the digestion process (Calder and King 1974). The pattern of afternoon activity displayed by Pre-nesting hens in 1989 was likely a response to reduced food availability. Low snow accumulations over the preceding winter resulted in soil frost persisting late into spring, with reduced availability of earthworms throughout the normal Pre-nesting period (Vander Haegen et al. in press a). Foraging conditions were likely best during the afternoon and evening hours, after solar radiation had warmed the soil and microclimate near the ground. By becoming most active during these times, the woodcock were apparently concentrating their foraging efforts when conditions were most suitable.

High levels of activity (>60%) during the afternoon hours in 1989 resulted in daily activity levels similar to those of 1988; however, activity bouts in 1989 were twice as long as those in 1988, suggesting that birds were foraging longer to obtain sufficient food. Low availability of earthworms and increased reliance on smaller prey in 1989 (Vander Haegen et al. in press a) likely increased the bird's foraging time. Foraging during the early morning hours was probably energetically inefficient, and was avoided in favor of roosting. When the females began laying, the activity pattern was again similar to that in 1988, with constant activity over the diel period. The Laying period in 1989 was 3-4 weeks later than usual (Longcore, Sepik, and McAuley, unpubl. data), and soil conditions and earthworm availability were comparable to those occurring during Laying in 1988 (Vander Haegen et al. in press a).

Activity patterns during Incubation were characterized by long periods of inactivity on the nest and short recesses devoted to feeding. As the sole incubator, the female incurs a negative energy balance through the incubation period, losing most of her fat reserves by the time the eggs hatch (Chapter 3). Females use these recesses to recoup losses, foraging intensively. Females collected on the nest after a recess had usually eaten earthworms, but the quantities obtained were not sufficient to maintain energy balance (Chapter 3). Spotted sandpipers (Actitus macularia) also feed more intensively while on incubation recesses, increasing their peck rates over those recorded during preincubation (Maxon and Oring 1980).

Activity patterns of brood females appeared to be governed by the thermoregulatory requirements of the chicks. Newly hatched chicks of most species are not homeothermic and develop this ability at varying ages (Ricklefs 1989). Low activity observed in female woodcock with very young chicks was likely due to the frequent brooding required at typical spring temperatures. The short activity bouts observed at this age suggest a pattern of intense feeding and frequent brooding, especially during the cool morning period (see Fig. 2.3). This pattern has been observed in young broods of other precocial species (Erikstak and Spidso 1982) and limits the time available for foraging. Beintema and Visser (1989) recorded a maximum of 10-15% non-brooding time for 1-3 day old chicks of 3 Charadriiform species at air temperatures <5 ^{o}C. Non-brooding times of 20-25% were reported for chicks of ringed plovers (Charadrius hiaticula) (Pienkowski 1984) and semi-palmated sandpipers (Calidris pusilla) (Ashkenazie and Safriel 1979) during the first week post-hatching. These values were similar to those of woodcock, where diel activity averaged 30% for females with broods 3-7 days old. Inactivity throughout the nighttime hours was probably in response to low air temperatures and the need for brooding. Nocturnal activity by hens did not occur until chicks approached fledging age and were likely homeothermic, or until the brood was lost.

When chicks attain thermal independence they are no longer restricted in foraging time by the frequent need to be brooded. Beintema and Visser (1989) identified threshold temperatures above which chicks did not require brooding for 3 Charadriiform species, and further observed that these temperatures decreased with age of the chicks. For the redshank (Tringa totanus), whose chicks are most similar in weight to an American woodcock's, this threshold temperature decreased from 20 °C at 1 day of age to 10 °C at 9 days of age. The black-tailed godwit (Limosa limosa) and redshank attained thermal independence at 40-50%, and the lapwing (Vanellus vanellus) at 70%, of fledging age. Similarly, Ashkenazie and Safriel (1979) observed brooding of semi-palmated sandpipers to occur up to 65% of fledging age, whereas Pienkowski (1984) reported a value of 75% for ringed plovers. Adult weights of these species varied from 26 to > 250 g, with no clear relationship between adult weight and age at thermal independence. Although cessation of brooding behavior in woodcock could not be determined definitively from telemetry data, the age-specific slopes of activity vs temperature suggest thermal independence occurs between 15 and 20 days of age (50-60% of fledging age). Beyond this age, regressions were not significant and slopes approached 0 or became negative (Table 2.3, Figure 2.7).

Dwyer et al. (1988) documented a negative relationship between rainfall during the brood period and production of woodcock chicks over a 4-year period in Maine. Wet plumage conducts heat more efficiently and increases the thermoregulatory requirements of birds (Lustick and Adams 1977). Beintema and

Visser (1989) observed longer brooding bouts and shorter foraging bouts on rainy days in 3 Charadriiforms; at air temperatures of 7-9 ^{o}C, this resulted in a 30-57% reduction in available foraging time. Similarly, Pienkowski (1984) reported reduced foraging by plover broods during rainy days. Similar effects have been reported among tetraonids. In Norway, willow grouse (Lagopus l. lagopus) chicks experienced a reduction in available foraging time during cool, wet weather (Erikstad and Spidso 1982). Moss (1986) observed an inverse relationship between productivity of Capercaillie (Tetrao urogallus) and number of days with rain during and immediately following hatching, whereas productivity of black grouse (Tetrao tetrix) on the same study area appeared unaffected.

If cool temperatures or precipitation necessitate increased brooding time, time available for foraging will decrease. Figure 2.8 represents the projected foraging time available to woodcock chicks from hatching to age 20 days over a range of mean ambient temperatures. This model was derived from the age-specific temperature/activity relationships illustrated in Figure 2.7. For very young chicks (age 1-2 days), the model suggests a decrease in foraging time of 50% with a drop in mean temperature from 10 to 5 ^{o}C. The projected loss in foraging time decreases with brood age. If the loss is carried through age 15 days the total loss of foraging time during this critical period would be 40%, and the addition of rain could increase the total loss to 74%. The chilling effect of rain may decrease with age, as has been observed in the black-tailed godwit (Beintema and Visser 1986).

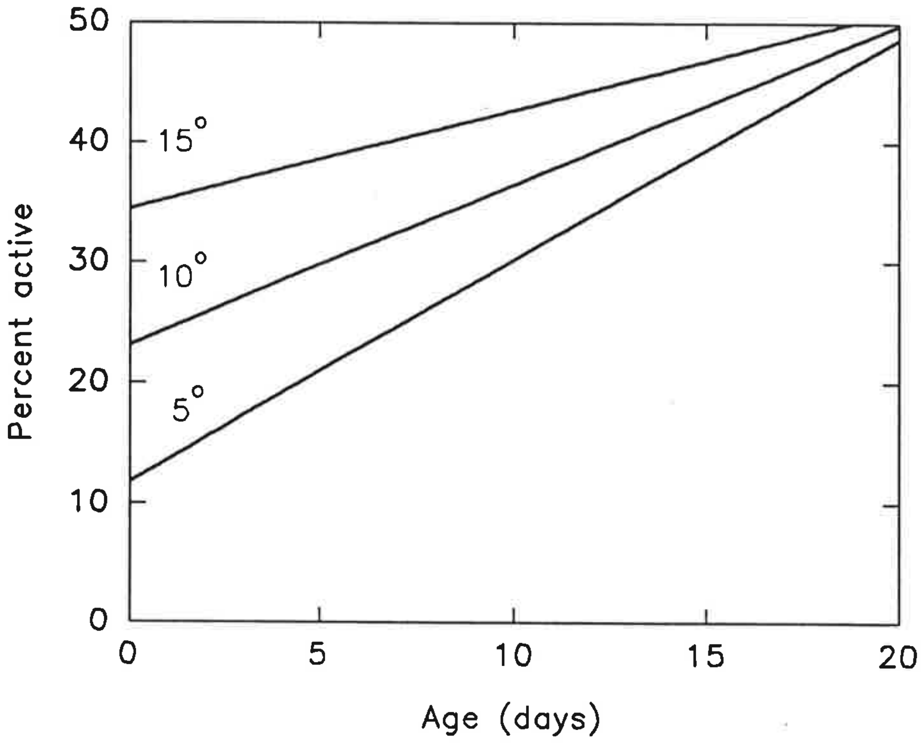

Figure 2.8. Predicted diel activity of American woodcock broods from hatching to age 20 days at different mean air temperatures. Lines were derived from activity/temperature relationships presented in Table 2.3.

Work with captive woodcock demonstrated that reduced intake rates can lead to reduced growth rates during early Brood-rearing (Vander Haegen et al. in press b). Beintema and Visser (1989) demonstrated a similar effect in black-tailed godwits and lapwings. Reduced growth rates could increase the flightless period of chicks, delaying fledging, molt, and migration and subjecting the chicks to increased predation and declining foraging opportunities at a time when energy stores are in great need. More detailed assessment of the effects of weather on chick growth and survival could be made by combining measurements of foraging rates and energy intake of growing chicks with the foraging times presented here.

SUMMARY

The activity patterns exhibited by breeding female woodcock indicate potential effects of weather on productivity. Pre-laying and Laying females foraged extensively throughout the diel period: when soil frost and cold temperatures limited availability of food, foraging was concentrated during the warmest hours of the day and nesting was delayed. Female woodcock with broods were inactive at night and both diel activity and length of activity periods increased with age of the chicks. Relationship between air temperature and activity of brood females indicates that woodcock chicks attain thermal independence between 15 and 20 days of age. Rain decreased the diel activity of females with young broods by 34%. Increased brooding times caused by low air temperatures or rain may adversely affect both females and chicks by reducing the time available for foraging.

LITERATURE CITED

Ashkenazie, S., and U. N. Safriel. 1979. Time-energy budget of the semipalmated sandpiper Calidris pusilla at Barrow, Alaska. Ecology 60:783-799.

Biedenweg, D. W. 1983. Time and energy budgets of the mockingbird (Mimus polyglottos) during the breeding season. Auk 100:149-160.

Beintema, A. J., and G. H. Visser. 1989. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77:181-192.

Bortner, J. B. 1990. American woodcock harvest and population status, 1990. U.S. Fish and Wildl. Serv., Washington, D.C. 12pp.

Calder, W. A., and J. R. King. 1974. Thermal and caloric relations in birds. Pages 259-413 in D. S. Farner and J. R. King, eds. Avian Biology, Vol. 4. 504pp.

Department of Commerce, 1990. Climatological Data, New England: Annual Summary. Vol. 102.

Derleth, E. L., and G. F. Sepik. 1990. Summer-fall survival of American woodcock in Maine. J. Wildl. Manage. 54:97-106.

Dwyer, T. J., G. F. Sepik, E. L. Derleth, and D. G. Mcauley. 1988. Demographic characteristics of a Maine woodcock population and effects of habitat management. U.S. Fish Wildl. Serv. Fish Wildl. Res. 4. 29pp.

Erikstad, K. E., and T. K. Spidso. 1982. The influence of weather on food intake, insect prey selection and feeding behaviour in willow grouse chicks in northern Norway. Ornis Scand. 13:176-182.

Ettinger, A. O., and J. R. King. 1980. Time and energy budgets of the willow flycatcher (Empidonax traillii) during the breeding season. Auk 97:533-546.

Lustick, S., and J. Adams. 1977. Seasonal variation in the effects of wetting on the energetics and survival of starlings (Sturnus vulgaris). Comp. Biochem. Physiol. 56:173-177.

Masman, D., S. Daan, and H. J. A. Beldhuis. 1988. Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. Ardea 76:64-81.

Maxon, S. J., and L. W. Oring. 1980. Breeding season time and energy budgets of the polyandrous spotted sandpiper. Behaviour 74:200-263.

McAuley, D. G., J. R. Longcore, and G. F. Sepik. In press. Methods for woodcock research: pitfalls, cravasses, and progress. Proc. 8th Woodcock Symp.

Moss, R. 1986. Rain, breeding success and distribution of Capercaillie Tetrao urogallus and black grouse Tetrao tetrix in Scotland. Ibis 128:65-72.

Pienkowski, M. W. 1984. Behaviour of young ringed plovers Charadrius hiaticula and its relationship to growth and survival to reproductive age. Ibis 126:133-155.

Ricklefs, R. E. 1989. Adaptations to cold in bird chicks. Physiology of Cold Adaptation in Birds 173:329-338.

Sheldon, W. G. 1967. The book of the American woodcock. Univ. Massachusetts Press, Amherst 227pp.

Vander Haegen, W. M., R. B. Owen, Jr., and W. B. Krohn. In press a. Effects of weather on earthworm availability and spring food habits of American woodcock. Proc. 8th Woodcock Symp.

Vander Haegen, W. M., W. B. Krohn, and R. B. Owen, Jr. In press b. Care, behavior, and growth of captive American woodcock. Proc. 8th Woodcock Symp.

CHAPTER 3

BIOENERGETICS OF FEMALE AMERICAN WOODCOCK DURING THE BREEDING SEASON

The American woodcock (Scolopax minor) is an upland shorebird that breeds in early successional forests of the northeastern and northcentral United States and Canada (Sheldon 1967). A decline in its eastern breeding population over the past decade has prompted concern about the welfare of the population (Bortner 1990). As one of the earliest nesting migrants in this region (early April [Mendall and Aldous 1943]), the woodcock often encounters environmental conditions that are potentially stressful. Research on the energy constraints acting on woodcock during the breeding season could help elucidate reproductive strategies and help interpret yearly variations in reproductive success. In the absence of empirical data for woodcock, a previous attempt to model woodcock energetics used metabolic parameters derived for other species (Rabe et al. 1983).

Research involving energetics is being used increasingly for analysis of factors influencing population dynamics in birds (Paladino 1989). Studies of energy expenditure by both modeling time-energy budgets and direct measurement via doubly-labeled water have provided insights into the seasonal demands on individuals (Mugaas and King 1981, Obst et al. 1987, Masman et al. 1988) and on populations (Wiens and Innis 1974, Holmes et al. 1979, Rotenberry 1980). The objective of this study was to model the energy budget of female woodcock during the breeding season and to identify periods where energetic stress could affect annual productivity or adult survival. Construction of a comprehensive, species-specific energy budget was facilitated by the availability of detailed time-budget (Chapter 2) and metabolism data (Chapter 1).

STUDY AREA

The study was conducted on the 6,580 ha Baring unit of Moosehorn National Wildlife Refuge, Washington County, Maine. The refuge is located in the spruce-fir (Picea-Abies) forest type. Farm abandonment, wildfire, and clearcutting during the early 1900's produced stands of birch (Betula spp.), red maple (Acer rubrum), and aspen (Populus spp.), while alder (Alnus rugosa) occurs on the wetter sites (Dwyer et al. 1988). Extensive patch-type clearcutting for woodcock management has taken place on the Baring Unit since 1976, with 7-57 forest clearings (totaling 40-60 ha annually) created each year (Derleth and Sepik 1990). Regional mean air temperatures for April, May, and June are 5, 11.4, and 16.7 $^{\circ}$C, respectively. Mean rainfall amounts for the region for the same months are 9.5, 9.2, and 8.3 cm, respectively (Dept. Commerce 1990).

METHODS

Microclimate

Woodcock were captured on the refuge and outfitted with back-pack radio transmitters (McAuley et al. in press) as part of this study and a related study on woodcock survival and habitat use (Longcore, McAuley, and Sepik unpubl. data). Microclimate was measured by remote microclimate stations in covers being used by radio-tagged woodcock from 01 April through 20 June, 1988-89. Ambient temperature (T_a) was measured by thermistor and thermocouple probes positioned 6 cm above the ground and shielded from solar radiation. Windspeed (u) was measured with a low- threshold cup anemometer (0.26 m/s stall speed) positioned 15 cm above the ground. Shortwave solar radiation was measured in covers without overhead vegetation using a solar pyranometer positioned 15 cm above the ground. All probes were sampled at 60 second intervals, and values averaged every 15 minutes by Campbell Scientific CR21 and CR21X microloggers. Hourly means were obtained by averaging the 15-minute readings.

Radio-tagged woodcock were selected randomly for microclimate monitoring, and data were collected until the bird moved to a different cover, at which time the station was moved to another bird. Preference was given to woodcock that were being monitored for activity patterns (Chapter 2). Use of 3 stations allowed simultaneous sampling in up to 3 separate covers. Representative values for microclimate variables affecting woodcock on the refuge were obtained by averaging the data collected at from 1 to 3 stations each day. Estimates of daily thermoregulatory costs were obtained by averaging energy expenditure values calculated for individual covers.

Thermoregulation model

Thermoregulatory costs were determined using an electrical-analog model (Robinson et al. 1976, Weathers et al. 1984) where heat-transfer resistances are derived from properties of the animals integument and from microclimate data. Estimates of daily thermoregulatory cost were generated using a FORTRAN program that used hourly averages of microclimate variables to calculate hourly energy expenditure. This procedure involved using metabolic rates (H_m) obtained from oxygen consumption experiments on captive woodcock (Chapter 1) and applying them to field measurements of operative temperature (T_e) and wind speed. Details of the model are described in Appendix B.

Energy Model

A model of seasonal energy expenditure was derived from data on metabolic, thermoregulatory, activity, and reproductive costs. Metabolic rates for standard and resting metabolism and physical activity were measured by indirect calorimetry (Chapter 1) and were assumed constant throughout the reproductive period. Thermoregulatory costs were obtained from the thermoregulation model described above, and were averaged for each period in the reproductive cycle. Diel activity for each period was derived from telemetric studies of wild woodcock

(Chapter 2), and was constant within each period except brooding. Activity during the brooding period was described by a regression equation relating time active to brood age (Chapter 2). Time allocated to flying was estimated at 1% of the diel period, as breeding female woodcock typically spend a very small proportion of the day in flight (personal observation). Allocation of energy to egg synthesis was modeled after King (1973). Production efficiency for egg synthesis was estimated as 77% (Brody 1945), whereas that for synthesis of the oviduct was estimated as 55% (Drobney 1980).

The model describes the energy requirements of a 190 g female with standard metabolic rate (SMR) of 1.09 kcal/hr, resting metabolic rate (RMR) of 1.36 kcal/hr, and active metabolic rate (AMR: walking, foraging) of 1.93 kcal/hr (energy equivalents derived from oxygen consumption data in Chapter 1). The cost of flight was estimated as 12.3 kcal/hour (ca. 11 X SMR) from equation 5.43 in Kendeigh et al. (1977). During pre-laying and laying, females were active throughout the diel period and RMR was applied to all periods of inactivity. During incubation and brooding, females were inactive at night and assumed to be in a resting phase; hence, SMR was applied to a 7-hour period designated as sleep, whereas RMR was applied to inactivity during the day.

Incubating and brooding females have an additional cost in heat transferred to eggs and young. For the incubation period, this cost was estimated as 20% of SMR (Weathers 1985) and was applied to periods of inactivity or rest. The brooding period was divided into an early (day 1-15) and a late (day 16-30) period, based on the thermoregulatory development of the young. Before age 15 days, woodcock chicks are not thermally independent and depend on brooding by the female (Chapter 2). The metabolic cost of brooding young was estimated as 20% SMR (equivalent to incubation) and was applied to the female during the resting and inactive phases of the early brood period. Heat increment of feeding was not included in the model because of the generally poor understanding of its effects in birds.

To examine the effects of assumptions in the model I conducted a sensitivity analysis, varying the values of key parameters obtained from the literature and measuring the effects on the predicted daily energy expenditure. Many parameters within the model were measured directly on woodcock in the field or in the laboratory and hence were not tested.

Body condition

Female woodcock were collected from late March through early June, 1987-89, either by shooting over a pointing dog or capturing the bird on the nest. Birds that died incidental to banding also were used. Birds were weighed on a top-loading balance, and then the feathers, reproductive tract, and contents of the proventriculus and ventriculus were removed. I weighed each ovary to the nearest 0.1 g, and measured the diameter of each yolky follicle to the nearest mm. The bird was then doubled-bagged and frozen for later analysis. Reproductive tracts were double-bagged and frozen separately. Birds were classified as:

Pre-RFG (rapid follicular growth) (no yolky ovarian follicles > 4mm diameter), RFG (1 or more follicles > 4mm diameter, but no post-ovulatory follicles), Laying (1 or more post-ovulatory follicles but not incubating), Hatching (collected on the nest during the last 1-2 days of incubation of first nest), or Renesting (collected on the nest 1-2 days after initiating incubation of renest). All renesting females were collected in 1989.

At the end of the field season, thawed birds were weighed, and the left breast (pectoralis, supracoracoideus, and coracobrachialis) and leg (all muscles having origin or insertion on the femur or tibiotarsus) muscles were removed, cleaned of adhering fat, and weighed. The remaining carcass (including fat removed from excised muscles) was then refrozen, cut with a band saw, and freeze-dried along with the excised breast and leg muscles. Dried tissues were then reweighed and ground in a food blender. Proximate analyses were conducted on duplicate samples of breast, leg, and carcass tissue using ether extraction in a Soxhlet apparatus for lipid, and the Kjeldahl procedure for protein.

Reproductive tissues were analyzed for fat, protein, and caloric content. Freshly-laid eggs were collected from woodcock nests on the refuge. Egg contents, and oviducts and developing follicles from RFG and laying females were freeze-dried and ground with mortar and pestle. Dry weights of oviducts and follicles from individual females were too small to analyze, so samples were combined. Duplicate samples of all tissues were then analyzed for caloric content by burning in an adiabatic calorimeter, and for lipid and protein as described above. Duplicate samples were ashed in a muffle furnace at 600 °C.

Allocation of energy and protein reserves to reproductive tissues in RFG and Laying hens was examined by regression analysis (Ankney and Afton 1988). Reproductive fat (fat contained in developing follicles and completed eggs) and reproductive protein (protein contained in oviduct and completed eggs) were regressed against body fat and body protein, respectively.

To examine the ability of females to regain nutrient reserves used during incubation, weights of brood-rearing females with known-age young were obtained from the refuge (Sepik, McAuley, and Longcore unpubl. data). Data from 7 years were analyzed, both combined and by year, using regression analysis to determine if the slopes were significantly different from zero.

Assimilation efficiency

Captive-reared woodcock were maintained on an ad libitum diet of nightcrawlers (Lumbricus terrestris), and housed in an environmental chamber at thermoneutral temperatures (Vander Haegen et al. in press a). Birds were kept in individual cages with removable stainless steel bottoms. Assimilation efficiency was measured during a 3-day period. Birds were weighed each morning, and a recorded number and mass of similarly-sized nightcrawlers were placed in each food tray. After 24 hours, the uneaten nightcrawlers were removed and replaced with fresh nightcrawlers. Each day, a sample of nightcrawlers was dried to constant weight at 40 ^{o}C to obtain a value for water content. Total intake for each bird each day was determined by subtracting the dry weight of uneaten nightcrawlers from the calculated dry weight of nightcrawlers fed. Woodcock excreta (feces and uric acid) and a sample of nightcrawlers were dried to constant weight at 40 ^{o}C and ground in a Wiley mill. Caloric values for excreta and nightcrawlers were obtained by burning duplicate samples in an adiabatic bomb calorimeter. Caloric values for earthworms consumed by woodcock in the wild were derived by bombing earthworms collected on reference transects in woodcock covers on the refuge in 1989 (Vander Haegen et al. in press b).

Required intake rates

The number of earthworms required to maintain energy balance was calculated for each period in the breeding season using the mean mass and caloric content of earthworms collected at reference transects and the daily energy expenditure and assimilation efficiency of woodcock. This value was then divided by the time spent active and available for foraging each day (Chapter 2) to derive the required intake rate in worms/minute.

RESULTS

Microclimate and thermoregulation

Microclimate variables for woodcock covers, values for solar shortwave radiation, and metabolic costs for thermoregulation are presented in Table 3.1.

Table 3.1. Mean values ($\bar{x}$ ± SE) for air temperature and wind speed measured at woodcock use sites, solar radiation recorded in the open, and metabolic cost for thermoregulation, during specific periods of the breeding season at Moosehorn National Wildlife Refuge, Maine. Levels of significance from Kruskal-Wallis test: ** = $P < 0.01$, * $P < 0.05$.

	Air temperature (C)		Wind speed (m/s)		Insolation (W/m^2)		Metabolism (kCal/day)	
Period	1988	1989	1988	1989	1988	1989	1988	1989
Prenesting[a]	4.72 ± 0.48 **	1.82 ± 0.57	0.68 ± 0.06 *	0.50 ± 0.06	0.15 ± 0.03	0.17 ± 0.03	18.9 ± 0.50 **	20.7 ± 0.35
Nesting[b]	7.17 ± 0.67 *	4.50 ± 0.73	0.50 ± 0.03	0.43 ± 0.03	0.14 ± 0.02	0.15 ± 0.03	16.0 ± 0.64 *	18.0 ± 0.68
Brooding[c]	13.1 ± 0.64	13.2 ± 0.32	0.31 ± 0.01	0.30 ± 0.01	0.21 ± 0.01	0.18 ± 0.02	10.1 ± 0.52	9.68 ± 0.30

[a] 1 April - 15 April
[b] 16 April - 8 May
[c] 9 May - 20 June

Mean air temperature and mean windspeed measured in woodcock covers during the pre-nesting period were lower in 1989 than in 1988. Solar shortwave radiation, measured in the open at the main weather station, did not differ between years. Metabolic cost for thermoregulation did not differ significantly among microclimate sites measured in 1988 ($\underline{P} = 0.843$) or 1989 ($\underline{P} = 0.614$) (Kruskal-Wallis test).

Energy requirements for thermoregulation were greatest during the pre-nesting period and decreased as the breeding season progressed (Figure 3.1). Mean values for each period depict a decrease of approximately 50% from pre-nesting to brood-rearing (Table 3.1). Thermoregulatory costs during the pre-nesting period were 10% higher in 1989 compared to 1988, largely because of lower air temperatures (Table 3.1, Figure 3.1). Although windspeed was significantly lower in 1989 during the pre-nesting period, it had little effect on DEE at the low velocity typically recorded.

Energy use

The thermoregulatory model was robust to changes in assumed parameters. When parameters (aA, as, d, L_g, and T_s) were varied ± 25% and applied to the pre-nesting period, the resulting values for DEE changed < 1%. Changing the assumed value for $T_b \pm 1\ ^{o}C$ had a greater effect, altering the predicted DEE by 2.5%. A greater chance for error existed in the partitioning of metabolic rates in the energy model. The assumption that female woodcock incur only SMR for a 7-

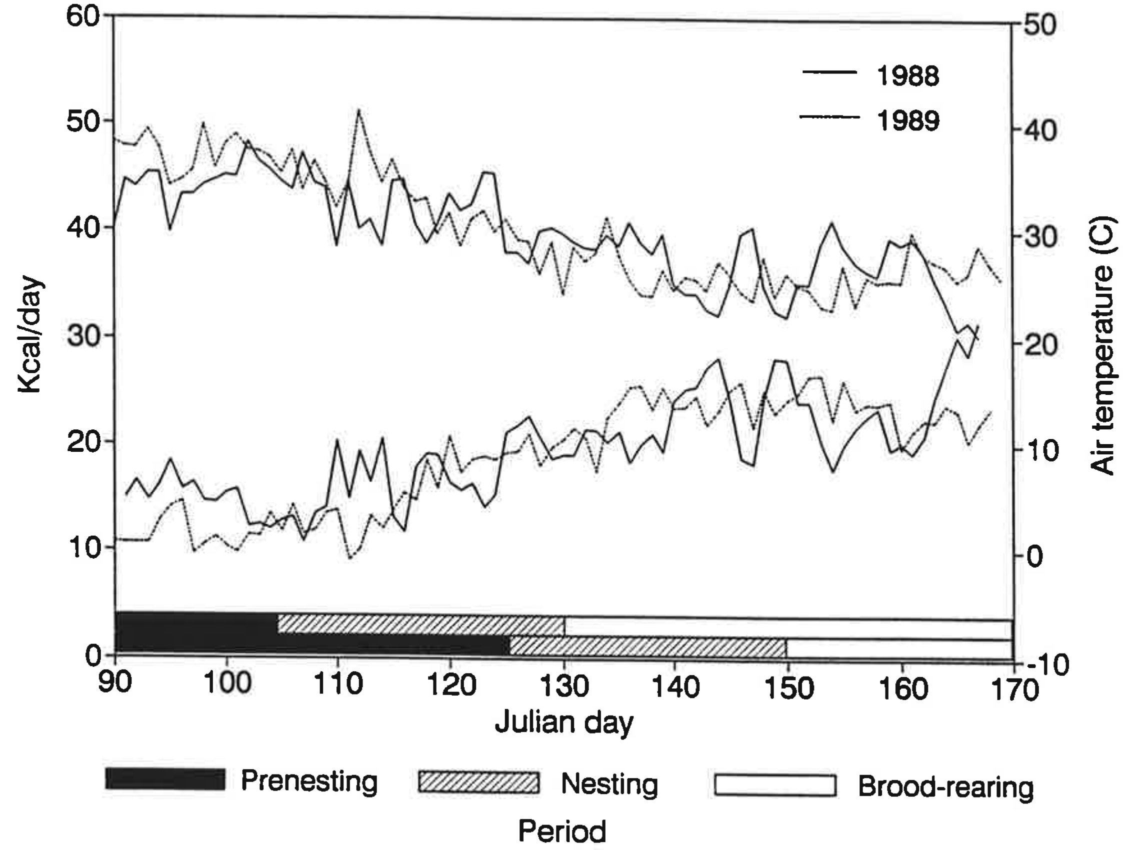

Figure 3.1. Mean daily energy expenditure for standard metabolism and thermoregulation (top) of American woodcock, and air temperature (bottom) measured in woodcock covers at Moosehorn National Wildlife Refuge, Maine, April-June 1988-89. Horizontal bars at bottom delineate timing of reproductive periods in 1988 (top) and 1989 (bottom).

hour period at night while incubating and brooding results in a DEE that is 3.4 to 3.8% below that predicted when the higher RMR is applied to all inactive periods. The assumption that incubating woodcock incur a cost equal to 20% of SMR for warming the clutch results in a 7.4% increase in DEE over a female experiencing no additional cost. An equal cost (20% of SMR) applied to brooding females increases DEE by 8.7% over brooding females incurring no additional cost. Finally, varying the cost of flying by ± 25% resulted in only a 1.3% change in DEE, a result of the minor occurrence of this activity in the time-budget of female woodcock.

Thermoregulatory costs composed 34% of the daily energy expenditure during the pre-nesting period, declining to 20% by the end of brood-rearing (Figure 3.2). Energy required for thermoregulation exceeded that required for activity during the pre-nesting, laying, and incubation periods (Figure 3.2). Despite increased activity rates during late brood-rearing, lower thermoregulatory demands at this time resulted in the lowest daily energy expenditure for the breeding period. Approximately half of the daily energy costs were allocated to standard metabolism, except during laying when energy costs peaked at 97 kcal/day (Figure 3.2).

Nutrient reserves

Twenty-three female woodcock were collected for analysis of body

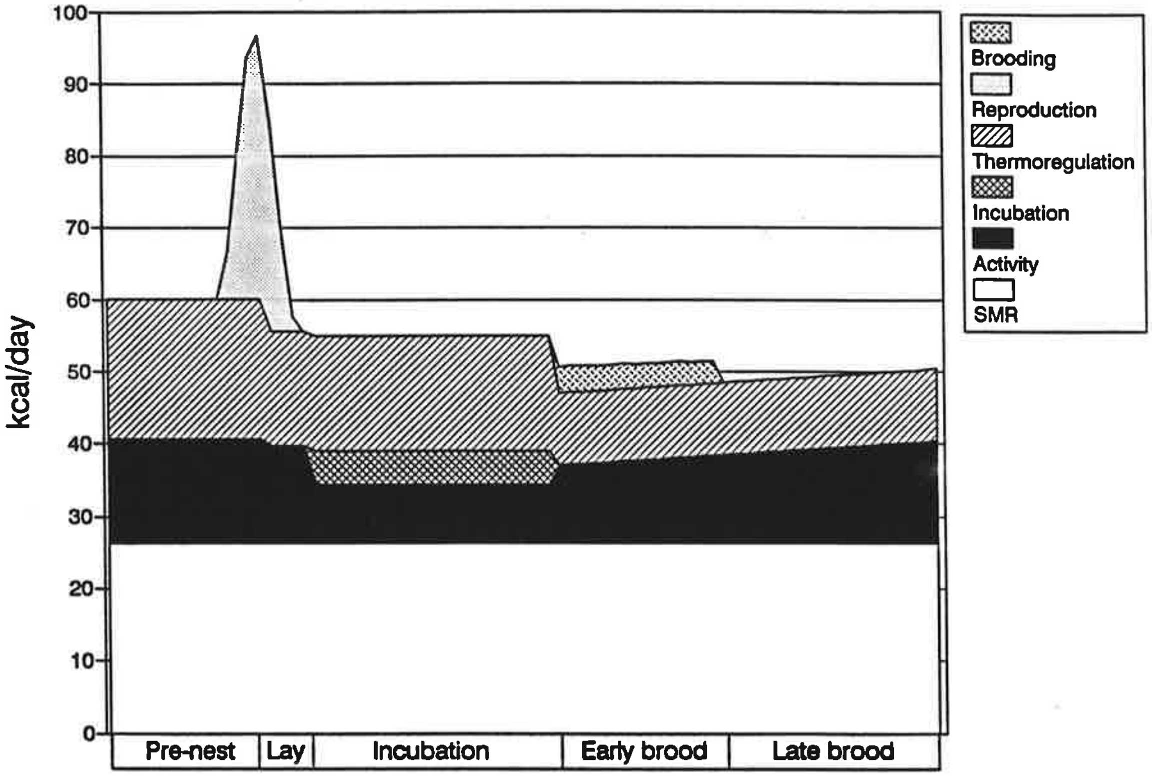

Figure 3.2. Model of daily energy expenditure of female American woodcock during pre-nesting, laying, incubation, early brood-rearing (chicks ≤15 days old) and late brood-rearing (chicks > 15 days old) at Moosehorn National Wildlife Refuge, Maine, April-June, 1988-89. Energy costs partitioned into Standard Metabolic Rate (SMR), Activity (cost of physical activity and increased metabolism associated with the active phase of the diel cycle), Incubation (cost of warming eggs), Thermoregulation (cost of maintaining body temperature), Reproduction (cost of producing oviduct and eggs), and Brooding (cost of warming chicks).

composition. Fresh body mass increased significantly from RFG to Laying (Tukey's test, P = 0.011), largely due to developing reproductive tissues and greater amounts of body fat (Table 3.2). A significant (Tukey's test, P = 0.003) decline in dry body mass from Laying to Hatching was due to a 75% decline in body fat (Table 3.2). Females lost an average 15 g of fat during incubation. Body fat was lower (Tukey's test, P = 0.005) in females at Hatching compared to Laying. There was no difference among reproductive classes in protein reserves in leg tissue (ANOVA, F = 1.692, df = 4, P = 0.196), whereas differences in breast (F = 2.642, df = 4, P = 0.068), and carcass (F = 2.788, df = 4, P = 0.058) tissues approached statistical significance. Fat reserves of females collected in March and April were lower in 1989 ($\bar{x}$ = 9.00 ± 1.95 (SE)g, n = 5, 14 April median collection date) than in the previous 2 years ($\bar{x}$ = 20.07 ± 1.70 g, n = 8, 7 April median collection date) (t = 4.281, df = 11, P = 0.002).

Dry mass of ovaries and oviducts increased from Pre-RFG through Laying, regressing to Pre-RFG mass by Hatching (Table 3.2). RFG females had a maximum of 4 developing follicles. Two Laying females had 1 egg in the oviduct, 1 developing follicle, and 2 post-ovulatory follicles, while a third had 1 egg in the oviduct and 3 post-ovulatory follicles. Based on follicle measurements from RFG and Laying females, follicle diameter sequence for a female preparing to ovulate the first egg in a 4-egg clutch would be 35, 21, 15, and 7 mm. Mean weight of 7 freshly-laid eggs was 17.2 ± 0.39 g. Dry weight of egg contents (minus shell) averaged 3.67 ± 0.03 g. Results of caloric and proximal analyses on reproductive

Table 3.2. Body composition ($\bar{x} \pm$ SE) of female American woodcock collected in Maine, March - May, 1987-89 (dry weights [g] except for fresh body mass). Statistical significance between adjacent columns tested using Tukey test. Significance levels: * = $P < 0.05$, ** = $P < 0.01$.

Variable	Pre-RFG(3)[a]	P	RFG (8)[b]	P	Laying (3)	P	Hatch (6)	P	Renest (3)
Fresh body mass[c]	189.4 ± 7.55	NS	214.5 ± 7.65	*	257.5 ± 12.49	*	189.8 ± 3.16	NS	198.9 ± 6.24
Dry body mass[d]	55.96 ± 3.66	NS	63.46 ± 2.96	NS	69.37 ± 2.99	**	47.77 ± 0.84	NS	52.14 ± 2.49
Fat mass	10.85 ± 2.95	NS	15.88 ± 2.40	NS	20.16 ± 2.08	**	4.90 ± 0.20	NS	7.42 ± 1.08
Protein mass									
carcass	36.43 ± 0.76	NS	38.71 ± 1.02	NS	40.43 ± 1.22	NS	35.23 ± 0.66	NS	38.04 ± 1.28
breast	6.11 ± 0.18	NS	6.58 ± 0.23	NS	6.87 ± 0.31	NS	5.74 ± 0.15	NS	6.61 ± 0.27
leg	2.44 ± 0.08	NS	2.48 ± 0.12	NS	2.81 ± 0.08	NS	2.33 ± 0.06	NS	2.46 ± 0.07
Ovary mass	0.057 ± 0.007	NS	1.226 ± 0.395	*	4.235 ± 1.661	**	0.039 ± 0.003	NS	0.087 ± 0.024
Oviduct mass	0.102 ± 0.017	NS	1.014 ± 0.169	NS	1.799 ± 0.480	**	0.101 ± 0.014	NS	0.298 ± 0.040

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[a] Sample size = 2 for oviduct mass.
[b] Sample size = 6 for oviduct mass.
[c] Body mass including feathers, stomach contents, and reproductive tracts.
[d] Body mass minus feathers, stomach contents, and reproductive tracts.

tissues are presented in Table 3.3. Total energy value of the contents of a woodcock egg averaged 24.58 ± 0.318 kcal ($n = 7$).

Rapid follicular growth likely occurs over a 4-day period, with most energy cost to the female occurring on the last 2 days of RFG and the first 2 days of laying (King 1973). Cost of synthesizing a clutch of 4 eggs was estimated as 127.69 kcal and was modeled after King (1973) over the 8-day RFG/Laying period. Development of the oviduct occurs over the period of RFG (King 1973) and required 18.22 kcal, or 4.55 kcal/day for the 4 days preceding laying.

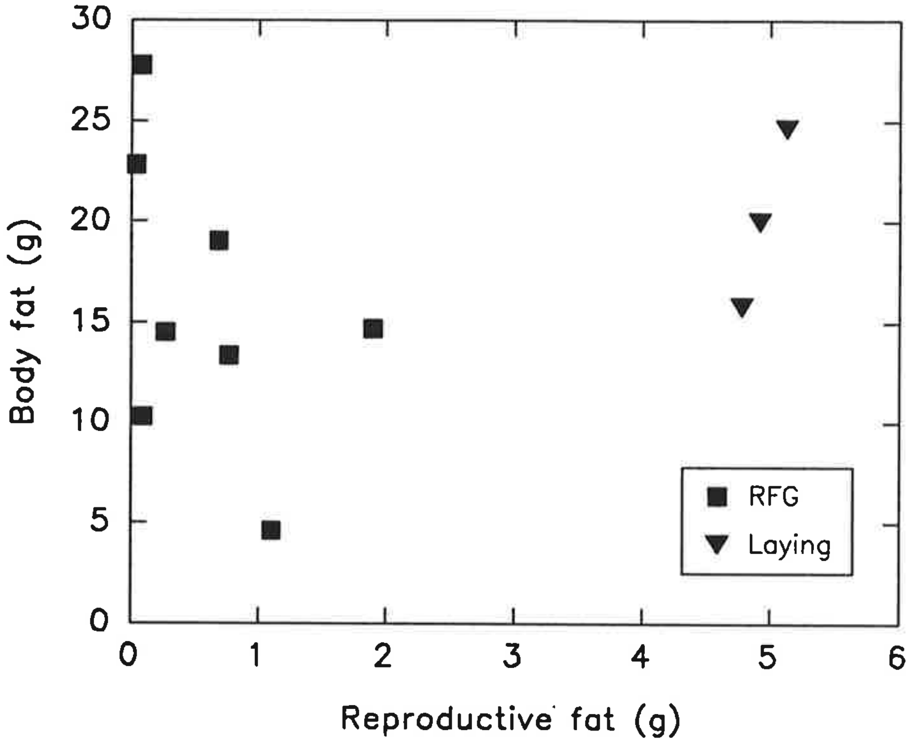
Females began RFG with a minimum 10 g of fat reserves, although there was evidence of yearly variation. Two females beginning RFG in 1989 had 10.2 and 14.5 g of fat reserves, whereas 2 females commencing RFG in earlier years had fat reserves of 22.8 and 27.8 g. There were no significant relationships between fat ($r^2 = 0.039$, $\underline{P} = 0.559$) and protein ($r^2 = 0.072$, $\underline{P} = 0.424$) committed to reproduction and body reserves in RFG and Laying hens (Figure 3.3). Similarly, there were no significant relationships in fat ($r^2 = 0.187$, $\underline{P} = 0.285$) or protein ($r^2 = 0.016$, $\underline{P} = 0.762$) when RFG females were considered alone. However, sample sizes were small and spread over 3 years. Although variability among years may have lowered the power of the regression analyses, the high levels of nutrient reserves retained by Laying females supports the conclusion that nutrient reserves were not used primarily for formation of the clutch. All Laying females in the analysis were collected in 1987 and 1988 and

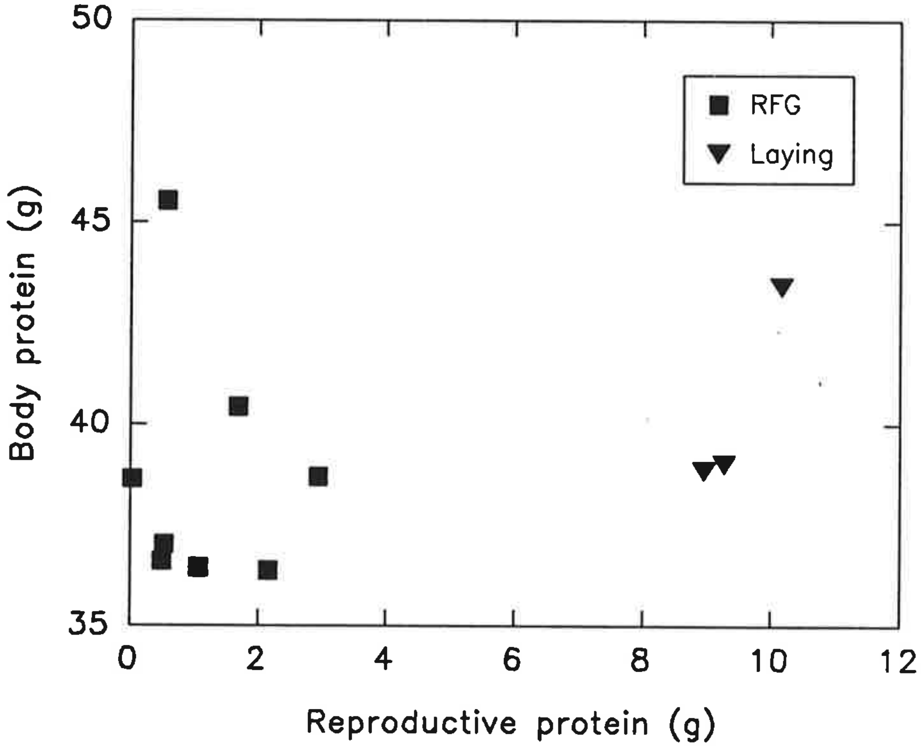
Table 3.3. Composition of reproductive tissues from American woodcock collected in Maine, March-May, 1987-89 ($\bar{x}$ ± SE) Sample size in parentheses.

Variable Class	Energy (kcal/g)	Fat (%)	Protein (%)	Ash (%)
Eggs (7)	6714 ± 23.0	33.5 ± 0.42	62.1 ± 0.49	4.3 ± 0.1
Follicles				
RFG (8)	7559[a]	52.9	43.4	3.7
Laying (2)	7054	39.9	55.9	4.1
Oviduct				
RFG (6)	5344	5.60	89.3	5.1
Laying (3)	5569	8.79	87.0	4.2

[a] follicle and oviduct samples were combined within classes and therefore lack measures of variance.

Figure 3.3. Relationships of nutrient stores (carcass fat and carcass protein) to nutrients committed to reproduction (contents of oviduct, developing follicles, and completed eggs) during periods of rapid follicular growth (RFG) and egg laying for female American woodcock collected at Moosehorn National Wildlife Refuge, Maine, 1987-89.


Body fat (g)
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Reproductive fat (g)
RFG
Laying


Body protein (g)
50
45
40
35
0
2
4
6
8
10
12
Reproductive protein (g)
RFG
Laying

had committed, at the time of collection, $\geq$ 88% of the energy required for a clutch of 4 eggs.

Mass of female woodcock with known-age young was not related to age of the chicks (Figure 3.4), indicating that females do not regain nutrient reserves lost over incubation during the early brood period. Slopes of regression lines relating female mass to age of brood were not significantly different from zero for any single year or for all years combined (Table 3.4).

Incubating woodcock leave the nest to feed several times each day, especially during the crepuscular periods (Chapter 2). Several incubating females were collected on the nest just after returning from a feeding recess. Two females collected after the morning crepuscular feeding period contained 13.5 and 2.3 g (wet weight) of earthworms in their esophagus, while a third, captured after a mid-morning recess (1000 hours) contained 17.7 g of earthworms. A fourth hen, captured (but not collected) on the nest after the evening crepuscular feeding period, had a well-distended crop that obviously was filled with food.

Assimilation efficiency

Nightcrawlers fed to woodcock during the assimilation trials had a caloric content of 4.87 kcal/g, a fat content of 3.9%, and an ash content of 14.9%. Metabolizable energy coefficients averaged 0.590 ± 0.016 ($n = 6$) and varied little, with the exception of one female designated BW (Table 3.5). Apparent metabolizable energy averaged 2.88 ± 0.077 kcal/g and was again higher for

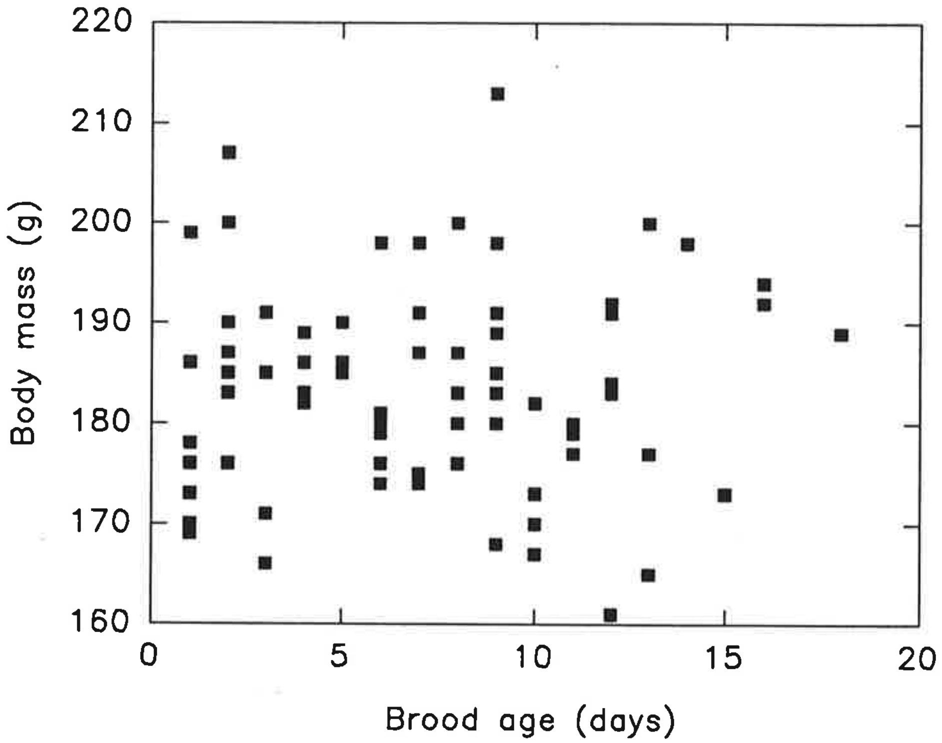


Figure 3.4. Mass of female American woodcock captured with known-age broods, Moosehorn National Wildlife Refuge, Maine, 1979-89 (n = 74). (Sepik, McAuley, and Longcore, unpubl. data.)

Table 3.4. Linear regressions relating body mass of female American woodcock captured on Moosehorn National Wildlife Refuge, Maine, with age of their broods (broods aged 1-18 days) (Sepik, McAuley, and Longcore, unpub. data).

Year	n	Constant	Slope	r^2	P
1979	10	179.1	0.534	0.035	0.607
1980	22	175.0	0.536	0.071	0.231
1982	9	193.8	-0.598	0.079	0.463
1987	17	183.3	0.073	0.003	0.862
1988	15	190.0	-0.584	0.021	0.609
1989	4	180.8	0.510	0.129	0.640
Combined	74	182.8	0.108	0.002	0.696

Table 3.5. Apparent metabolizable energy (AME)(kcal/g) and metabolic energy coefficients (MEC) for American woodcock fed a diet of nightcrawlers during a 3-day trial. Weights are dry weight.

	Food consumed		Excreta			
Bird	Grams	kcal	Grams	kcal	AME	MEC
R	69.00	336.3	41.15	147.9	2.73	0.56
RR	50.54	246.3	29.86	104.7	2.80	0.58
G	50.87	247.9	28.96	103.3	2.84	0.58
W	56.62	276.0	33.32	120.3	2.75	0.56
BW	63.72	310.6	29.19	104.2	3.24	0.67
RW	58.45	284.9	33.76	116.3	2.89	0.59
Mean	58.20	283.7	32.71	116.1	2.88	0.59
SE	2.97	14.1	1.89	6.98	0.08	0.02

individual BW (Table 3.3). Average caloric value and percent ash of earthworms sampled on transects in woodcock covers on the refuge in 1989 were 3.65 kcal/g and 34.5%, respectively (Table 3.6). Ash-free caloric values (kcal/g) for nightcrawlers fed to woodcock during the assimilation trials (5.73) and earthworms collected on the refuge (5.62) were similar.

DISCUSSION

The energy demands incurred by female American woodcock on the northern breeding grounds were greatest during the pre-nesting and laying periods. High DEE during these periods resulted from low operative temperatures and resultant high thermoregulatory costs, high activity levels, and the cost of egg formation. The peak in total energy demand during egg production is typical of birds in general (King 1973) and indicates the need for sufficient food, or body reserves, to support tissue production during this period. The combination of thermoregulatory, activity and production costs, combined with uncertainty of weather and food conditions, make the Pre-nesting and Laying periods a time of potential stress for woodcock.

Female woodcock likely arrive on the northern breeding grounds with some fat reserves but must increase stores before laying. They achieve this by entering a condition of hyperphagia, foraging throughout the diel period from arrival through initiation of incubation (Chapter 2). However, this rapid nutrient gain

Table 3.6. Caloric and ash content of earthworms collected on sample transects in woodcock feeding habitat, April-June 1989, Moosehorn National Wildlife Refuge, Maine.

Period	kcal/g	Ash (%)
1-30 April	3.903	30
1-15 May	3.881	32
16-31 May	3.207	42
1-15 June	3.618	34

can be interrupted by vagaries in the weather. Spring snow storms can limit the areas available for feeding (Mendall and Aldous 1943), whereas persistent soil frost can severely limit the availability of earthworms, the woodcock's principal prey (Vander Haegen et al. in press b). During such poor conditions, woodcock have demonstrated the ability to alter their behavior to maximize energy balance. In the spring of 1989, when soil frost on the refuge persisted into May, female woodcock shifted their activity to afternoon hours when the sun had warmed the soil and microclimate near the ground, while remaining mostly inactive at night when foraging conditions were probably poor (Chapter 2). Although this may have allowed them to maximize energy balance under existing conditions, energy intake was evidently too low to initiate egg production as nesting did not occur until the frost melted and earthworm availability and woodcock activity patterns returned to normal, 3-4 weeks later than the usual nesting period.

Constant feeding during the pre-nesting and laying periods served both to provide nutrients for reproductive tissues and to store energy (fat) for use during incubation. High foraging rates during pre-nesting and laying have been recorded in time-budget studies of female semipalmated sandpipers (Actitis macularia) (Ashkenazie and Safriel 1979) and spotted sandpipers (Calidris pusilla) (Maxson and Oring 1980). Numerous studies of waterfowl have documented that nutrients are reduced during egg production (e.g., Korschgen 1977, Alisaukus and Ankney 1985, Ankney and Afton 1988). Woodcock, however, lay fewer eggs with lower caloric value compared with waterfowl (Ricklefs 1974) and under normal conditions can obtain nutrients at a sufficient rate to support egg production. Erckmann (1983) concluded that most shorebirds do not depend on stored nutrient reserves during egg-laying.

Energy stored during pre-nesting and laying may be critical to the incubating female. Although activity costs during incubation are reduced, thermoregulatory costs remain high. The use of fat reserves during incubation allows the birds to remain on the nest with only limited feeding recesses. Use of energy reserves by incubating females has been documented for numerous species including American eiders (*Somateria mollissima dresseri*)(Korschgen 1977) and northern shovelers (*Anas clypeata*)(Ankney and Afton 1988). The pectoral sandpiper (*Calidris melanotos*) also begins incubation with a substantial fat reserve and apparently nests only when body fat levels are high (MacLean 1969). Like the woodcock, this arctic-nesting shorebird also is polygynous and the female does all the incubating (Johnsgard 1981).

Energetic relationships during the brood-rearing period likely play a major role in determining productivity for the year. The female has not only her own needs to satisfy, but those of her brood as well. Woodcock chicks are not homeothermic during the early brood period and require frequent brooding by the female (Chapter 2). Further, there is an inverse relationship between air temperature and brooding requirements of the chicks. The model in Chapter 2 demonstrates how, at temperatures typical of the brood period, a decline in mean air temperature of 5 ^{o}C can result in a 40% decrease in time spent active, with a concomitant loss of foraging time. Similarly, rainfall increases the brooding requirements of woodcock chicks, with a demonstrated 30% reduction in time spent active for chicks < 10 days old (Chapter 2). This reduction in available foraging time affects the female as well as the chicks at a time when both require substantial energy intake; for growth in the case of the chicks, and for maintenance while caring for the brood for the female. In addition to time spent brooding, the female also must forage to feed the chicks, at least for the first week after hatching (Gregg 1984). Condition of the female at the end of incubation may dictate how much time she can dedicate to brooding and feeding the chicks at the expense of feeding herself. Females with adequate reserves could probably carry their brood through several days of inclement weather by vigilant brooding, with periodic short bouts of foraging to feed the chicks. Exactly this pattern of behavior is documented in the activity data reported in Chapter 2. Females with depleted energy reserves and faced with cold, wet weather may lose their brood through neglect while foraging to meet their own energy needs.

Constraints on the woodcock's energy budget can be examined further by comparing energy intake requirements with available foraging time and intake rates observed in the field. When compared with intake rates of captive-reared (0.46 worms/minute: 6 birds observed for a total of 12, 10-minute measurements) and wild (1.65 worms/minute: 5 birds observed for a total of 11, 10-minute measurements) woodcock observed in the field, intake rates required during pre-RFG and laying seem reasonable, given an adequate food supply (Table 3.7).

Table 3.7. Intake requirements of female American woodcock during Pre-RFG (no Rapid Follicular Growth), RFG (mean for the 4 peak days of egg production), Incubation, and Brood-rearing (chicks age 15 days). Calculations based on daily energy expediture (DEE), caloric value of earthworms, assimilation efficiency of woodcock, and available foraging time (Time active).

			Required intake	
Period	DEE (kcal/day)	Time active (Minutes)	Dry wt. (g)	Worms/minute
Pre-RFG	60.3	576	28.0	0.76
RFG	89.1	550	41.4	1.18
Incubation	55.3	118	25.7	3.41
Brooding	51.7	576	24.0	0.65

When food is not sufficiently available, as occurred during persistent spring frost in 1989 (Vander Haegen et al. in press b) follicular growth and nesting is delayed until food becomes adequate.

High daily energy expenditure and short time available for foraging during incubation result in the maximum required intake rates for the breeding period (Table 3.7). Females left the nest a mean of 4.8 times/day, and both recess length and percent time active each day varied little among years (Chapter 2). An incubating female going on 5 feeding recesses and obtaining 18 g of earthworms each time would meet only 70% of her daily energy needs. This discrepancy is supported by the mass loss observed in females collected at the end of incubation and underscores the importance of endogenous energy reserves during this period. Converting 15 g of endogenous fat to energy (at 9.0 kcal/g [Ricklefs 1974:160]) would supply 12% of the females DEE over the typical 21-day incubation period.

Although required intake rates are lowest (Table 3.7) and earthworm densities highest (Rabe et al. 1983, Vander Haegen et al. in press b) during the brood-rearing period, the failure of females to regain lost reserves during the early brood period suggest that other factors are having an effect. Time spent feeding the young, and perhaps an increase in time spent watching for predators (e.g., Ashkenazie and Safriel 1979, Maxson and Oring 1980), decreases the time available for feeding by the female. The added foraging effort required to feed a brood of 4 chicks can be estimated by using daily intake rates documented for captive-reared woodcock. Eleven, 5-day old chicks consumed a mean of

5.42 ± 0.38 g (dry weight) of earthworms (Vander Haegen et al. in press a). When the food requirement of the brood is added to the intake requirements of the female (23.7 g), the required foraging rate for the 5th day of brood-rearing is 1.64 worms/minute--equivalent to foraging rates observed in the field. This is a conservative estimate, as energy requirements of captive chicks are probably lower that those of chicks in the wild.

The timing of avian reproduction has been linked with availability of food on the breeding grounds (Lack 1968, Drent and Daan 1980, Daan et al. 1988). Early nesting by American woodcock on the northern breeding grounds may be a strategy to time hatching with peak prey availability, while running the risk of encountering uncertain weather during the pre-nesting and nesting periods. In normal years availability of food is increasing during the pre-nesting and nesting periods (Rabe et al. 1983, Vander Haegen et al. in press b) and is at suitable levels to support females preparing to nest. When food availability is low, as occurred on the refuge in 1989, nesting is delayed until conditions improve and foraging opportunities increase. Delay in nesting associated with low availability of food has been documented for another shorebird, the spotted sandpiper (Lank et al. 1985). If woodcock were to delay initial nesting attempts until food resources were more reliable, the brood-rearing period would be extended into the time when foods are declining (Rabe et al. 1983, Vander Haegen et al. in press b), and may be unsuitable for rearing young. Earthworm biomass on sample transects on the refuge peaked in late May, declining through summer to pre-nesting levels by August (Phelps 1986, Vander Haegen et al. in press b).

Renesting is an important component of the woodcock's reproductive strategy (McAuley et al. 1990). Snow in spring or persistent soil frost can delay initial nesting attempts, thus reducing the time available for renesting. In 1989, when spring conditions delayed nesting on the refuge by 3-4 weeks, the proportion of woodcock renesting after losing a nest or brood was < 50% (Longcore, Sepik and McAuley, unpubl. data), compared to > 90% in normal years (McAuley et al. 1990). Low energy reserves obtained by those females that did renest in 1989 may have resulted from a compromise between delaying nesting until additional reserves could be acquired, or foregoing renesting altogether. Renesting females were collected between 12 and 28 May 1989, during the normal brood-rearing period, and contained about 1/3 the fat reserves of first-nesters beginning incubation in previous years (Table 3.2). These low energy reserves likely put renesting females at a disadvantage, increasing their reliance on exogenous energy sources. The negative energy balance of incubating woodcock and their failure to regain reserves during early brood-rearing indicate the tenuous balance that exists during these periods; reduced food availability during either period could also lower the probability of renesting.

The environmental conditions prevailing in spring 1989 provided an opportunity to observe how nutrient availability can affect the reproductive behavior and subsequent productivity of woodcock. Table 3.8 summarizes the

Table 3.8. Comparison of key variables affecting reproduction of American woodcock during years of normal and low earthworm availabiltiy, Moosehorn National Wildlife Refuge, Maine.

Variables	Earthworm availability normal (1987-88)	Earthworm availability low (1989)
Food habits < 15 April [a]	Diet > 90% earthworms	Diet 42% earthworms
Activity pattern of females during pre-nesting [b]	37% of diel period active; constant activity over 24 hours	41% of diel period active; high activity 0800-1900, low activity 2000-0700 hours
Fat reserves of females during March and April	20.07 g (dry weight)	9.00 g (dry weight)
Fat reserve of females begining rapid follicular growth	> 22 g fat (dry weight)	< 15 g (dry weight)
Initiation of first nests	Average mid April	Average early-mid May
Females renesting after losing a nest or brood [c,d]	> 90% renesting	< 50% renesting
Productivity [d]	Immature/mature female ratio 4.04	Immature/mature female ratio 3.13

[a] Vander Haegen et al. (in press b).
[b] Chapter 2.
[c] McAuley et al. (1990).
[d] Longcore, Sepik, and McAuley (unpublished data).

pertinent variables and their values in 1989 as compared to the previous 2 years. The primary outcome of the persistent soil frost and associated reduced availability of earthworms that occurred in 1989 was a shift in woodcock diets and activity patterns that led to a delay in nutrient acquisition. As a result, nesting was delayed 3-4 weeks and at least some females initiated rapid follicular growth with lower fat reserves. A further delay in nesting to allow time for acquisition of additional reserves was likely avoided, as it may have put the females at a disadvantage with regard to foraging opportunities for their chicks. Females renesting in 1989 began incubation with low fat reserves, which suggests that woodcock will attempt nesting in sub-optimal condition. However, the proportion of females renesting was low, probably a result of the delayed nesting season. The lower productivity observed on the refuge in 1989 was an apparent consequence of low renesting and suboptimal foraging conditions for female woodcock that was likely manifest in reduced ability to incubate eggs and care for the brood.

The pattern of energy use and food availability over the breeding season also has implications for adult survival. During the pre-nesting period, high thermoregulatory costs combined with uncertain weather and food conditions may result in mortalities in some years, especially during persistent frost or following deep snow accumulations (Mendall and Aldous 1943). Such weather-related mortality may affect males more than females, whose greater body size should allow them to endure longer periods of fasting (Calder 1974). The negative energy balance of incubating females and females brooding young through extended periods of inclement weather may result in those with insufficient energy reserves falling into weakened condition. Similar results could arise when food availability is inadequate due to drought. During a summer drought in 1978, low earthworm availability on the refuge resulted in woodcock in poor condition with some near the point of starvation (Sepik et al. 1983).

The energy costs predicted from this model differ from those derived from the model in Rabe et al. (1983), primarily in relative expenditures for activity and thermoregulation. The model of Rabe et al. (1983) overestimates cost of activity by >100%, apparently including the cost of standard metabolism (already included in the maintenance component of their model) along with the energy increment for activity. The predicted DEE of the 2 models differ substantially when this extraneous cost is subtracted. By using literature values for SMR and LCT, the model of Rabe et al. (1983) underestimates thermoregulatory costs by >100% when compared to our model using parameters derived from captive woodcock. The differences in the values predicted by these models underscore the importance of using measured values when modeling animal energetics.

SUMMARY

The energy demands incurred by female American woodcock on the northern breeding grounds were highest during the pre-nesting and laying periods. Energy required for thermoregulation was substantial, exceeding that required for activity during the pre-nesting, laying, and incubation periods. High daily energy expenditure and short time available for foraging during incubation result in the maximum required intake rates for the breeding period. By metabolizing fat reserves during incubation, females reduced their exogenous energy needs by 12%. Food supply prior to nesting may be critical, because condition of the female at the end of incubation may dictate how much time she can dedicate to brooding and feeding the chicks at the expense of feeding herself. Females with depleted energy reserves and faced with cold, wet weather may lose their brood through neglect while foraging to meet their own energy needs. If woodcock were to delay initial nesting attempts until food resources were more reliable, the brood-rearing period would be extended into the time when foods are declining, and may be insufficient for rearing young. Persistent soil frost and reduced availability of earthworms that occurred on the refuge in 1989 caused a shift in woodcock diets and activity patterns that led to a delay in nutrient acquisition. The lower productivity observed on the refuge in 1989 was an apparent consequence of low renesting and suboptimal foraging conditions for female woodcock that was likely manifest in reduced ability to incubate eggs and care for the brood.

LITERATURE CITED

Alisauskas, R. T., and C. D. Ankney. 1985. Nutrient reserves and the energetics of reproduction in American coots. Auk 102:133-144.

Ankney, C. D., and A. D. Afton. 1988. Bioenergetics of breeding northern shovelers:diet, nutrient reserves, clutch size, and incubation. Condor 90:459-472 .

Ashkenazie, S., and U. N. Safriel. 1979. Time-energy budget of the semipalmated sandpiper Calidris pusilla at Barrow, Alaska. Ecology 60:783-799.

Brody, S. 1945. Bioenergetics and growth. Reinholt Publ. Co., New York.

Bortner, J. B. 1990. American woodcock harvest and population status, 1990. U.S. Fish and Wildl. Serv., Washington, D.C. 12pp.

Calder, W. A. 1974. Consequences of body size for avian energetics. Pages 86-144 in R. Paynter, ed. Avian energetics. Nuttall Ornithol. Club., Cambridge, Massachusetts. 334pp.

Calder, W. A., and J. R. King. 1974. Thermal and caloric relations of birds. Pages 259-413 in D. S. Farner and J. R. King, eds. Avian Biology, Vol. IV. Academic Press, New York.

Campbell, G. S. 1977. An introduction to environmental biophysics. Springer-Verlag, New York. 159pp.

Daan, S., C. Dijkstra, R. Drent, and T. Meijer. 1988. Food supply and the Annual timing of avian reproduction . Proc. Int. Ornithol. Congr. 19:392-407.

Department of Commerce, 1990. Climatological Data, New England: Annual Summary. Vol. 102.

Derleth, E. L., and G. F. Sepik. 1990. Summer-Fall Survival of American Woodcock in Maine. J. Wildl. Manage. 54:97-106.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

Drobney, R. D. 1980. Reproductive bioenergetics of wood ducks. Auk 97:480-490.

Dwyer, T. J., G. F. Sepik, E. L. Derleth, and D. G. Mcauley. 1988. Demographic characteristics of a Maine woodcock population and effects of habitat management. U.S. Fish Wildl. Serv., Fish Wildl. Res. 4. 29pp.

Erckmann, W. J. 1983. The evolution of polyandry in shorebirds: An evaluation of hypotheses. Pages 113-168 in S. K. Wasser, ed. Social behaviour of female vertebrates. Academic Press, New York.

Gates, D. M. 1980. Biophysical Ecology. Springer, New York, 611pp.

Gregg, L. E. 1984. Population ecology of woodcock in Wisconsin. Wisc. Dept. Nat. Resour. Tech. Bull 144, 51pp.

Holmes, R. T., C. P. Black and T. W. Sherry. 1979. Comparative population bioenergetics of three insectivorous passerines in a deciduous forest. Condor 81:9-20.

Johnsgard, P. A. 1981. The plovers, sandpipers, and snipes of the world. Univ. of Nebraska Press, Lincoln.

Jorde, D. G. 1986. Nutritional and thermodynamic aspects of the ecology of black ducks wintering in Maine. Ph.D. Thesis, Univ. of Maine, Orono, 114pp.

Kendeigh, S. C., V. R. Dol'nik, and V. M. Gavrilov. 1977. Avian energetics. Pages 127-204 in J. Pinowski and S. C. Kendeigh, eds. Granivorous birds in ecosystems., Cambridge Univ. Press.

Korschgen, C. E. 1977. Breeding stress of female eiders in Maine. J. Wildl. Manage. 41:360-373.

King, J. R. 1973. Energetics of reproduction in birds. Pages 78-120 in D. S. Farner, ed. Breeding biology of birds, Natl. Acad. Sci., Washington, D.C.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lank, D. B., L. W. Oring, and S. J. Maxon. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. Ecology 66:1513-1524.

MacLean, S. F., Jr. 1969. Ecological determinants of species diversity of arctic sandpipers near Barrow, Alaska. Ph.D. Diss., Univ. of California.

Masman, D., S. Daan and G. J. A. Beldhuis. 1988. Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. Ardea 76:64-81.

Mathiu, P. M., O. W. Johnson, and P. M. Johnson. 1989. Basal metabolic rate of Pacific Golden-Plovers . Wilson Bull. 101:652-654.

Maxon, S. J., and L. W. Oring. 1980. Breeding season time and energy budgets of the polyandrous spotted sandpiper. Behaviour 74:200-263.

McAuley, D. G., J. R. Longcore and G. F. Sepik. 1990. Renesting by American Woodcocks (Scolopax minor) in Maine. Auk 107:407-410.

McAuley, D. G., J. R. Longcore, and G. F. Sepik. In press. Methods for woodcock research: pitfalls, crevasses, and progress. Proc. 8th Woodcock Symp.

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

Monteith, J. L. 1973. Principles of environmental physics. Edward Arnold Publications, London.

Mugaas, J. N., and J. R. king. 1981. Annual variation of daily energy expenditure by the black-billed magpie: a study of thermal and behavioral energetics. Studies in avian biology No. 5, Cooper Ornithological Society, 78pp.

Obst, B. S., K. A. Nagy, and R. E. Ricklefs. 1987. Energy utilization by Wilson's storm-petrel (Oceanites oceanicus). Physiol. Zool. 60:200-210.

Paladino, F. V. 1989. Constraints of bioenergetics on avian population dynamics. Physiol. Zool. 62:410-428.

Phelps, N. E. 1986. The influence of earthworm abundance on woodcock diurnal habitat use in Maine. M. S. Thesis, Penn. State Univ., 76pp.

Rabe, D. L., H. H. Prince and E. D. Goodman. 1983. The effect of weather on bioenergetics of breeding American woodcock. J. Wildl. Manage. 47:762-771.

Reifsnyder, W. E., and H. W. Lull. 1965. Radiant energy in relation to forests. U.S. Dept. Agric. Forest Service Tech. Bull. No. 1344.

Ricklefs, R. 1974. Energetics of reproduction in birds. Page 152-292 in R. Paynter, ed. Avian energetics. Nuttall Ornithol. Club., Cambridge, Massachusetts. 334pp.

Robinson, D. E., G. S. Cambell, and J. R. King. 1976. An evaluation of heat exchange in small birds . J. Comp. Physiol. 105:153-166 .

Rotenberry, J. T. 1980. Bioenergetics and diet in a simple community of shrubsteppe birds. Oecologia 46:7-12.

Sepik, G. F., R. B. Owen, Jr., and T. J. Dwyer. 1983. The effects of drought on a local woodcock population . Trans. N.E. Fish and Wildl. Conf. 40:1-8 .

Sheldon, W. G. 1967. The book of the American woodcock. Univ. Massachusetts Press, Amherst, 227pp.

Vander Haegen, W. M., W. B. Krohn, and R. B. Owen, Jr. In press a. Care, behavior, and growth of captive American woodcock. Proc. 8th Woodcock Symp.

Vander Haegen, W. M., R. B. Owen, Jr., and W. B. Krohn. In press b. Effects of weather on earthworm availability and spring food habits of American woodcock. Proc. 8th Woodcock Symp.

Veghte, J. H., and C. F. Herreid. 1965. Radiometric determinations of feather insulation and metabolism of arctic birds. Physiol. Zool. 38:267-275.

Walsberg, G. E., and J. R. King. 1978. The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76:185-189.

Weathers, W. W. 1985. Energy cost of incubation in the canary. Comp. Biochem. Physiol. 81A:411-413.

Weathers, W. W., W. A. Buttermer, A. M. Hayworth, and K. A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. Auk 101:459-472.

Wiens, J. A., and G. S. Innis. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. Ecology 55:730-746.

APPENDIX A

Effect of ambient temperature on oxygen consumption by individual woodcock.

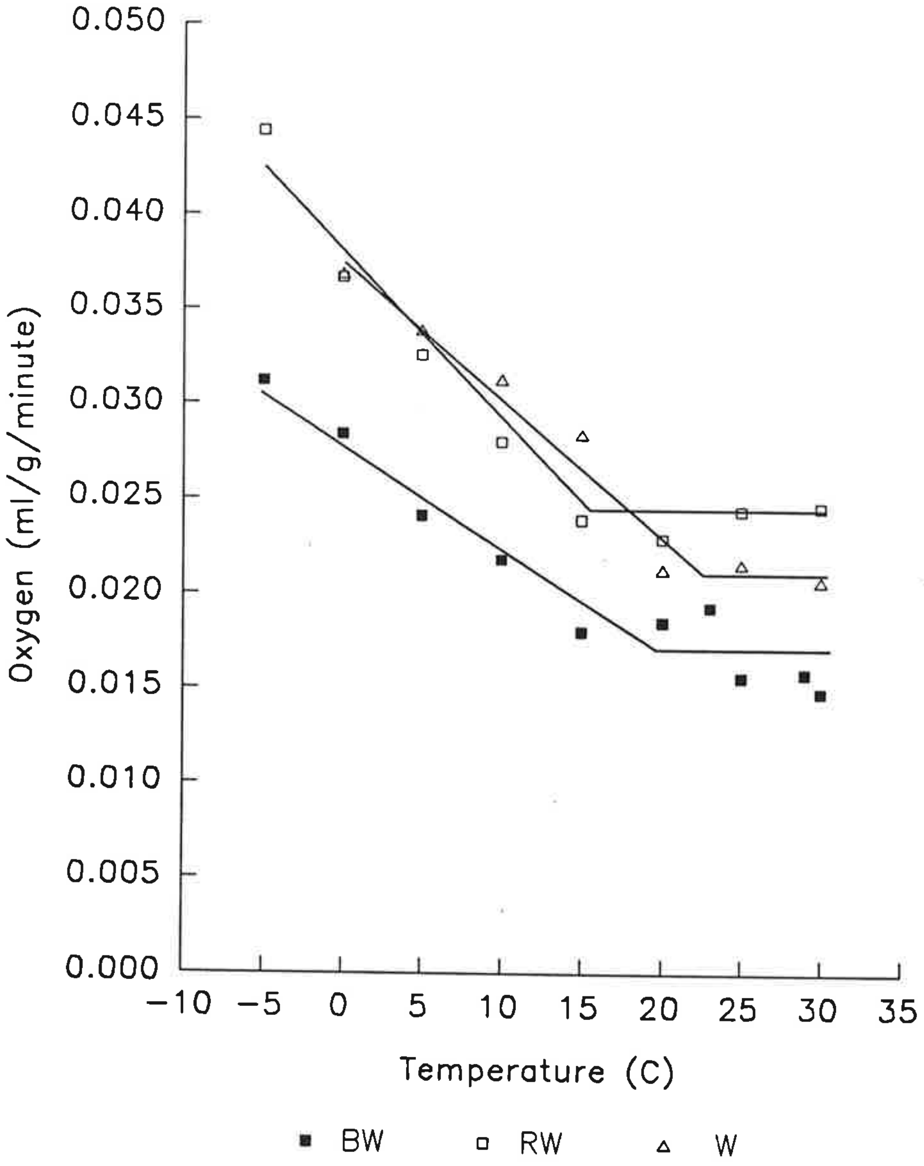


Figure A.1. Effect of ambient temperature on oxygen consumption by captive-reared female American woodcock. Individual birds designated by leg-band color codes.

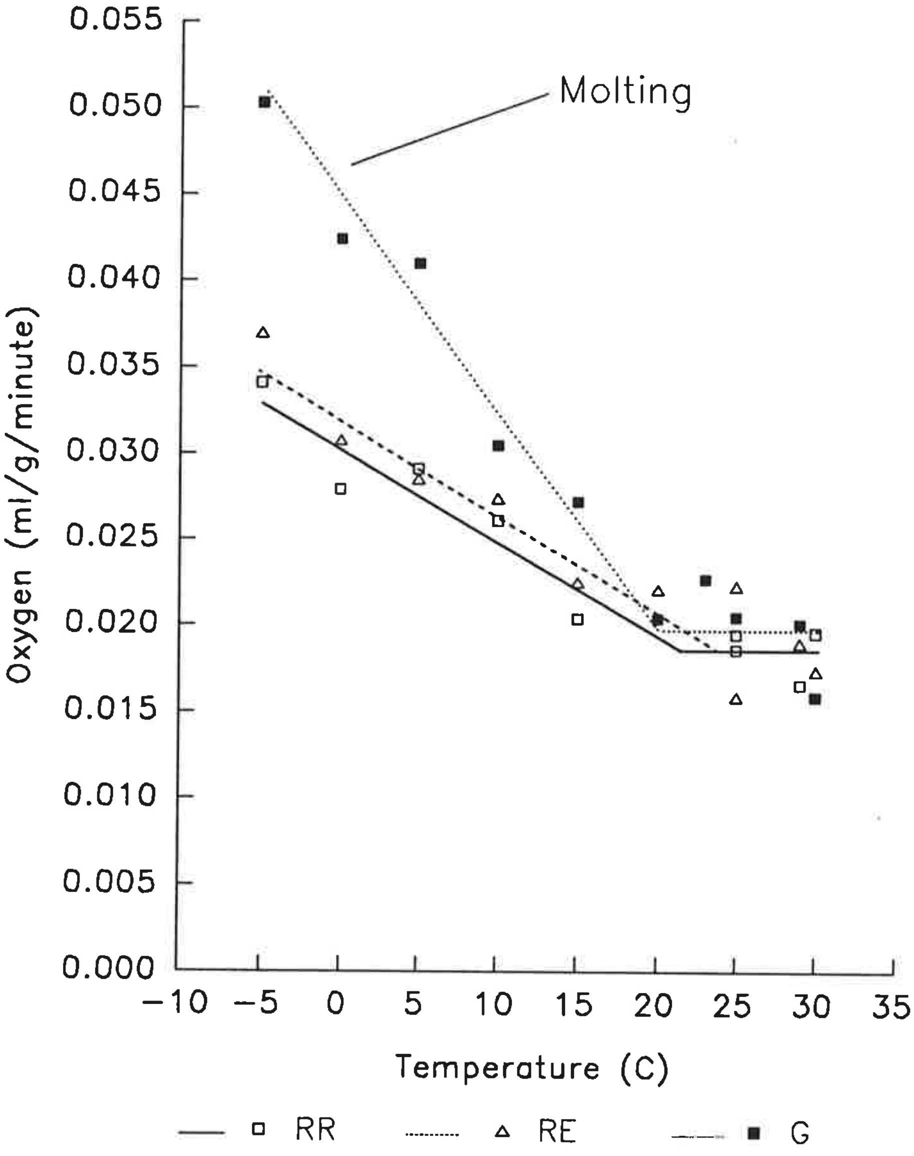


Figure A.2. Effect of ambient temperature on oxygen consumption by captive-reared male American woodcock. Individual birds designated by leg-band color codes.

APPENDIX B

THERMOREGULATION MODEL

The first step involved determining r_t (total resistance) from measurements of H_m obtained from captive woodcock. The program calculated r_t from hourly averages of microclimate temperature using the formula:

$$r_t = \rho c_p(T_b - T_e)/H_m - (H_m E_f) \qquad (1)$$

where H_m is the metabolic heat production and is expressed in W/m^2 (surface area of a 190g woodcock was estimated from the formula in Walsburg and King [1978]). E_f is the fraction of metabolic heat lost through evaporation and was estimated from equation 56 in Calder and King (1974), and the volumetric heat capacity of air (ρc_p) is a constant (1,200 j/m^3/C) (Campbell 1977:6). Body temperature was estimated as 40 ^{o}C (Mathiu et al. 1989).

Whole-body thermal resistance (r_b) was then calculated from the equation:

$$r_b = r_t - r_e, \qquad (2)$$

where r_e is the parallel equivalent resistance of a radiative resistance (r_r) and a convective resistance (r_a), such that

$$r_e = r_r r_a/(r_r + r_a). \qquad (3)$$

Radiative resistance is derived from the equation:

$$r_r = \rho c_p/4\sigma\epsilon T_a^3, \qquad (4)$$

where σ is the Stephan-Boltzman constant, ϵ is the emissivity of the bird's plumage (estimated as 0.98 [Gates 1980:249]), and T_a is air temperature in degrees K. Convective resistance to heat flow in the boundary layer of air around a birds plumage (r_a) is defined as the parallel sum of a forced convective resistance (r_{fo}) and a free convective resistance (r_{fr}), and is calculated as

$$r_a = r_{fr}r_{fo}/(r_{fr} + r_{fo}), \qquad (5)$$

where

$$r_{fo} = 310(d/u)^{0.5} \qquad (6)$$

and

$$r_{fr} = 820[d/([T_s - T_e])^{0.25}. \qquad (7)$$

In calculating r_a, d is the diameter of the bird in meters (0.07 m, measured on 4 adult females), u is wind speed in m/s, and T_s is the surface temperature of the birds plumage (estimated from the equation in Veghte and Herreid [1965], where $T_s = 12.5 + 0.7T_a$). Wind speed in the metabolic chamber was negligible and was estimated as 0.05 m/s (Weathers et al. 1984).

Using this procedure, a value for r_b was derived for birds in the metabolic chamber while exposed to temperatures equivalent to those in the field. Extrapolation of r_b values from chamber to field conditions required modification for the effects of wind, using the formula:

$$r_b' = r_b - ([0.10u^{0.5}]r_b). \qquad (8)$$

This formula (Weathers et al. 1984) is based on an observed 10-15% decrease in r_b per unit increase in $u^{0.5}$. Whole-body resistance in the field (r_b') was then combined with r_e to derive a field r_t for each hour (to account for turbulent wind flow in the field, r_e was recalculated using $r_{fo} = 246(d/u)^{0.5}$ [Weathers et al. 1984]). These values were then used in equation (1) to derive net metabolic heat production (H_m - H_mE_f), which was used to calculate field metabolic rate (H_f):

$$H_f = [H_m - (H_mE_f)]\ [(1/(1 - E_f)]. \qquad (9)$$

The driving variable in this model of thermoregulatory costs is the operative temperature affecting the bird (T_e). Operative temperature is derived from T_a, shortwave radiation absorbed by the bird, and longwave radiation both striking the bird and emitted from the birds' plumage. Because woodcock under a forest canopy would likely receive little significant shortwave radiation, and because microenvironments beneath a closed canopy approximate a blackbody radiating environment (Gates 1980:149), T_a should approximate T_e for birds beneath a forest canopy. These conditions existed for incubating and brood-rearing hens after leaf-out (ca. 15 May), and for prenesting and incubating hens using coniferous cover. Prior to leaf-out, the birds' radiative environment depended on canopy type and sky conditions. Birds in open cover received direct shortwave radiation during the daylight hours under a clear or partly cloudy sky, while their longwave radiant flux depended upon cloud conditions. Longwave radiation emitted from the sky depends upon the atmospheric temperature and is greater under cloudy conditions (Campbell 1977:58).

Operative temperature was estimated from equation 7.17 in Campbell (1977;94):

$$T_e = T_a + (r_e/\rho c_p)(R_{abs} - \epsilon\sigma T_a^4), \quad (10)$$

where R_{abs} is the total radiation absorbed by the birds, and $\epsilon\sigma T_a^4$ is the estimated longwave radiant loss from the birds surface. Absorbed radiation was estimated from the equation:

$$R_{abs} = KT(0.5)(1 - aA) + KT(0.5)(as-(aAas)) + L_s(0.5)(1-rA) + L_g(0.5)(1-rA), \quad (11)$$

based on the equation in Jorde (1986), where KT = total shortwave radiation (W/m^2), aA = shortwave reflectivity of the birds plumage (0.28 for the dorsal surface of a bobwhite quail [Gates 1980:260]), as = shortwave reflectivity of the ground surface (estimated as 0.2 [Campbell 1977:54]), L_g is the longwave radiation emitted by the ground (estimated as 0.98 [Reifsnyder and Lull 1965]), rA = longwave reflectivity of the birds plumage (estimated as 0.02 [Gates 1980:249]), and L_s is the longwave radiation emitted by the sky. Values for L_s were determined from average cloud cover as estimated from mean insolation data recorded at the main weather station. Mean insolation values of < 0.1, 0.1 - 2.0, and > 2.0 W/m^2 were estimated to represent cloud cover values of 0, 50, and 100%, respectively, after comparing a sample of insolation data and visually-estimated cloud cover. Under partly cloudy or overcast skies, L_s was determined from the Stephan-Boltzman equation (Campbell 1977:49):

$$L_s = \epsilon \sigma T_a^{\,4}, \qquad (12)$$

where ϵ is the emissivity of the sky, σ is the Stephan-Boltzman constant, and T_a is the air temperature in degrees K. For overcast days, emissivity was set equal to 1 (Gates 1980:150). Under partly cloudy conditions (50% cloud cover), ϵ was estimated from equation 5.14 in Campbell (1977:58):

$$\epsilon_{ac} = \epsilon_a + C\,(1-\epsilon_a-(4\,\Delta T/T_a)), \qquad (13)$$

where C is the proportion of the sky in clouds (set at .50), ΔT is the difference in temperature between the cloud base and the air at the ground (estimated as a constant of 2 K [Montieth 1973]), and ϵ_a is the emissivity of a clear sky, estimated from equation 5.13 in Campbell (1977:58):

$$\epsilon_a = 0.72 + 0.005(T_a). \qquad (14)$$

Estimates of ϵ_{ac} are relatively insensitive to errors in estimating C and ΔT (Campbell 1977:58). Under clear skies, L_s was estimated from equation 7.2 in Gates (1980:152):

$$L_s = (53.1 \times 10^{-14})(T_a{}^6), \qquad (15)$$

where T_a is in degrees K.

Sky and ground components were multiplied by 0.5 because primarily the upper hemisphere of the bird receives direct and diffuse shortwave radiation and longwave radiation from the sky, while the bird's lower hemisphere receives reflected shortwave radiation and longwave radiation from the ground. Shortwave radiant flux was measured by pyranometers at the microclimate sites.

LIST OF SYMBOLS

aA	Shortwave reflectivity of plumage
as	Shortwave reflectivity of ground surface
C	Proportion of sky in clouds
d	Bird diameter
E_f	Fraction of metabolic heat lost to evaporation
H_b	Standard (Basal) metabolic rate
H_m	Metabolic heat prodution
H_f	Field metabolic rate
KT	Total shortwave radiation
L_g	Longwave radiation emmitted by ground surface
L_s	Longwave radiation emmitted by sky
R_{abs}	Total absorbed radiation
T_a	Ambient temperature
T_b	Body temperature
T_s	Temperature of plumage surface
T_e	Operative temperature
rA	Longwave reflectivity of plumage
r_a	Boundry layer resistance
r_b	Whole-body thermal resistance
r_b'	Whole-body thermal resistance corrected for wind
r_e	Equivalent resistance

r_{fo}	Resistance to forced convection
r_{fr}	Resistance to free convection
r_r	Resistance to radiative heat transfer
r_t	Total resistance
u	Wind speed
σ	Stephan-Boltzman Constant
ϵ_a	Emissivity of clear sky
ϵ_{ac}	Emissivity of partly cloudy sky
ρc_p	Volumetric heat capacity of air

BIOGRAPHY

William Matthew Vander Haegen was born on 8 June 1959, in Winchester, Massachusetts. He attended public schools in Reading Massachusetts and graduated from Reading Memorial High School in June 1977.

From 1978 through 1980 Matt attended Salem State College in Salem, Massachusetts, studying biology and geology, and transferred into the wildlife program at the University of Massachusetts, Amherst, in January 1981. He received his Bachelor of Science in Wildlife Management in 1983 and his Master of Science in Wildlife and Fisheries Biology in 1987. Matt entered the Doctoral program in Wildlife Biology at the University of Maine, Orono, in February 1987.

Matt is a member of The Wildlife Society and served on the national Student Affairs Committee. He also belongs to the American Ornithologists' Union and the Cooper Ornithological Society. He is currently employed as a research wildlife biologist with the U. S. Forest Service, Northeastern Forest Experiment Station. Matt is a candidate for the Doctor of Philosophy degree in Wildlife at the University of Maine in May 1992.