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BIOENERGETICS OF THE WILD TURKEY
IN MICHIGAN

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Brian Thomas Gray

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BIOENERGETICS OF THE WILD TURKEY
IN MICHIGAN

By
Brian Thomas Gray

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ABSTRACT

BIOENERGETICS OF THE WILD TURKEY IN MICHIGAN

By

Brian Thomas Gray

The bioenergetics of the eastern wild turkey (Meleagris gallopavo) in Michigan was studied from December, 1983 through March, 1985. The objective of this study was to estimate daily energy expenditure (DEE) in relation to ambient temperature and activity of free-ranging turkeys during winter months. This was accomplished by monitoring metabolism and gross energy (GE) intake of captive turkeys as a function of ambient temperature, and through time-activity observations on free-ranging birds.

DEE models predicted juvenile females as the most susceptible to winter starvation followed by juvenile males, adult females, and adult males, respectively. During periods of severe cold and zero food intake, juvenile females were predicted to succumb within 8 days, whereas adult males were predicted to survive 20 days.

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INTRODUCTION

The original range of the eastern wild turkey (Meleagris gallopavo silvestris) included the southern portion of Michigan's lower peninsula, roughly south of a line from Saginaw Bay to Muskegon County (Leopold 1931 in Lewis 1962). The wild turkey disappeared from the Michigan area around 1900 (Ignatoski 1973), with the last recorded observation in Van Buren County in 1897 (Barrows 1912 in Aldrich 1967). This disappearance coincided with the end of a 40 year era of logging that swept across the entire southern peninsula (Petersen 1979). As the pine forests of the north were cleared mixed stands of oak (Quercus spp.), beech (Fagus grandifolia), and maple (Acer spp.) developed in their place, changing the composition of these northern forests.

In an effort to reintroduce turkeys in Michigan, Pennsylvania game farm turkeys (3/4 wild hens serviced by wild toms) were released at 15 different locations in the southern peninsula between 1954 and 1963. Fourteen of these release sites were located north of the birds' original range in large tracts of second growth hardwoods created by the logging era. The releases were considered successful and annual hunting seasons have been held in designated areas since 1965. Current distribution of the reintroduced birds remains north of the original range, with only 1 flock of game farm descendants in the southern part of the state (Ignatoski 1973). Bronner (1983) reported 75% of the northern birds winter on private lands consisting of hunting clubs

and farm lands. This study focuses on these flocks of turkeys.

Snow depth during winter is one of the most important physical factors influencing turkey populations in the upper midwest (Porter et al. 1980, Porter 1983), with depths over 25 cm greatly reducing mobility (Austin and DeGraff 1975). Turkeys wintering in forested areas become dependent upon localized food sources and are restricted to these small areas during periods of deep powder snow even after food sources become depleted (Hayden 1980). In addition to hindering movement, heavy snowfall also makes localized winter foods such as mast and waste grain unavailable. Northern lower Michigan receives over 150 cm of snow annually, with accumulations over 30 cm common from late December through early March (Stromme 1967). In late fall, large flocks of northern Michigan turkeys return to established wintering areas where food was available the previous year (Kulowiec and Haufler 1985a). Successful flocks are associated with active farms where grain is readily available from feedlots, corn cribs, or as waste in the field, or private lands where artificial feeding programs are practiced. Michigan Department of Natural Resources (MDNR) wildlife biologists report that the majority of starvation related mortalities occur on public lands isolated from agricultural and artificial feeding areas. Populations wintering on these areas fluctuate according to the severity of winter, whereas populations on private lands appear more stable. Before the suitability of winter habitat on both public and private lands can be adequately assessed, the energetic needs of wintering turkeys must be quantified.

Temperature and changes in the time allocated to various activities are the major determinants of changes in a bird's daily energy expenditure

(DEE). Knowledge of metabolic rates at different temperatures, coupled with knowledge of time allocated to activities during these temperatures, would help researchers better understand energy budgets of wild birds. Standard methods used to estimate DEE include: (1) extrapolations from laboratory measurements of oxygen consumption or metabolizable energy intake, (2) time-activity studies of free-ranging birds, quantified in energy terms by extrapolations of laboratory data, and (3) estimates of energy consumption by indirect methods in free-living birds (King 1974). This study was designed to estimate DEE in relation to temperature and activity of free-ranging turkeys, during winter months, using a combination of methods 1 and 2. With this information the importance of public lands, agricultural areas, and artificial feeding programs to the turkeys' winter survival could be assessed, and management plans geared toward improving the winter habitat developed.

METHODS

Source of Captive Turkeys

A captive flock of turkeys was established in the spring of 1983. The flock originated from 3 sources: eggs collected from nests of wild birds in northern Michigan, eggs obtained from the Van Atta Game Farm located in Haslett, Michigan, and eggs obtained from the Pilarski Game Farm located in Fairview, Michigan. All eggs were incubated and hatched at the Mason Wildlife Facility. Poults were pedigree hatched, leg banded and moved to brooder houses. At 2 weeks of age they were moved to 3 x 20 m outdoor pens with food and water available ad libitum. Purina Startena was fed the first 4 weeks. Diets were shifted to Purina Turkey Growena through the first winter and Purina Maintenance Chow thereafter.

Metabolic Measurements

Metabolic measurements were made in a conventional open circuit system (Hill 1972), using a Beckman paramagnetic oxygen analyzer. Pressurized ambient air flowed through Drierite (a drying agent), through flowmeters (Brooks rotameters), into the metabolic chambers, back through Drierite through an automated flow selector, through Ascarite (used to absorb CO₂), through more Drierite and into the oxygen analyzer (Fig. 1). Two PVC metabolic chambers, measuring 32 x 64 x 40 cm for

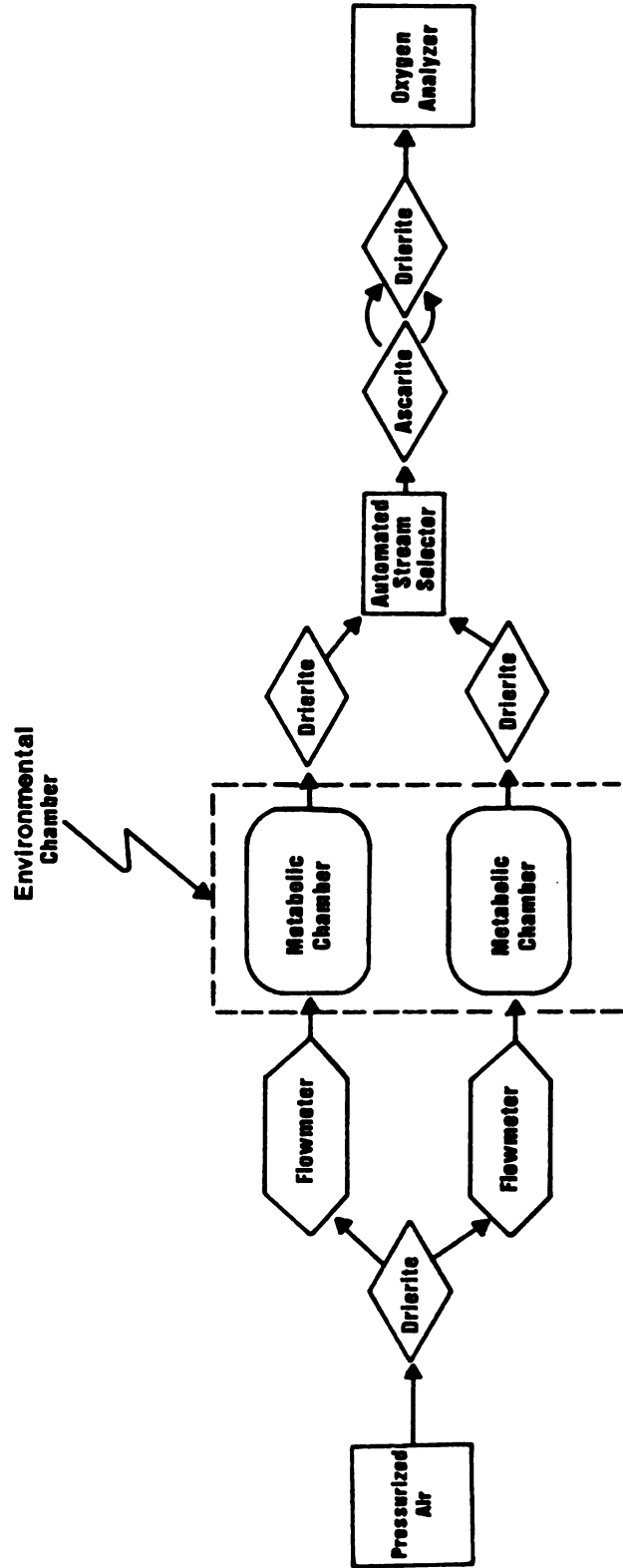


Fig. 1. Flow diagram of the open circuit system used to measure oxygen consumption in captive wild turkeys.

females and 36 x 76 x 46 cm for males, were housed inside an environmental chamber with a temperature range of -15°C to $+50^{\circ}\text{C}$. Copper-constantan thermocouples with a Honeywell chart recorder were used to monitor temperatures ($\pm 1^{\circ}\text{C}$) in the metabolic chambers. A mercury barometer was used to determine atmospheric pressure and a mercury-in-glass thermometer was used to monitor flowmeter temperature.

Metabolic rates of turkeys were measured during 2 winter and 1 summer periods (Table 1). Winter measurements were taken from February 16 to March 18, 1984, on juvenile females. Winter tests conducted on juvenile males and adults of both sexes were run from December 29, 1984, through March 20, 1985. Measurements during the summer were taken on adults of both sexes from July 5 to September 10, 1984.

Test sequences of metabolic measurements are referred to as chronological periods; "winter juvenile" and "winter adult" represent measurements conducted on juveniles and adults during winter months, and "summer adult" represents measurements conducted on adults during summer. During each chronological period, metabolic measurements were obtained at 5 target temperatures (-10°C , -5°C , $+5^{\circ}\text{C}$, $+15^{\circ}\text{C}$, and $+25^{\circ}\text{C}$) for each bird. Values at the 3 highest temperatures were obtained sequentially while measures at the 2 lowest temperatures were obtained on separate runs. The test schedule was randomized, and the same test birds were not utilized more than once with a 5-day period.

Two birds were run simultaneously through each metabolic test. Birds were fasted 24 h prior to the metabolic measurements. Following this, the birds were weighed to the nearest gram, transported to the laboratory and placed into the metabolism chambers. The metabolism

Table 1. Sex, age, source and number of captive turkeys used in metabolic experiments during each seasonal period.

Season	Sex	Age	Source		Total
			Wild	Pilarski	
Winter	Female	Juvenile	2	5	7
		Adult	4	5	9
	Male	Juvenile	-	6 ^a	6
		Adult	1	5	6
Summer	Female	Adult	4	5	9
	Male	Adult	1	5	6

^aBirds were progeny of Pilarski males x Wild females raised in captivity.

chambers were then placed into the darkened climate chamber. The birds were then allowed to adjust for 3 h, as recommended by Prince (1979). Summer metabolic measurements started after 21:50 hrs and winter measurements after 18:00 hrs. When testing a bird at more than 1 temperature per night (i.e., highest 3 temperatures), 1 h was allowed for adjustment after the new target temperature was reached. Temperatures were always lowered for successive tests and never raised as this could result in a difference in the temperature-metabolism slope (Pohl 1969). After the adjustment period, four 5-minute oxygen (O_2) samples were collected over a 1 h period for each bird (i.e., one 5-minute sample was collected every 15 minutes for each bird). The lowest 3 of the 4 O_2 values obtained for each bird were averaged to obtain a mean rate of consumption for the given temperature. Mean O_2 values were corrected, without knowledge of the respiratory quotient, using the table in Hill (1972). Rate of oxygen consumption ($\dot{V}O_2$) was obtained by:

$$\dot{V}O_2 \text{ (ml } O_2/\text{g/hr)} = [\text{corrected } O_2 \text{ difference} \times \text{flow rate (ml/hr)} \\ \times \text{STP}]/\text{Body weight (g)}$$

Where $\text{STP} = 273/[(273 + \text{flowmeter temp. (}^\circ\text{C)})] \times \text{Barometric pressure (mm Hg)}/760\text{mm}$. $\dot{V}O_2$ values were converted into energy values (kJ/g/hr) using the following formula:

$$\text{kJ/g/hr} = \text{ml } O_2/\text{g/hr} \times 0.02009$$

where $\text{ml } O_2 = 0.0048\text{kcal}$ (Hill 1976) and $\text{kcal} = 4.185\text{kJ}$ (Scott et al. 1982).

Least squares linear regression was used to evaluate the effect of temperature on metabolic rate. Differences in regression equations between sources and between sexes were tested using a t-test procedure.

Differences in regression equations between test periods were tested with an analysis of covariance (Zar 1973).

Gross Energy Intake

Gross energy (GE) intake of captive turkeys was monitored during 1 summer and 2 winter periods (Table 2). Food consumption of juvenile birds was measured on alternate days from January 10 to March 16, 1984. Food consumption of adults was measured on alternate days from July 3 to August 2, 1984, and from February 20 to March 22, 1985. Purina Turkey Growena (18.08 kJ/g) was fed ad libitum the first winter and Purina Gamebird Maintenance Chow (16.49 kJ/g) was fed the following summer (1984) and winter (1985). Birds were placed in individual 2 x 3 m outdoor pens during the food trials, and allowed 1 week for adjustment. Body weight was measured every 6 days. Water or snow was supplied ad libitum. Gross energy intake was standardized for each bird by determining the kiloJoule intake per gram body weight per day. Mean temperature $((\text{max} + \text{min})/2)$ was recorded daily using max/min thermometers. The effect of temperature on GE intake was analyzed using the least squares regression techniques discussed in Nie et al. (1975). Differences in GE intake between chronological periods were tested in each sex using an analysis of variance design and Duncan's Multiple Range test (Steel and Torie 1980). Differences in GE intake between sexes and within chronological period, were tested using the two-sample t-test (Gill 1981).

Table 2. Sex, age, source and number of captive turkeys used in food trials during each seasonal period.

Season	Sex	Age	Source			Total
			Wild	Pilarski	Van Atta	
Winter	Female	Juvenile	4	2	2	8
		Adult	3	2	2	7
	Male	Juvenile	1	-	3	4
		Adult	1	3	1	5
Summer	Female	Adult	3	-	2	5
	Male	Adult	1	3	2	6

Time Activity Observations

Behavioral observations of free-ranging turkeys were made on a 165 ha dairy farm south of Fairview, Michigan (Fig. 2). The property consisted of a mixture of cornfields, pasture, fallow fields, and second growth woodlots. Woodlots were characterized by red maple (Acer rubrum), sugar maple (A. saccharum), and oak (Quercus spp.). MDNR 1985 winter count estimated 500 birds wintering on the area. This was one of the larger flocks of wintering turkeys in northern Michigan.

Time-activity observations were made on January 26, 27; February 2, 3, 4, 16, 17, 23, 24; and March 2, 3, 11, 12, 1985. Each day (1/2 hr before sunrise to 1/2 hr after sunset) was divided into 3 equal time blocks: (1) early morning; (2) midday; and (3) late afternoon. Each block was further divided into 2 periods, first and last half. One period per block was chosen randomly, without replacement, every other sampling day, with observations made during the opposite period the following sampling day.

Observations were made from a vehicle (Fig. 2). Five male and 5 female turkeys were observed per time block each day, weather permitting. Each bird was observed individually for 5 minutes using a 20-45x zoom spotting scope. If a bird was lost from view before 3 minutes of observation, the data were not used and another bird was chosen for observation. Potential sample birds were selected by first visually estimating size of various flocks on the study site (i.e., field, woodlot, feedlot, barn area) and using a weighted procedure (Quinlan and Baldassarre 1984) to determine what flocks

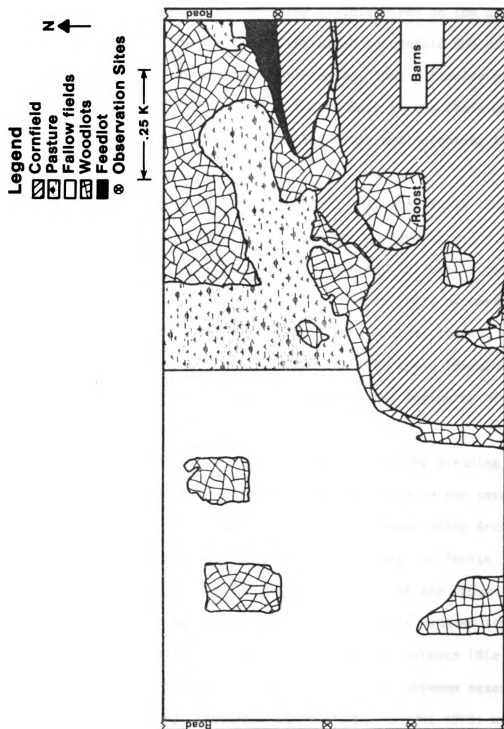


Fig. 2. Dairy farm used for winter behavioral observations.

to select samples from. Once a flock was selected, the number of samples obtained for each sex was determined by estimating the size of the flock relative to the remaining visible birds on the study area. For example, if a flock was estimated to contain 60% of the visible females and 40% of the visible males, then 3 females and 2 males were sampled from the flock. Individuals in the flock were chosen by randomly focusing the spotting scope and selecting the first bird that came into focus.

Activity of individuals was recorded instantaneously (Altman 1974) every 15 seconds. Activities were categorized as: (1) feeding, (2) resting, (3) comfort movements, (4) walking, (5) alert, and (6) courtship/antagonistic. Ambient temperature (°F), barometric pressure (mm Hg), precipitation (none, light, medium, heavy), cloud cover (0-25%, 26-50%, 51-75%, 76-100%), and wind speed (Beaufort scale in Platt and Griffiths 1964) were recorded at the beginning of each individual observation.

Percent time spent per activity was obtained by dividing the number of instantaneous recordings of each activity by the total number of recordings. All percentage data were transformed using Arcsin transformation before statistical analysis (Steele and Torrie 1980).

A one way analysis of variance technique (Kim and Kohout 1975) was used to test for differences in activity levels between time periods for each sex x activity combination. "Student's" t-tests (Nie et al. 1975) were used to test for daily differences between sexes in each activity category. Spearman correlations (Siegal 1956) were used to identify relationships between climatic variables and activities during the different periods of the day.

RESULTS

Metabolism Measurements

$\dot{V}O_2$ at 25° C did not differ ($P>0.05$) between sources of turkeys of the same sex during any chronological period, therefore values for Pilarski and Wild birds were pooled in each sex (Table 3.). $\dot{V}O_2$ at 25° C also did not differ ($P>0.05$) between males and females within any chronological period. $\dot{V}O_2$ of juvenile turkeys in winter and adults in summer were not significantly different ($P>0.05$), and both were higher than that of adults measured in winter ($P<0.05$).

Within each chronological period, measurements made at 15° C appeared to be above T_{lc} (lower critical temperature) in some turkeys and below T_{lc} in others (i.e., $\dot{V}O_2$ at 15° C was equal to $\dot{V}O_2$ at 25° C in some birds, while in others $\dot{V}O_2$ at 15° C was greater). Therefore, including 15° C measurements in regression analysis resulted in smaller regression coefficients and higher estimated T_{lcs} in each equation. Due to this potential error, $\dot{V}O_2$ consumption measured at 15° C was deleted from analysis.

Metabolic readings at +5°, -5°, and -10° C were used in regression analysis of temperature and metabolic rate. A negative linear relationship ($P<0.001$) existed between temperature and $\dot{V}O_2$ for all ages and sexes of turkeys tested below the T_{lc} (Fig. 3). There were no differences in regression coefficients (slopes) or elevations ($P>0.05$) between sources of females or males within chronological period.

Table 3. $\dot{V}O_2^a$ (ml/g/hr) of fasted turkeys during 3 chronological periods at 25° C.

Sex	Chronological Period			
	Winter Juvenile	(n) ^c	Summer Adult	Winter Adult
Female	0.403 $\pm$ 0.014	(7)	0.422 $\pm$ 0.007	0.336 $\pm$ 0.007
Male	0.388 $\pm$ 0.008	(6)	0.424 $\pm$ 0.009	0.337 $\pm$ 0.008
Pooled	0.398 ^A $\pm$ 0.010 ^b	(13)	0.423 ^A $\pm$ 0.005	0.336 ^B $\pm$ 0.005

^a

$\bar{x} \pm$ S.E.

^bPooled $\dot{V}O_2$ with different capital letters differ (P < 0.05).

^cNumber birds tested.

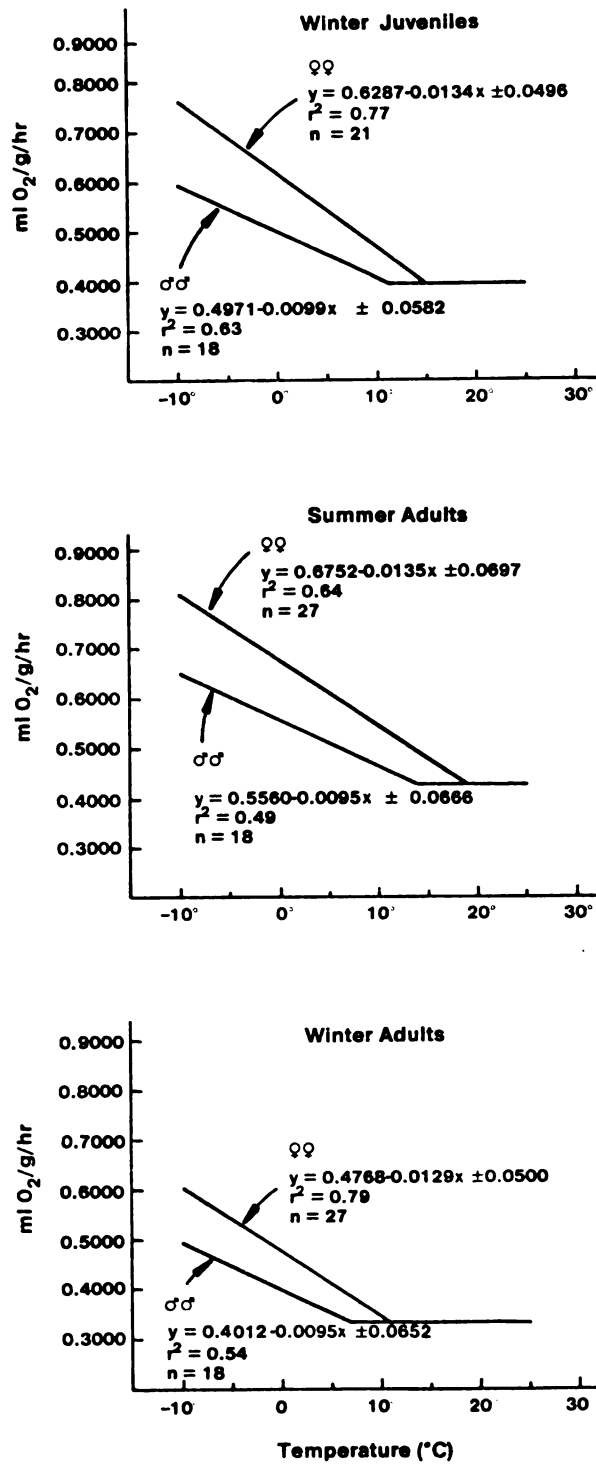


Fig. 3. Metabolic rates (ml O₂/g/hr) of juvenile and adult turkeys measured at various temperatures during 3 chronological periods.

The regression coefficients for males, however, were significantly lower than females ($P < 0.05$) within each chronological period. Analysis of covariance revealed turkeys of the same sex had equal regression coefficients ($P > 0.05$) across chronological periods, but the elevations of regression equations varied ($P < 0.05$) consistently across chronological periods. Regression equations for adults of both sexes in summer had the highest intercepts, juveniles tested in winter had the next highest, and adults tested in winter, the lowest.

Lower critical temperatures were estimated by placing $\dot{V}O_2$ equal to $\dot{V}O_{2c}$ at 25° C and solving for x in each regression equation in Fig. 3 (Table 4). The trend for T_{lc} across chronological periods was, from highest to lowest, adults in summer, juveniles in winter, and adults in winter, with females consistently the highest.

Gross Energy Intake

Gross energy intake and body weight of captive turkeys changed with season (Fig. 4). Temperatures ranged from -20° C to +5° C during the winter of 1984. Body weights of juvenile females in winter 1984 food trials averaged 3350 ± 174 g ($\bar{x} \pm$ S.E.) at the beginning and gradually increased by 9% to 3650 ± 265 g 66 days later. Body weights of juvenile males averaged 6370 ± 620 g at the beginning and increased by 23% to 7840 ± 1095 g at the end. GE intake during the winter of 1984 averaged 0.552 ± 0.015 kJ/g/day and 0.498 ± 0.017 kJ/g/day for females and males respectively. The response of GE intake to varying temperature was obtained by comparing mean daily GE intake over 6-day periods with mean temperatures of those periods. The response was linear

Table 4. Estimated T_{lc} ($^{\circ}\text{C}$) of fasted turkeys during 3 chronological periods.

Sex	Chronological Period		
	Winter Juvenile	Summer Adult	Winter Adult
Female	15	19	11
Male	11	14	7

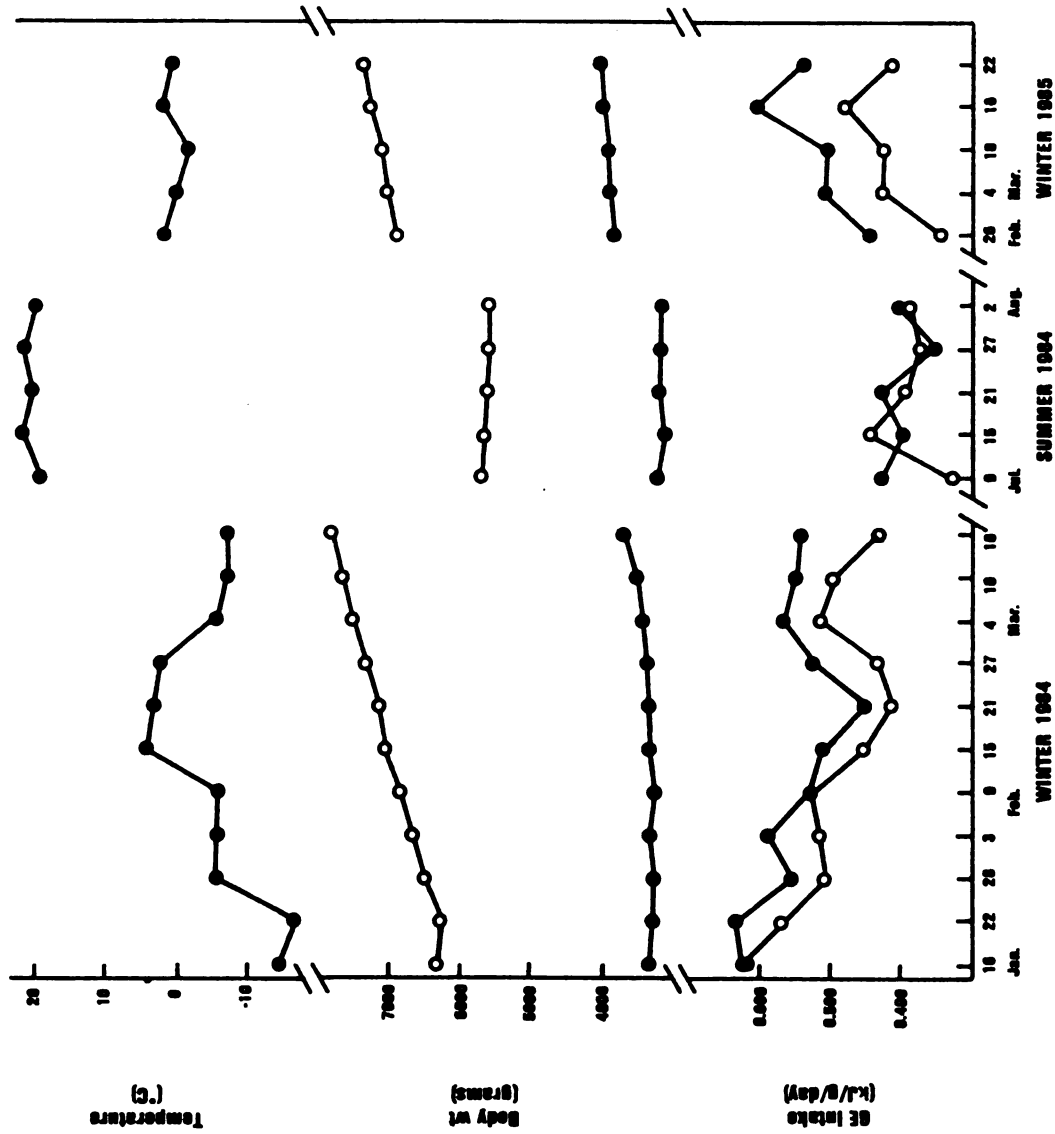


Fig. 4. Seasonal changes in G.E. intake, body weight, and ambient temperature in caged male (o) and female (•) turkeys housed out-of-doors. N=8 juvenile females and 4 juvenile males for winter 1984, N=5 adult females and 6 adult males for summer 1984, and N=7 adult females and 5 adult males for winter 1985.

with the equation for females:

$$y = 0.5185 - 0.0071x \quad (R^2 = 0.129) \quad (P < 0.01)$$

and males:

$$y = 0.4545 - 0.0088x \quad (R^2 = 0.242) \quad (P < 0.01)$$

where $y = \text{kJ/g/day}$, $x = ^\circ\text{C}$. The relation between GE intake and temperature was likely confounded by increasing body size.

Temperatures ranged from 16.1°C to 25.6°C during the food trials in the summer of 1984. Body weights of adult females decreased slightly from $3250 \pm 143\text{g}$ at the beginning to $3200 \pm 170\text{g}$ at the end of the 30-day trial. Body weights of adult males declined gradually from $5890 \pm 434\text{g}$ to $5660 \pm 371\text{g}$. GE intake averaged 0.404 ± 0.015 and $0.388 \pm 0.013 \text{ kJ/g/day}$ for females and males respectively. No relationship existed ($P > 0.05$) between temperature and GE intake.

Temperature ranged from -5.0°C to $+6.1^\circ\text{C}$ during the winter 1985 food trials. As in the winter of 1984, body weights increased during the food trials. Body weights of adult females gradually increased by 7% from $3810 \pm 98\text{g}$ at the beginning of the food trials to $4070 \pm 144\text{g}$ at the end. Body weights of males increased by 8% from $6880 \pm 447\text{g}$ at the beginning to $7400 \pm 537\text{g}$ at the end of the 30-day trial. GE intake during the winter of 1985 averaged $0.524 \pm 0.018 \text{ kJ/g/day}$ in females and $0.426 \pm 0.019 \text{ kJ/g/day}$ in males. No relationship existed between temperature and GE intake during the winter of 1985.

Birds of both sexes consumed more energy, on a per gram basis, in the winter than in summer ($P < 0.01$). Although temperatures were considerably lower during winter 1984 food trials than winter 1985 food trials, energy consumption of either sex, on a per gram basis, was not different ($P > 0.05$). Body weights of both sexes were heaviest

in winter and lightest in summer. In males, juvenile body weights in winter were heavier than adults due to the source of birds used (Table 2); Van Atta birds were heavier than Pilarski and Wild. Although, on a per gram basis, males consistently consumed less energy than females, only the difference during the winter of 1985 was significant ($P < 0.05$).

Time-Budgets

Observations of a flock of approximately 500 free-ranging turkeys were made from January 26 to March 12, 1985. During this time, most birds restricted their home range to the 160 ha farm (Fig. 1.), feeding in the cornfields, feedlot, and barn area. At night the entire flock roosted in the woodlot west of the barn area. The main source of food appeared to be corn obtained by: (1) eating directly from the corn crib in the barn area, (2) from undigested corn in cattle manure, located in manure piles or spread on fields, or (3) waste corn in fields. In late March, as the snow melted, turkeys foraged heavily in exposed areas, consuming what appeared to be grasses, mast, and waste grain. Although sex could be readily determined during the observations, differences between adult and juvenile birds were not distinguishable.

Temperature during the observations averaged $-5.0^{\circ} \pm 0.6^{\circ} \text{ C}$ ($\bar{x} \pm \text{S.E.}$), ranging from a low of -30° to a high of 6° C . Snow depth averaged 29.5 cm. Percent time allocated to each of the 6 activities remained similar ($P > 0.05$) across daily time periods in both sexes (Fig. 5), and mean daily activities were similar ($P > 0.05$) between

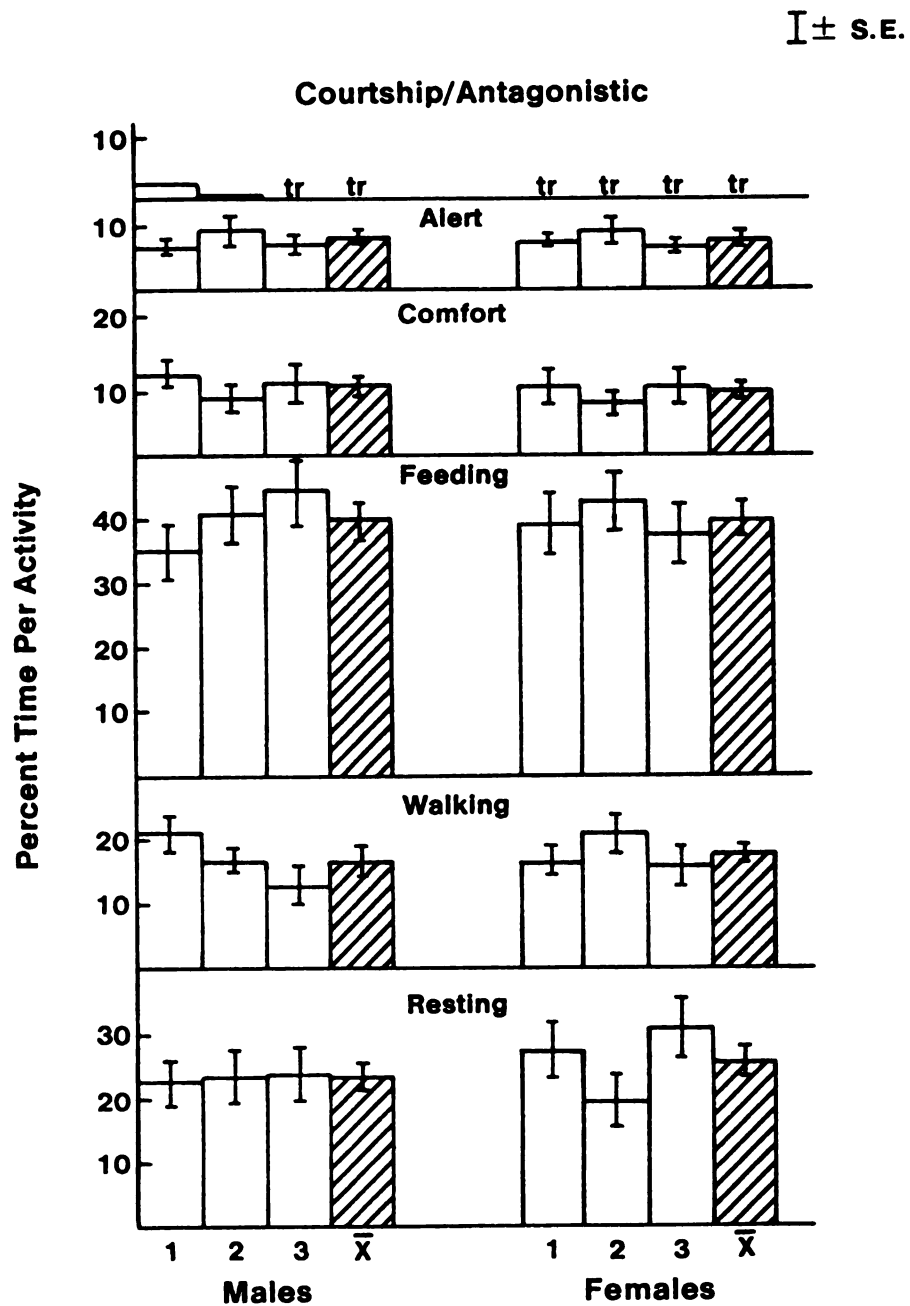


Fig. 5. Percent time spent in activities by turkeys during the first, middle, and last third of the diurnal period. Data shown are seasonal means for diurnal period $\pm$ SE (crosshatched) and time blocks $\pm$ SE within diurnal period (solid). N = 59 turkeys of each sex observed during each time block.

sexes. Feeding was the predominant activity comprising an average of 40% of the day in both sexes, resting was the next at 25%, followed by walking at 17%; comfort movements comprised 10%, alert, 7.5%, and courtship/antagonistic, 0.5%. Although turkeys occasionally flew short distances during the observations, flight amounted to a minute percent of the daily activities; therefore the activity was omitted from observations.

Several activities were correlated with climatic variables within time periods (Table 5). Temperature was correlated negatively with comfort and resting, and positively with feeding during the first 2 diurnal periods. Precipitation was correlated negatively with comfort and resting during the first 2 periods, but positively during the third period. Feeding was the reverse, correlated positively with precipitation during the first 2 periods and negatively during the third period. Cloud cover followed the same trend as precipitation but the correlations were not as strong.

Wind velocity was correlated negatively with percent time alert and positively with walking during the third period. Barometric pressure was negatively correlated with comfort during the third time period and positively correlated with resting during the second time period.

Table 5. Spearman correlations (ρ) among activities of free-ranging turkeys and climatic variables for each time period^a in northern lower Michigan. N = 118 birds observed for each correlation.

Activity	Time Period	Temperature	Precipitation	Cloud Cover	Wind Velocity	Barometric Pressure
Courtship/ Antagonistic	1	0.07	-0.10	0.08	0.01	-0.09
	2	0.11	0.15	0.08	-0.03	0.02
	3	0.14	-0.09	-0.14	0.14	0.01
Alert	1	0.01	0.05	0.06	-0.06	-0.07
	2	0.01	0.03	0.05	-0.16	0.06
	3	0.06	-0.06	-0.14	-0.20*	-0.16
Comfort	1	-0.30***	-0.23*	-0.27**	0.02	0.06
	2	-0.30**	-0.09	-0.06	-0.03	-0.09
	3	0.15	0.24*	0.10	-0.07	-0.31**
Feeding	1	0.53***	0.34***	0.26**	-0.02	-0.12
	2	0.53***	0.22	0.03	0.12	-0.18
	3	-0.17	-0.42***	-0.18	-0.04	0.16
Walking	1	-0.12	0.02	-0.01	-0.15	0.04
	2	0.04	-0.04	-0.01	0.04	-0.03
	3	0.06	0.06	-0.08	0.36**	0.10
Resting	1	-0.48***	-0.27**	-0.31***	0.06	0.14
	2	-0.54***	-0.21*	-0.09	-0.11	0.24**
	3	-0.02	0.47***	0.21*	0.01	-0.01

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

^aFirst, middle, and last third of the diurnal period.

DISCUSSION

Metabolism Measurements

Measurements of oxygen consumption obtained from animals during their normal resting period, in a thermoneutral environment, and in a postabsorptive state, approximate the standard or basal metabolic rate (BMR). Measurements made under these same conditions but at air temperatures outside the thermoneutral range are a linear or near-linear function of air temperature below the thermoneutral range (King 1974). In this study, I refer to these measurements below thermoneutrality as measurements of the existence metabolic rate (EMR).

Kendeigh et al. (1977) noted that although differences in BMR between males and females are sometimes observed, their occurrences are erratic and inconsistent except when there are pronounced differences in body weight. Male turkeys were roughly twice the size of females in this study, yet there was no difference in BMR per gram body weight.

The BMR within a group of related animals is strongly weight-dependent and often adheres to the equation:

$$M = aW^b$$

where M = metabolic rate, W = body mass, a = constant, and b = exponent that describes the effect of size within the group (Calder 1974).

King (1974) developed an equation for non-passerines based on Aschoff and Pohl's (1970) equation:

$$\text{kcal/h} = 3.6W^{0.734}$$

where W = body weight in kg. A comparison of the a values from my data should give some indication of the applicability of their equation to turkeys or other large birds. I compared data from adult turkeys used in my studies (Table 6) and found significant differences among the calculated a values for male and female turkeys. All a values from my data were lower than the value of 3.6 for non-passerines, therefore King's equation appears to overestimate BMR in turkeys. BMRs of adult turkeys, expressed per unit body weight (mlO₂/g/hr), were significantly lower in winter than in summer. The ecological significance of this is complicated by the differences in body weights that existed between winter and summer. Males and females were 26% and 23% heavier, respectively, in winter than summer. Therefore, the difference in metabolism between seasons is confounded by body size. Winter and summer BMRs of adult turkeys expressed per bird (kJ/bird/hr), however, are not significantly different between seasons (P>0.05, paired t-test).

Male turkeys in this study, due to their larger body size, consistently had smaller temperature coefficients than females in all chronological periods. Kendeigh et al. (1977) reported 24 out of 31 species of birds reviewed had lower temperature coefficients in winter than in summer. Temperature coefficients of turkeys in this experiment did not differ between seasons in either sex. Regression equations between resting metabolism and air temperature in each sex differed between seasons due to varying elevations caused by varying T_{lc}, not varying temperature coefficients. Kendeigh et al. (1977) stated that as birds increase in weight the T_{lc} declines at the same

Table 6. The $\bar{a}^c$ values calculated from the equation $M = aW^b$, where M = kcal per hour, $\bar{a}$ = constant, W = weight in kg, and $b = 0.734$.

Chronological Stage	Female		Male	
	N	$\bar{a}$	N	$\bar{a}$
Adult Summer	9	2.7 ± 0.05	6	3.2 ± 0.05
Adult Winter	9	2.3 ± 0.05	6	2.8 ± 0.06

$\bar{a}^c$
 $\bar{x} \pm \text{S.E.}$

rate in all taxa at all seasons. Male turkeys in this study had lower T_{lcs} than females during all chronological periods, but a seasonal difference in T_{lc} was evident in both sexes, with winter T_{lcs} consistently lower than summer. Lower T_{lcs} in avian species during winter could result from better insulation from the plumage or added body fat or a combination of both (Pohl 1971). Kendeigh et al.'s (1977) equation estimating T_{lc} for non-passerines ($T_{lc} = 47.17W^{-0.1809} \pm 1.382$, where W = body weight in grams) predicted T_{lcs} of $9.4 \pm 1.4^{\circ} \text{C}$ for adult males ($\bar{x} = 7300\text{g}$) and $10.6 \pm 1.4^{\circ} \text{C}$ for adult females ($\bar{x} = 3900\text{g}$) used in winter metabolism measurements. These figures compare reasonably with my estimates of 7°C and 11°C for males and females, respectively. Their equation estimates of $10.0 \pm 1.4^{\circ} \text{C}$ for adult males ($\bar{x} = 5400\text{g}$) and $11.1 \pm 1.4^{\circ} \text{C}$ for adult females ($\bar{x} = 3020\text{g}$) used in summer metabolism measurements, however, were considerably lower than my estimates of 14°C and 19°C , respectively.

Gross Energy Intake

Energy intake is a linear function of air temperature in a variety of avian species. Most studies have focused on the relationship of existence (metabolized) energy and temperature (e.g., West 1960, West 1968, Owen 1970), while a few (e.g., Hart 1962) have studied the relationship of temperature and GE intake. I found GE intake to be inversely related to ambient temperature during the first winter of food trials but not the second. The second winter never had temperatures substantially below the thermoneutral zone (i.e., $\bar{x} = 1.3^{\circ} \text{C}$); this is probably why a relationship was not observed.

My captive turkeys tended to increase in weight during the winter food trials and maintain or lose weight during the summer food trials. Adult body weights of both sexes were approximately 25% greater during winter experiments. Bailey and Rinell (1967) reported the same trend; wild turkeys increase in weight throughout the winter, attaining maximum weight just prior to mating season. Weight then declines throughout the spring and reaches a minimum in July and August.

Time Budgets

Turkeys observed during the time budget studies spent most of the day feeding in crop fields or around barnyards, and resting in woodlots adjacent to these areas. Porter (1977) reported the same trend; wild turkeys in southeastern Minnesota fed extensively in cornfields during winter.

Temperature and precipitation were the weather variables most often correlated with activity. Birds tended to feed more on mornings with snowfall, but later in the afternoon, snowfall tended to reduce time spent feeding. Comfort and resting activities were inversely related to feeding activities during all 3 periods. In the morning, when temperatures were bitterly cold, birds would remain inactive until the sun came up or the temperature increased. In the late afternoon, however, temperature had no measurable effect on resting, comfort, or feeding activities.

On windy days, turkeys tended to rest on the leeward side of hills and woodlots, with feeding patterns not markedly different. Wind velocity or calculated wind chill were not correlated with any

activity. There were no correlations between barometric pressure and activity.

Davis (1949) reported turkeys have 2 distinct periods of heavy feeding, mid-morning and mid-afternoon. The remainder of the day is spent resting. Mosby and Handley (1943) found the late afternoon to be the time of heaviest feeding. Bailey (1967), however, believed during periods of snow cover turkeys may be forced to feed or search for food throughout most of the day. Snow completely covered the ground during all the time-budget observation periods except March 11 and 12, when an earlier warm rain exposed patches of bare ground. My results agree with Bailey; on the average turkeys tended to feed at the same rate all day.

Lewis (1962) reported turkeys staying on the roost during snowstorms and following storms when the snow was deep and soft. Turkeys observed in this study remained active during morning and early afternoon snowstorms, but tended to become inactive during late afternoon storms. None of the time-budgets were conducted after a heavy snowstorm (>10 cm) so I could not determine if deep new snow affected activity. The average snow depth during my time budgets was 29.5 cm. Snow depth, either less than or greater than the depths recorded during the time budgets could affect the turkeys' activity budgets and consequently the daily energy expenditure (DEE). Different habitats and food availability could also potentially alter activity.

Estimates of Total Daily Energy Expenditure in Winter

Daily energy expenditure (kJ/bird/day) can be estimated from the model:

$$1) \text{ DEE} = [(TR \times DHL) + (BMR \times DH) (2.2Pf + 1.5Pr + 2.2Pw + 1.8Pc + 2.1Pa + 3.0Pco) + (EMR \times NH)]BW$$

where:

TR = EMR - BMR, day time thermoregulatory costs (kJ/g/hr).

EMR = Resting Metabolic rate (kJ/g/hr) at temperatures below T_{lc} estimated by converting the appropriate equation in Fig. 3 to energy units.

DHL = Total hours of daylight below T_{lc} .

BMR = Basal metabolic rate (kJ/g/hr) estimated from captive turkeys at 25° C (Table 3).

DH = Total hours of daylight.

Pf = Proportion of daylight spent feeding.

Pr = Proportion of daylight spent resting.

Pw = Proportion of daylight spent walking.

Pc = Proportion of daylight spent in comfort activities.

Pa = Proportion of daylight spent alert.

Pco = Proportion of daylight spent in courtship/antagonistic activities.

NH = Night time hours.*

BW = Body weight of turkeys in grams.

*This model assumes all night time temperatures during winter and early spring are below the T_{lc} in wild turkeys.

The energy requirements for activity (multiples of BMR) are included as numerical coefficients in the third bracketed set, with each being a multiplier for the proportion of daylight spent in the associated activity.

Energy requirements for activity were estimated from data on other species of birds. Resting has been estimated to be 1.4 x BMR in black ducks (Anas rubripes) (Wooley and Owen 1978), 1.5 x BMR in purple martins (Progne subis) (Utter and LeFebvre 1973), 1.7 x BMR in ferruginous hawks (Buteo regalis) (Wakely 1978), and 2.6 x BMR in willow flycatchers (Empidonax traillii) (Ettinger and King 1980). I used the figure of 1.5 x BMR as an estimate of the energetic cost of resting in wild turkeys.

Wooley and Owen (1978) estimated alertness to be 2.1 x BMR in black ducks and Wakely (1978) estimated it to be from 2.0-2.5 x BMR in ferruginous hawks. I used the average figure of 2.1 x BMR.

Feeding activities have been estimated to be 2.0 x BMR in American ibis (Eudocimus albus) (Kushlan 1977), 1.3 x Existence metabolism in dickcissels (Spiza americana) (Schartz and Zimmerman 1971), and 1.7 x BMR in black ducks (Wooley and Owen 1978). I used the factor of 2.2 x BMR in this model because I feel turkeys have potentially a more costly form of foraging (i.e., scratching and digging) than the 3 other species.

I defined comfort movements in turkeys as preening, ruffling feathers, stretching, or wing-flapping. Wooley and Owen (1978) estimated the cost of preening and wing-flapping in black ducks to be 1.6 x BMR and 3.0 x BMR respectively. Mugaas and King (1981) estimated preening to be 1.8 BMR in black-billed magpies (Pica pica).

The energetic cost of comfort movements in this model is $1.8 \times \text{BMR}$ because preening composed the majority of the comfort movements that I observed.

Wooley and Owen (1978) estimated the cost of walking and swimming in black ducks to be $1.7 \times \text{BMR}$ and $2.2 \times \text{BMR}$ respectively. Mugaas and King (1981) estimated the cost of walking in black-billed magpies to be $2.0 \times \text{BMR}$ and Prange and Schmidt-Nielson (1970) estimated the cost of swimming in mallards (Anas platyrhynchos) to be $3.2 \times \text{BMR}$. I used the average figure of $2.2 \times \text{BMR}$ as an estimate of the energetic cost of walking in wild turkeys.

Finally, I could not find any estimates in the literature for the energetic costs of courtship or antagonistic activities. Since these activities are usually vigorous, an estimate of $3.0 \times \text{BMR}$ was assigned.

The energetic cost of molt was not included in the model. Eastern wild turkeys in the southern parts of their range do not begin their prenuptial molt until mid-February (Bailey and Rinell 1967). I observed this molt beginning in early March in my captive birds, but could not find any evidence of it occurring in the wild birds during the time-budget analysis.

The heat increment of feeding ("SDA" or "SDE") can account for a 10-30% increase in heat production above BMR, depending on the composition of the diet (Barrot et al. 1938, Scott et al. 1982). Below the thermoneutral zone, part or all of the heat increment of feeding may be utilized for thermoregulation, but the subject is still controversial (Calder and King 1974). For this model, I assumed it was utilized for thermoregulation and excluded it from the model.

In addition to the above, this model does not account for energy expenditures of growth nor the influences of wind, thermal radiation, and humidity.

The relationship between heat produced as a by-product of activity and an endotherm's thermostatic requirement has been the subject of much confusion (Walsberg 1983). The unanswered question is whether the waste heat of activity substitutes for the resting thermostatic requirement of endotherms at temperatures below thermoneutrality. Pohl and West (1973) found activity metabolism of common redpolls (Acanthis flammea) additive to thermostatic metabolism at temperatures above -30° C. In a more recent study, Bryant et al. (1985) also found no evidence for substitution in dippers (Cinclus cinclus) and treated foraging costs as additive to thermoregulatory costs. Walsberg (1977) developed a model for phainopepla (Phainopepla nitens) which incorporated 2 assumptions on the interaction of cold and exercise thermogenesis. First, exercise metabolism at low work levels of nonflight activity were considered additive to maintenance metabolism at temperatures below thermoneutrality. Second, exercise metabolism of flight was assumed to substitute for cold-induced thermogenesis. No information was available on the relationship of cold and exercise thermogenesis for large non-passerines, therefore I incorporated Walsberg's assumptions into the model. If heat produced as a by-product of activity does substitute for the thermostatic requirement of resting in turkeys, this model will overestimate DEE.

When constructing energy budgets from time budgets, miscalculated conversion factors for computing the energy equivalents of timed activities can be a major source of error (Kendeigh et al. 1977,

Walsberg 1983). Secondly, as Williams and Nagy (1984) observed, failure to include daytime thermoregulatory requirements could also lead to considerable error.

I used the procedure of Ettinger and King (1980) to illustrate the magnitude of error in estimated DEE associated with error in estimates of conversion factors. I selected DEEs of adult females estimated by the model, and increased each conversion factor by 50% (Table 7). The greatest error in DEE (+ 8.8%) results from an error in quantifying the factor for feeding, because it is a relatively costly activity, predominating the time budget. An error this large seems unlikely, because the factor would be equal to $3.3 \times \text{BMR}$, which is 65% greater than the highest factor for foraging found in the literature for a ground feeding bird.

Errors of DEE resulting from errors in quantifying the factors for resting, walking, comfort, alert and courtship/antagonistic are small. It is unlikely that all errors in power factors will be simultaneously additive (by chance some will cancel others of opposite sign). Ettinger and King (1980) reported a higher percent deviation in their model by increasing each power consumption factor by 25% than I did by increasing my model by 50%. They concluded their estimates of DEE were accurate to within roughly 5% of the true value.

Energetics models of wintering birds have recently become of interest to population biologists. Stalmaster (1983) modeled energy consumption to estimate energy demands of wintering bald eagles. His model indirectly used activity cost as being additive to energetic costs of thermogenesis. Koplin et al. (1980) modeled the energetics of 2 wintering raptors, also including activity costs as additive

Table 7. Sensitivity of DEE to error in estimating factors for activity in adult females during winter (DEE^a = 1691 kJ/bird/day).

+ 50% Error in Factor for:	Estimated DEE (kJ/bird/day)	Percent Deviation from Original Estimate
Feeding	1840	+ 8.8
Resting	1755	+ 3.8
Walking	1754	+ 3.7
Comfort	1722	+ 1.8
Alert	1718	+ 1.6
Courtship/Antagonistic	1694	+ 0.2

^aDEE estimated using the model, with ambient temperature = -10° C, body weight = 4500g, activity equal to my time budget observations, and 11 hours daylight.

to the cost of thermogenesis. Their model's DEE estimates compared favorably with DEEs calculated from food intake estimated from free-ranging birds. Using an approach similar to Koplin et al. (1980), I calculated DEE in captive birds and tested the accuracy of my model against the calculated DEE.

Daily expenditures of captive turkeys were calculated during periods of minimal weight change (i.e., 6-day periods during the winter food trials when the average body weight did not change more than $\pm 1\%$) to estimate existence energy. The "actual" DEE was obtained by estimating the ME intake (75% of the GE intake; Farrell 1974) during this period of minimal weight change. Average ambient temperature, body weight, activity, and approximate daylength of these periods were entered into the model allowing for a comparison of DEE "predicted" by the model with "actual" DEE (Table 8). Activities of captive turkeys were assumed to equal activities of free-ranging turkeys recorded in my observations (i.e., feeding = 40%, resting = 25%, walking = 17%, comfort movements = 10%, alert = 7.5%, and courtship/antagonistic = 0.5% of the diurnal period). Model estimates were lower than "actual" DEE estimates for captive adult females and males of both age classes, and only slightly higher for juvenile females. This discrepancy could have resulted from the method used to estimate "actual" DEE in captive birds. Digestive efficiency ($ME/GE \times 100$) of a species is influenced by many factors including season and temperature, with reports ranging from 62% to 87%. (Kendeigh et al. 1977). If ME values in the captive turkeys averaged 70% of the GE instead of the estimated 75%, then my estimates of "actual" DEE would be smaller, reducing the model's underestimation from -20% in adult females and -13% in juvenile males

Table 8. Percent deviation of DEEs "estimated" by the model from "actual" DEEs obtained from captive wild turkeys during winter.

Sex	Age	Percent Deviation
Female	Juvenile	+ 2%
	Adult	- 20%
Male	Juvenile	- 13%
	Adult	- 9%

to -11% and -5%, respectively. The discrepancy between "actual" DEE and DEE estimated by the model could also have resulted from incorrect inputs into the model. Activity budgets of the captive turkeys were not recorded and probably differed from those of free-ranging turkeys used in the model.

The model can be used to predict energetic demands of a specific age or sex of turkey during the winter period (Table 9). Equations in Figure 3 predicting $\dot{V}O_2$ were converted to equations predicting energy consumption (kJ/g/hr) and used to estimate the appropriate EMR. $\dot{V}O_2$ values from Table 3 were converted to energy values (kJ/g/hr) to estimate the appropriate BMR. Models in Table 9 were used to predict DEEs for different ages and sexes of turkeys at various winter temperatures using activity information based on my time budgets (feeding = 40%, resting = 25%, walking = 17%, comfort = 10%, alert = 7.5%, and courtship/antagonistic = 0.5% of the daylight hours) (Table 10). If the average daily temperature is below the T_{lc} then DHL = DH. DEEs estimated from -15° C and -30° C are based on the assumption that the regression equation describing cost of thermogenesis remains accurate below my lowest laboratory measurement of -14° C. Body weight and activity are assumed constant for each sex x age combination. Therefore the change in DEE with each temperature change is a result of thermogenetic costs. As age and weight increase the cost of thermogenesis, expressed as a multiple of DEE in a thermoneutral environment, remains constant in each sex, with the cost being considerably lower in males. For example, DEE of juvenile and adult females at -30° C is 2.2 x DEE at thermoneutrality, while DEE of juvenile and adult males at the same temperature is 1.7 x DEE at

Table 9. Models used to estimate winter DEE (kJ/bird/day) for each age and sex of wild turkey.

Sex	Age	Equation
Female	Juvenile	$DEE = [(0.0126 - 0.0003x^a - 0.0080)(DHL) + (0.0080)(DH) (2.2Pf + 1.5Pr + 2.2Pw + 1.8Pc + 2.1Pa + 3.0Pco) + (0.0126 - 0.0003x)(NH)]BW$
	Adult	$DEE = [(0.0096 - 0.0003x - 0.0068)(DHL) + (0.0068)(DH) (2.2Pf + 1.5Pr + 2.2Pw + 1.8Pc + 2.1Pa + 3.0Pco) + (0.0096 - 0.0003x)(NH)]BW$
Male	Juvenile	$DEE = [(0.0101 - 0.0002x - 0.0080)(DHL) + (0.0080)(DH) (2.2Pf + 1.5Pr + 2.2Pw + 1.8Pc + 2.1Pa + 3.0Pco) + (0.0101 - 0.0002x)(NH)]BW$
	Adult	$DEE = [(0.0081 - 0.0002x - 0.0068)(DHL) + (0.0068)(DH) (2.2Pf + 1.5Pr + 2.2Pw + 1.8Pc + 2.1Pa + 3.0Pco) + (0.0081 - 0.0002x)(NH)]BW$

^ax = Temperature ° C.

Table 10. DEEs (kJ/bird/day) estimated by the model^a for each sex x age combination of wild turkey at various winter temperatures.

Sex	Age	Weight (g)	-30° C	-15° C	0° C	Thermoneutral
Female	Juvenile	3200	1935	1589	1244	890
	Adult	4500	2339	1853	1367	1064
Male	Juvenile	4600	2174	1843	1512	1280
	Adult	8000	3294	2718	2142	1892

^a11 hours daylight.

thermoneutrality. These results can be explained by referring back to Figure 3. Temperature coefficients, within each sex, were equal between adults and juveniles; and males, due to their larger body size, had smaller temperature coefficients than females.

Estimates of Winter Survival

If wild turkeys experience negative energy balances during winter, it is important for managers and biologists to understand the impacts of limited energy intake and cold temperatures on survival.

Estimates of expected days of survival for each sex and age of wild turkey were calculated based on the interaction of temperature and energy intake (Fig. 6). Estimates were derived by dividing total energy available from body reserves by rate of energy loss per day, for each temperature. Energy loss per day was estimated by subtracting daily energy intake (ME) from DEE. Estimates were based on the following assumptions:

- 1) Juvenile females = 3200g, juvenile males = 4600g, adult females = 4500g and adult males = 8000g.
- 2) DEEs were estimated from equations in Table 9 based on an 11 hour day and 13 hr night, with activities based on my time budget data and assumed constant for all energy intake levels except 0.0% of DEE. At 0.0% DEE, all feeding activity is shifted to resting.
- 3) Regression equations in Figure 3 accurately predict the metabolic response to temperatures below my lowest measurements at -14° C.
- 4) Body weight losses of 35% and 25% result in death of adults and juveniles, respectively.

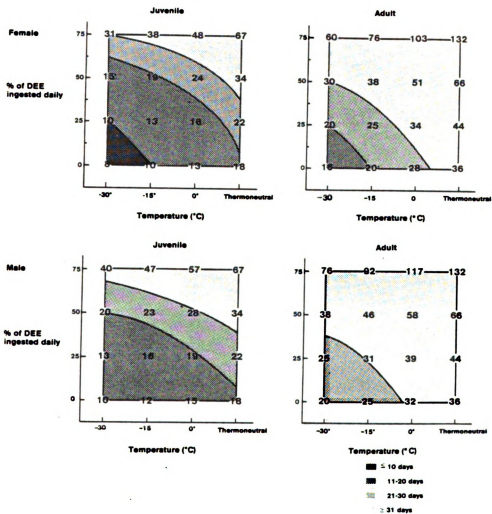


Fig. 6. Estimates of expected days of survival for juvenile and adult turkeys during winter at various temperatures and restricted levels of energy intake.

- 5) Adipose tissue composes 25% and 15% of winter body weights of adults and juveniles, respectively.
- 6) Turkeys succumb with 2% of the initial body weight remaining as adipose tissue. Therefore, adults and juveniles in this example utilize adipose tissue for energy amounting to 23% and 13% of the body weight, respectively.
- 7) Adults and juveniles utilize muscle tissue for energy amounting to the difference between the maximum reduction in body weight before death and the percent body weight of adipose tissue utilized.
- 8) Adipose tissue = 31.4kJ/g.
- 9) Muscle tissue = 4.94kJ/g.

Porter et al. (1980) reported reduced activity in free-ranging turkeys experiencing negative energy budgets during midwinter in southeastern Minnesota, but the cause is unclear. As avian species near starvation, some exhibit a decrease in activity (Brady et al. 1978, Le Maho et al. 1981), some an increase (Ketterson and King 1977, Stuebe and Ketterson 1982), and some, no change (Mortensen and Blix 1985). Due to the conflicting information on the relationship of food availability and feeding activity, I kept activity levels constant for all levels of energy intake except 0.0% of DEE. Error in estimating activity does not change estimated survival time by more than ± 1 day for any energy intake level x temperature combination.

Lehninger (1981) traced the pattern of tissue utilization in starving mammals. First, the small stores of glucose and glycogen are used up in less than a day. Next, body fat is utilized with body protein degraded at minimal rates. Finally, after the fat supply is exhausted, energy requirements of the body are met from muscle

protein. Brady et al. (1978) and Le Maho et al. (1981) documented the same pattern in birds.

Mosby and Handley (1943) reported turkeys may lose one third of their body weight during winter without permanent injury. In an experiment conducted in Mississippi, Gardner and Arner (1968) reported winter body weight losses averaging 21% in captive juvenile female turkeys and 35% in captive adult females without ill effects. They did not report temperatures during the experiment, but due to the location, it is doubtful temperatures paralleled average northern winter temperatures. Roberts (1958 in Bailey and Rinell 1967) reported weight loss of 38% body weight appeared to be the critical point of no recovery. I set weight losses of 35% and 25% as critical for adults and juveniles, respectively, based on reference weights of my captive birds. Cold temperatures, combined with susceptibility to predators in the wild, make survival below this critical mark unlikely in the northern range.

Bailey and Rinell (1967) report adult wild turkeys have a seasonal fluctuation in body weight of about 15%, being heaviest in winter and lightest in late summer. My captive adult turkeys underwent a 25% fluctuation during this period. Wild northern Michigan turkeys, not existing in the benign environment of my captive birds, probably fall in between at about 20% fluctuation. This fluctuation in body weight can be attributed to the fluctuation of adipose tissue. No information was available on the body composition of wild turkeys but it is logical to assume they have minimal fat of about 5% body weight during summer and add about 20% more before the onset of winter. Juveniles, on the other hand, are still growing body tissue prior to winter, therefore do not have as much body fat. I feel 15% of

the body weight is a reasonable estimate.

Not all body fat can be utilized by starving birds. Nonrecoverable reserves ranging from 0.3 to 1.3% of the body weight have been reported in small birds (Robbins 1983). I used a conservative value of 2% for turkeys; therefore adults and juveniles were assumed to utilize adipose tissue for energy amounting to 23% and 13% of their body weight, respectively. Percent body weight of protein utilized was estimated by subtracting percent body weight of fat utilized from percent reduction in body weight resulting in death.

Johnston (1970) reported caloric densities of avian adipose tissue ranging from 25.5 to 38.1 kJ/g. I used the average energy value of 31.4 kJ/g (Mortensen and Blix 1985) for turkeys. Muscle tissue contains about 75% water, 20% protein, 4% fat, and 1% glycogen and mineral matter (Maynard et al. 1979), giving it an energy value of approximately 4.94 kJ/g.

Northern Michigan winters last around 100 days with temperatures averaging -5.6°C (Stromme 1967). Figure 6 illustrates how big an impact cold weather and a limited food supply could have on a flock of wild turkeys. Juvenile birds during severe winters are the most vulnerable, with adults having over twice the expected survival time at all temperature x energy intake combinations. Juveniles and adults, within each sex, have equal thermoregulation costs per unit body weight at low temperatures, but adults have the survival edge due to greater endogenous reserves (i.e., adipose and muscle tissue). Within each age category, males have a slight edge at low temperatures due to their lower metabolic power required for thermoregulation.

Gerstill (1942 in Markley 1967) fasted wild turkeys and found

them capable of surviving at least 7 days of severe weather and 24 days at temperatures between 1° C and 10° C. In another study, Wunz (1962 in Markley 1967) reported turkeys could survive at least 15 days without food, but did not report temperature. Although sex, age, and weight of the birds were not specified in these reports, the numbers appear to fit reasonably within my estimates.

Future Research Needs and Management Implications

Food habits and the nutritive value of foods available to northern Michigan turkeys in the winter should be evaluated. Although Billingsley and Arner (1970) looked at the nutritive value and digestibility of 8 winter turkey foods, only one of these foods is common in northern Michigan.

Once the nutritive values of winter foods to turkeys are determined, areas can be assessed to give an estimate of the winter carrying capacity for turkeys. After the carrying capacity or suitability of an area is assessed, decisions can be made whether or not managed food plots or supplemental winter feeding are desired to maintain or increase flock size.

Hayden and Nelson (1963) demonstrated captive wild turkeys could live for 2 weeks without food and lose up to 40% of their normal body weight before dying. After 2-week fasts, hens were allowed to fully recover body weight prior to the laying period. The investigators observed that these imposed fasts did not significantly reduce fecundity of the surviving hens. In a similar study, Gardner and Arner (1968) reported up to 47.8% weight loss for surviving hens. They did, however,

notice an effect on fecundity; egg fertility was not different, but the number of eggs laid by birds on the marginal diet was significantly lower than that laid by the control birds. Unlike Hayden and Nelson, Gardner and Arner maintained birds on marginal diets through the egg laying period and never allowed the birds to recover the lost body weight. Therefore, it appears hens can lose significant amounts of body weight during winter without affecting fecundity as long as they can regain it prior to the laying period.

The average date of initiation of laying in northern Michigan wild turkeys begins around April 20 (Kulowiec and Haufler 1984, 1985b). Therefore, females have about 1 month to recover from winter before the onset of laying. The quantity and nutritive value of foods available to northern turkeys at this time of year should also be assessed in the future to determine if this is a nutritionally stressful or productive time for hens. If it is deemed a nutritionally stressful period, then food plots that remain covered during deep snow, only becoming accessible after the thaw, such as chufa and winter wheat, might be desirable.

Small, mature stands of conifers such as white or red pine, in close proximity to feeding areas are desirable as winter roosting habitat. Wunz and Hayden (1975) found conifer stands to be preferred roosting cover during harsh winters. I also observed heavy utilization of conifers for roosting cover during my time budget observations. These roosts reduce thermal radiation losses compared to regular hardwoods. By selecting coniferous roosts, turkeys conserve energy, thus reducing energy expenditure.

Lewis (1962) found open streams and seeps or springs to be an

important winter habitat of turkeys in southwestern Michigan. If these areas exist during winter in northern Michigan they will probably be utilized.

Periodic winter mortality due to starvation is a common occurrence in northern turkey populations. During severe winters, over 40% mortality may occur in isolated northern flocks (Wunz and Hayden 1975, Austin and DeGraff 1975, Porter 1983) as a result of malnutrition. If management goals are to stabilize as well as raise this fluctuating northern Michigan population, managed food plots or supplemental winter feeding might be necessary.

Considerable debate has arisen concerning winter starvation losses and the problem of providing supplementary food for turkeys during prolonged periods of deep snow. Winter feeding stations are viewed by most biologists as undesirable. Arguments point out that they are expensive, impractical, inefficient, and promote disease transmission. Emergency winter feeding stations operated only during severe weather have proven ineffective. If feeding stations are to be effective at all, they must be maintained the entire winter, not just during periods of severe weather. If not, stations often remain isolated from turkeys just when they are needed most (Wunz and Hayden 1975).

Food plots or plantings that remain accessible during periods of prolonged deep snow seem to be the most attractive management tool. Porter et al. (1980) reported low winter mortality in flocks of turkeys feeding in standing cornfields, suggesting these areas constitute an important feeding habitat. They felt small, appropriately placed corn food plots could provide an effective means of maintaining

populations in areas of prevalent deep snow.

Indeed, planting food plots on public lands or paying farmers to leave portions of their crops in the fields, seems more cost effective than buying grain from elevators and redistributing it. Arguments that deer will feed in these plots are a major consideration. Local deer populations would be a factor in determining size or feasibility of winter food plots. Deer can be beneficial by creating paths through deep snow allowing turkeys easier mobility. Deer also can effectively dig into snow, uncovering food normally inaccessible to turkeys. But, large numbers of deer in areas with small numbers of turkeys would make winter food plots impractical. Food plots are also attractive because they do not concentrate birds at a single focal point like feeders, thus limiting easy predation and disease transmittal.

Use-days (Prince 1979) can be calculated to determine the size of food plots needed in specific areas. Use-days for turkeys can be calculated according to the equation:

$$(\text{bird-days/ha}) = [\text{ME of Food (kJ/g)} \times \text{Yield (g/ha)}] / \text{DEE (kJ/bird-/day)}.$$

Crop yield data must be converted to dry weight values for inclusion in the equation (Prince 1979). Yield represents the net yield to turkeys; therefore estimated losses to deer and other wildlife should be considered. DEE represents the predicted average energy expenditure, per day, over the entire winter obtained from equations in Table 9. Projected temperature, daylength, and activity levels are entered into the appropriate equations to determine average DEE for each sex and age of wild turkey. For example, if a cornfield is planted that

yields a net of 3,750,000 g/ha (ME of corn = 14.1 kJ/g), the total energy available to turkeys would be 52,875,000 kJ/ha. Using activities based on my time budget observations and assuming temperature averages -5° C and daylight 11 hours, then this area would be capable of supporting 322 adult females/ha or 203 adult males/ha for a 90 day period.

Use-days can also be used to calculate winter carrying capacity of natural areas, such as hardwood stands, once the nutritive values of natural foods are determined.

LITERATURE CITED

- Aldrich, J. W. 1967. Historical background. Pp. 3-16. In Oliver H. Hewitt, ed., The wild turkey and its management. The Wildl. Soc. 589pp.
- Altman, J. 1974. Observational study of behavior; sampling methods. Behavior 99:228-295.
- Aschoff, J., and H. Pohl. 1970. Rythmic variations in energy metabolism. Fed. Proc. 29:1541-1552.
- Austin, D. E., and L. W. DeGraff. 1975. Winter survival of wild turkeys in southern Adirondacks. Natl. Wild Turkey Symp. 3:55-60.
- Bailey, R. W. 1967. Behavior. Pp. 93-111. In Oliver H. Hewitt, ed., The wild turkey and its management. The Wild. Soc. 589pp.
- _____, and K. T. Rinell. 1967. Events in the turkey year. Pp. 73-92. In Oliver H. Hewitt, ed., The wild turkey and its management. The Wildl. Soc. 589pp.
- Barrott, H. G., J. C. Fritz, and E. M. Pringle. 1938. Heat production and gaseous metabolism of young male chickens. J. Nutri. 15:145-167.
- Billingsley, B. B., Jr., and D. H. Arner. 1970. The nutritive value and digestibility of some winter foods of the eastern wild turkey. J. Wildl. Manage. 34:176-182.
- Brady, L. T., D. R. Romsos, P. S. Brady, W. G. Bergen, and G. A. Leveille. 1978. The effects of fasting on body composition, glucose turnover, enzymes, and metabolites in the chicken. J. Nutri. 108:648-656.
- Bronner, W. N. 1983. Summary of wild turkey management workshop. Mich. Dept. of Nat. Resour. Typewritten manuscript. 16pp.
- Bryant, D. M., C. J. Hails, and R. Prys-Jones. 1985. Energy expenditure by free-living dippers (Cinclus cinclus) in winter. Condor 87:177-186.
- Calder, W. A., III. 1974. Consequences of body size for avian energetics. Pp. 86-151. In R. A. Paynter, Jr., ed., Avian

- energetics. Nuttall Ornithol. Club Publ. 15. 334pp.
- _____, and J. R. King. 1974. Thermal and caloric relations of birds. Pp. 259-413. In D. S. Farner and J. R. King, eds., Avian biology. New York, Academic Press.
- Davis, H. E. 1949. The american wild turkey. Small Arms Tech. Publ. Co., Georgetown, S. C. 328pp.
- Dejong, A. A. 1976. The influence of simulated solar radiation on the metabolic rate of white-crowned sparrows. Condor 78:174-179.
- Ettinger, A. O., and J. R. King. 1980. Time and energy budgets of the willow flycatcher during the breeding season. Auk 97:535-546.
- Farell, D. J. 1974. General principles and assumptions of calorimetry. In T. R. Morris and B. M. Freeman, eds., Energy requirements of poultry. Br. Poul. Sci. Ltd. 199pp.
- Gill, J. L. 1981. Design and analysis of experiments in the animal and medical sciences, Vol. I. Iowa State Univ. Press, Ames, IA. 410pp.
- Gardner, D. T., and D. H. Arner. 1968. Food supplements and wild turkey reproduction. Trans. N. Am. Wildl. Conf. 33:250-258.
- Hart, J. S. 1962. Seasonal acclimation in four species of small wild birds. Physiol. Zool. 35:224-236.
- Hayden, A. H. 1980. Dispersal and movements of wild turkeys in northern Pennsylvania. Transactions of the Northeast Sect. of the Wildl. Soc. 37:258-265.
- Hayden, H., and E. Nelson. 1963. The effects of starvation and limited rations on reproduction of game farm wild turkeys. Proc. NE Wildl. Cong., Portland, ME.
- Hill, R. W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261-263.
- _____. 1976. Comparative physiology of animals: an environmental approach. Harper and Row, New York. 656pp.
- Ignatoski, F. J. 1973. Status of wild turkeys in Michigan. Pp. 49-53. In Glen C. Sanderson and Helen C. Schultz, eds., Wild turkey management: current problems and programs. Univ. of Mo. Press, Columbia.
- Johnston, D. W. 1970. Caloric density of avian adipose tissue. Comp. Biochem. Physiol. 34:827-832.

- Kendleigh, S. C., V. R. Dol'Nik, and V. M. Gavrilov. 1977. Avian energetics. Pp. 127-204. In Jan Pinowski and S. Charles Kendleigh, eds., Granivorous birds in ecosystems. Cambridge Univ. Press, London.
- Ketterson, E. D. and J. R. King. 1977. Metabolic and behavioral responses of fasting in the white-crowned sparrow (Zonotrichia leucophrys gambelli). *Physiol Zool.* 50:115-129.
- Kim, J. and F. J. Kohout. 1975. Analysis of variance and covariance: subprograms anova and oneway. Pp. 398-433. In Norman H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds., Statistical package for the social sciences. McGraw-Hill, Inc., New York.
- King, J. R. 1974. Seasonal allocation of the time and energy resources in birds. Pp. 4-70. In R. A. Paynter, Jr., ed., Avian energetics. Nuttall Ornithol Club. Publ. 15. 334pp.
- Koplin, J. R., M. W. Collopy, A. R. Barmann, and H. Levenson. 1980. Energetics of two wintering raptors. *Auk* 97:795-806.
- Kulowiec, T. G. and J. B. Haufler. 1984. Habitat utilization and population characteristics of resident Michigan turkeys. Biannual progress report to Mich. Dept. of Nat. Resour. 20pp.
- . 1985a. Winter dispersal movements of wild turkeys in Michigan's northern lower peninsula. Pp. 145-153. In James Earl and Mary C. Kennamer, eds., Proc. Fifth Natl. Wild Turkey Symp.
- . 1985b. Habitat utilization and population characteristics of resident Michigan turkeys. Biannual progress report to Mich. Dept. of Nat. Resour. 15pp.
- Kushlan, J. A. 1977. Population energetics of the American white ibis. *Auk* 94:114-122.
- Lehninger, A. L. 1981. Biochemistry. Worth Publishers, Inc., New York. 1104pp.
- Le Maho, Y. V., H. Vu Van Kha, H. Koubi, G. Dewasmes, J. Girard, P. Ferre, and M. Cagnard. 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. *Am. J. Physiol.* 241:342-354.
- Lewis, J. C. 1962. Wild turkeys in Allegan County, Michigan. M.S. Thesis, Mich. State Univ., E. Lansing. 35pp.
- Maynard, L. A., J. K. Loosli, H. F. Hintz, and R. G. Warner. 1979. Animal nutrition. McGraw-Hill Book Co., New York. 602pp.
- Markley, M. H. 1967. Limiting factors. Pp. 199-244. In Oliver

- H. Hewitt, ed., The wild turkey and its management. The Wildl. Soc. 589pp.
- Mortensen, A., and A. S. Blix. 1985. Seasonal changes in the effects of starvation on metabolic rate and regulation of body weight in Svalbard ptarmigan. *Ornis Scand.* 16:20-24.
- Mosby, H. S., and C. O. Handley. 1943. The wild turkey in Virginia: its status, life history and management. Va. Comm. Game and Inland Fish., Richmond. 281pp.
- Mugaas, J. N., and J. R. King. 1981. The annual variation in daily energy expenditure of the black-billed magpie: a study of thermal and behavioral energetics. *Stud. Avian Biol.* 5:1-78.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences. McGraw-Hill Book Co., New York. 675pp.
- Owen, R. B., Jr. 1970. The bioenergetics of captive blue-winged teal under controlled and outdoor conditions. *Condor* 72:153-163.
- Petersen, E. T. 1979. Hunter's heritage, a history of hunting in Michigan. MUCC, Lansing, MI. 56pp.
- Platt, R. B., and J. F. Griffiths. 1964. Environmental measurement and interpretation. Reinhold Publ. Co., New York. 235pp.
- Pohl, H. 1969. Some factors influencing the metabolic response to cold in birds. *Fed. Proc. Fed. Am. Socs. Exp. Biol. Med.* 28:1059-1064.
- _____. 1971. Seasonal variation in metabolic functions of bramblings. *Ibis* 113:185-193.
- _____, and G. C. West. 1973. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the common redpoll. *Comp. Biochem. Physiol. A.* 45:851-867.
- Porter, W. F. 1977. Utilization of agricultural habitats by wild turkeys in southeastern Minnesota. XIII Int. Congr. Game Biol. 13:319-323.
- _____. 1983. Effects of winter conditions on reproduction in a northern wild turkey population. *J. Wildl. Manage.* 47:281-290.
- _____, R. D. Tangen, G. C. Nelson, and D. A. Hamilton. 1980. Effects of corn food plots on wild turkeys in the upper Mississippi Valley. *J. Wildl. Manage.* 44:456-462.
- Prange, H. D., and K. Schmidt-Nielson. 1970. The metabolic cost of swimming in ducks. *J. Exp. Biol.* 53:763-777.

- Prince, H. H. 1979. Bioenergetics of postbreeding dabbling ducks. Pp. 103-117. In T. A. Bookhout, ed., Waterfowl and wetlands-an integrated review. Proc. 1977 Symp., Madison Wisc., N. Cent. Sec. The Wildl. Soc. 147pp.
- Quinlan, E. E., and G. A. Baldassarre. 1984. Activity budgets of nonbreeding green-winged teal on playa lakes in Texas. J. Wildl. Manage. 48:838-845.
- Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York. 343pp.
- Schartz, R. L., and J. L. Zimmerman. 1971. The time and energy budget of the male dickcissel (Spiza americana). Condor 73:65-76.
- Scott, M. L., M. C. Nesheim, and R. J. Young. 1982. Nutrition of the chicken. M. L. Scott and Assoc. Ithaca, NY. 312pp.
- Siegal, S. 1956. Non-parametric statistics. McGraw-Hill Book Co., New York. 312pp.
- Stalmaster, M. V. 1983. An energetics simulation model for managing wintering bald eagles. J. Wildl. Manage. 47:349-359.
- Steele, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill Book Co., New York. 633pp.
- Stromme, N. D. 1967. Climate of Michigan. U. S. Dept. of Comm., Washington, D. C. 25pp.
- Stuebe, M. M., and E. D. Ketterson. 1982. A study of fasting in tree sparrows (Spizella arborea) and dark-eyed juncos (Junco hyemalis): Ecological implications. Auk 99:299-308.
- Utter, J. M., and E. A. Lefebvre. 1973. Daily energy expenditure of purple martins (Progne subis) during the breeding season: estimates using D_2O^{18} and time budget methods. Ecology 54:597-604.
- Wakely, J. S. 1978. Activity budgets, energy expenditures, and energy intakes of nesting ferruginous hawks. Auk 95:667-676.
- Walsberg, G. E. 1977. Ecology and energetics of contrasting social systems in Phainopepla nitens. Univ. Calif. Berkeley Publ. Zool. 108:1-63.
- _____. 1983. Ecological energetics: what are the questions? Pp. 135-158. In Alan H. Brush and George A. Clark, Jr., eds., Perspectives in ornithology. Cambridge Univ. Press, Cambridge.
- West, G. C. 1960. Seasonal variation in the energy balance of the tree sparrow in relation to migration. Auk 77:306-329.

- _____. 1968. Bioenergetics of captive willow ptarmigan under natural conditions. *Ecology* 49:1035-1045.
- Williams, J. B., and K. A. Nagy. 1984. Daily energy expenditure of savannah sparrows: comparison of time-energy budget and doubly-labeled water estimates. *Auk* 101:221-229.
- 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.
- Wunz, G. A., and A. H. Hayden. 1975. Winter mortality and supplemental feeding of turkeys in Pennsylvania. *Natl. Wild Turkey Symp.* 3:61-69.
- Zar, J. H. 1973. Using regression techniques for prediction in homeotherm bioenergetics. Pp. 115-133. In James A. Gessamen, ed., *Ecological energetics of homeotherms: a view compatible with ecological modeling*. Mono. Ser. Utah St. Univ. Press. Logan, UT. Vol. 20.