# REPRODUCTIVE BIOENERGETICS OF WOOD DUCKS[1]

RONALD D. DROBNEY[2]

*School of Forestry, Fisheries, and Wildlife, University of Missouri–Columbia, Gaylord Memorial Laboratory, Puxico, Missouri 63960 USA*

ABSTRACT.—A model for the daily energy requirements during egg production was developed for Wood Duck (*Aix sponsa*) hens laying a 12-egg clutch. Reproductive requirements are high, because Wood Ducks lay large clutches of relatively large eggs that have a high energy density. Costs totaled 5,996 kJ and included 2,969 kJ for carbohydrates and lipids, 1,595 kJ for protein, and an estimated 1,432 kJ for biosynthesis. Both are the temporal distribution of costs and the use of stored fat reserves are thought to be important factors enabling hens to meet these large requirements. Costs equivalent to that of an entire egg are incurred for only 6 days during the cycle, because costs are distributed over an 18-day period rather than the 12 days of laying. The energy content of body fat expended by hens was sufficient to account for 88% of the estimated requirements for biosynthesis and the nonprotein fraction of the oviduct and clutch. Protein and minerals are primarily dietary requirements and are obtained by foraging for invertebrates during laying. Although an egg contains only about 5 g of protein, hens must consume large numbers of invertebrates to meet this requirement. The ability to meet most nonprotein requirements with stored fat may therefore be essential to ensure that hens have enough time to forage for invertebrates. *Received 12 February 1979, accepted 15 February 1980.*

DESPITE extensive research on the breeding biology of waterfowl, surprisingly little is known about the bioenergetics of the reproductive cycle. With the exception of the Maccoa Duck (*Oxyura maccoa*) (Siegfried et al. 1976), most of the information available for waterfowl consists of estimates of the cost of producing an egg or clutch (King 1973, Ricklefs 1974) based on extrapolations of data on the chemical composition or caloric content of duck and goose eggs (Romanoff and Romanoff 1949). Cost estimates for reproduction in birds (King 1973, Ricklefs 1974) show that anseriforms incur considerably higher costs for egg production than other groups, because they produce large clutches of relatively large eggs that have a high energy density. It is therefore of particular interest to determine how waterfowl have adapted to meet these high costs.

Although total cost estimates are of value for making interspecific comparisons, a knowledge of the temporal distribution of costs and how resources are obtained and allocated to meet these costs is needed to understand breeding strategies. Studies of caged birds have provided data on the bioenergetics of breeding Zebra Finches (*Poephila guttata*) (El-Wailly 1966) and Ring Doves (*Streptopelia* sp.) (Brisbin 1969). The results of pen studies, however, are of only limited value in understanding how free-living birds interact with the environment to meet the requirements for reproduction.

---

[1] Contribution from Gaylord Memorial Laboratory (School of Forestry, Fisheries, and Wildlife, University of Missouri–Columbia, and Missouri Department of Conservation cooperating), Division of Wildlife Refuges, U.S. Fish and Wildlife Service, Edward K. Love Fellowship, Missouri Agricultural Experiment Station, Project 170, Journal Series Number 8157, and the School of Natural Resources, University of Michigan-Ann Arbor.

[2] Present address: School of Natural Resources, Samuel Trask Dana Building, University of Michigan, Ann Arbor 48109 USA.

The purpose of this paper is to show how costs are distributed during the reproductive cycle and how reproductive requirements are apportioned between dietary and stored sources under free-living conditions.

## Methods

During 1975–77, 154 Wood Ducks (79 females, 75 males) were collected in southeast Missouri for detailed analyses of food habits (Drobney and Fredrickson 1979), weights of digestive organs, and changes in weights and composition of the carcass during the reproductive cycle (Drobney 1977). Selected portions of these data are included here to demonstrate how the behavioral, morphological, and physiological adjustments of hens during breeding relate to the bioenergetics of reproduction.

All estimates of requirements during the reproductive cycle were calculated from values derived by calorimetric and proximate analyses of the tissues produced. Estimates of the water and energy content of yolk, albumen, and oviduct tissue were based on an average from three replicate samples of each tissue that were freeze dried and subsequently burned in a bomb calorimeter. Proximate analyses were performed using AOAC procedures (Horwitz 1970). Energy equivalents of 17.58 kJ/g for carbohydrates, 23.86 kJ/g for protein, and 39.77 kJ/g for fat (Kleiber 1961) were used to compute energy values from chemical composition data obtained by proximate analyses. A slightly lower value of 37.67 kJ/g, suggested by Ricklefs (1974: 160), was used for determining the energy content of extracted carcass lipids.

In addition to the energy content of materials produced, there are costs associated with biosynthesis that are commonly expressed in terms of a partial or net production efficiency (PE). Because actual production efficiencies for Wood Duck eggs are not known, Brody's (1945) estimate of 77% for synthesis of eggs in chickens was used. The PE for the synthesis of body tissue (Kleiber and Dougherty 1934, Brody 1945, Pullar and Webster 1977) is lower than that for eggs. The wide range of values reported in the literature, however, required the selection of an arbitrary, representative PE value of 55% for calculating the energy required for synthesis of the oviduct.

Female Wood Ducks were subdivided into seven categories on the basis of morphological changes that occur in the ovary and brood patch during the reproductive cycle as follows: (1) fall courtship (FC), hens collected in September and October that had begun courtship activities; (2) prebreeding (PB), hens collected in the spring prior to the rapid growth phase of ovarian development, largest ovum $\leq$ 7 mm; (3) follicle growth (FG), hens that initiated the rapid growth phase of ovarian development, largest ovum $>$ 7 mm; (4) laying (L), laying hens (as evidenced by one or more ruptured follicles), with three or more enlarged follicles yet to be ovulated; (5) terminal laying (TL), hens in the final stages of the laying cycle that contained ovaries with fewer than three enlarged follicles left to be ovulated; (6) early incubation (EI), hens with a brood patch and an ovary weighing $\geq$1 g with all follicles ruptured or regressing; and (7) incubation (I), hens with a well developed brood patch and ovaries weighing $<$1 g.

Data were analyzed using Mann-Whitney $U$-tests (Siegel 1956). Plus or minus values following data presented in the text represent the standard error of the mean.

## Results

### Egg Composition and Cost

A sample of 13 freshly laid Wood Duck eggs selected from 13 different nests was used to determine mean egg weight and the average weights and relative proportions of shell, yolk, and albumen. Eggs averaged 42.6 g and were composed of 53.5% albumen (22.8 g), 35.8% yolk (15.2 g), and 10.7% shell (4.6 g). Proximate analysis of a homogenate of the contents of eight eggs showed that the major constituents were water (69.5%), lipid (14.1%), and protein (13.5%), with lesser amounts of ash (1.7%) and carbohydrates (1.2%).

The yolk contained 43.5% water and had an energy content of 33.82 kJ/g dry weight. Albumen had a higher water content (84.2%) than yolk and was lower in energy (21.85 kJ/g dry weight).

On the basis of the preceding data, the energy content of materials in the egg is 369.2 kJ. At a production efficiency of 77%, hens would need to expend 479.5 kJ

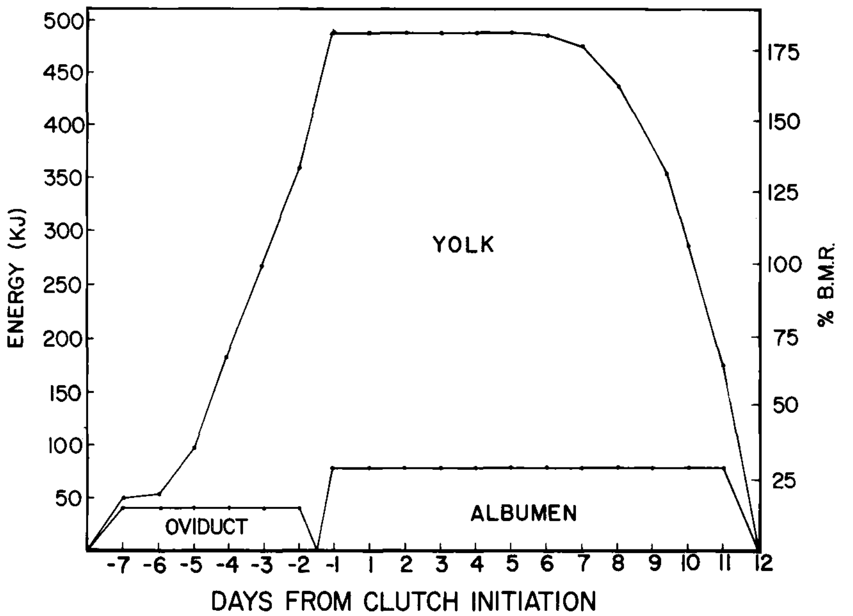


Fig. 1. Estimated daily energy requirements during the period of follicular growth and laying for the synthesis of yolk albumen and an oviduct expressed in kJ and as a percentage of the daily basal metabolic rate (BMR).

for each egg produced. The average clutch size for successful Wood Duck nests (excluding dump nests) in the vicinity of the study area was 11.8 eggs during a 5-y period (Hansen 1971). Assuming an average of 12 eggs, the cost of producing a clutch would total 5,754.0 kJ.

## TEMPORAL SEQUENCE OF ENERGY EXPENDITURE

*Costs during gonadal recrudescence.*—Estimates of the energy cost of gonadal recrudescence were based on the follicular growth accomplished each day prior to laying, the period of formation of the oviduct, and the energy contents of the yolk and oviduct. A fully functional but nonovulating ovary in Wood Ducks normally contained seven developing follicles. The average weights of the ova from nine Wood Duck hens were 0.38 (±0.05), 1.34 (±0.16), 2.90 (±0.25), 5.47 (±0.31), 8.90 (±0.23), 12.55 (±0.22), and 15.20 (±0.25). On the basis of the number of developing follicles, the period of ovarian development lasts 7 days. Yolk material is secreted into these ova simultaneously by their follicle cells throughout the period of development and laying. Because the Wood Duck has a laying rate of one egg per day (Leopold 1951: 212), the difference in weight between any two ova in the series provides a measure of the growth rate (Romanoff and Romanoff 1949: 204).

Daily energy requirements for growth of the follicles were determined using a model developed by Ricklefs (1974: 188). Because ova in the early stages of growth contain more water than those in later stages (Romanoff and Romanoff 1949: 206), a correction for differences in water content was made. The water content of the four largest ova was similar and averaged 43.5%. The water content of the three

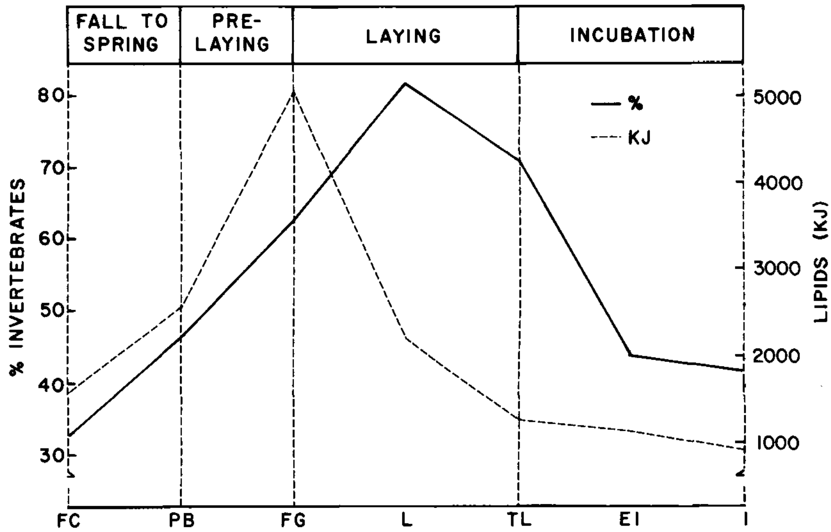


Fig. 2. Invertebrate composition of the diet (aggregate percent volume) and energy content of the body fat of hens during the reproductive cycle. Stages in the reproductive cycle and sample sizes (open figure = *n* for food habits, figure in parenthesis = *n* for body fat): FC = fall courtship 20(10); PB = prebreeding 9(5); FG = follicle growth 10(6); L= laying 10(6); TL = terminal laying 10(6); EI = early incubation 10(5); I = incubation 10(5).

smallest ova in order of decreasing size was 60, 81, and 82%, respectively. To compensate for differences in water content, weights of the ova were converted to dry weight values. Daily energy costs were then calculated by multiplying the daily growth increment by the dry weight energy density of yolk (33.82 kJ/g).

The daily energy requirements for ovarian synthesis at a production efficiency of 77% are depicted by the period from day −1 to day −7 in Fig. 1. Daily costs increase progressively from 3.0 kJ on day −7 before laying to a maximum of 377.3 kJ on the day before the first egg is laid. The sum of the daily cost increments shows that hens expend an estimated 1,109.4 kJ before laying commences to develop a fully functional but nonovulating ovary.

The other energy-demanding event prior to clutch initiation is the synthesis of an oviduct. The mean weight of the oviduct increased by 23.62 g between the regressed (0.27 g ± 0.05, $n$ = 10) and fully developed (23.89 g ± 2.5, $n$ = 15) state. Nearly all of this growth occurred during the period when the follicles were developing, presumably in response to estrogen elaborated by the maturing ovary (Sturkie 1965: 577). Because the exact form of the growth curve for the oviduct could not be determined, the weight increase was averaged for the 6 days of development. On the basis of the average daily weight change (3.94 g/day) and energy density (5.65 kJ/g wet weight), the daily cost for production of the oviduct was estimated to be 40.47 kJ (at 55% PE) and the total cost 242.8 kJ.

*Costs of egg formation.*—Once gonadal recrudescence is complete, the period of egg formation begins. The daily energy expenditures become maximal during egg formation because yolk and albumen must be synthesized simultaneously. As a consequence of the laying rate (one egg per day), albumen must be deposited in less than 24 h. Thus, the daily rate of albumen formation is equivalent to the albumen

TABLE 1. Summary of the requirements for reproduction in Wood Ducks and the energy available from body fat expended during laying. Data presented in kJ.

| | | |
|---|---|---|
| Energy content of production | | |
| Energy content of 12-egg clutch[a] | 4,430.4 | |
| Energy content of oviduct[b] | 133.4 | |
| Total energy content of clutch and oviduct | 4,563.8 | 4,563.8 |
| Cost of biosynthesis | | |
| Clutch at 77% PE | 1,323.4 | |
| Oviduct at 55% PE | 109.1 | |
| Total cost of biosynthesis | 1,432.5 | 1,432.5 |
| Total cost for reproduction | | 5,996.3 |
| Energy content of protein | | |
| Protein in clutch[c] | 1,468.8 | |
| Protein in oviduct[d] | 126.5 | |
| Total energy content of protein | 1,595.3 | −1,595.3 |
| Nonprotein requirements | | 4,401.0 |
| Energy available from expended lipids[e] | | 3,880.0 |

[a] 12 eggs at 369.2 kJ/egg (derived by bomb calorimetry).
[b] Change in weight of oviduct (23.62 g) at 5.65 kJ/g (derived by bomb calorimetry).
[c] Protein = 13.5% of egg contents (derived by proximate analysis) (38 g) at 23.86 kJ/g [energy equivalent of protein (Kleiber 1961) and fat (Ricklefs 1974)].
[d] Protein = 22.4% (derived by proximate analysis) of oviduct weight (23.62 g) at 23.86 kJ/g [energy equivalent of protein (Kleiber 1961) and fat (Ricklefs 1974)].
[e] Net change in body fat during laying (103.0 g) at 37.67 kJ/g [energy equivalent of protein (Kleiber 1961) and fat (Ricklefs 1974)].

content of a single egg and remains constant throughout laying (Fig. 1). Maximum daily energy requirements (479.4 kJ) begin on the last day before laying, because the first egg must be fully formed before laying can begin. This high rate of energy expenditure lasts for only 6 days. The daily energy requirements begin to decline on the sixth day after clutch initiation, because at that time the ovary still contains enough developing ova to complete the clutch without bringing new follicles into rapid growth. Hence, energy requirements are reduced during the latter stages of laying by an amount equivalent to the energy expended in the developing ovary during gonadal recrudescence. This strategy distributes the cost of producing eggs over a longer time interval and reduces the duration of the period of maximum energy expenditure.

*Costs in relation to* BMR.—To provide a standard for comparing the energy budgets of birds of different sizes, energy requirements are often expressed as a percentage of basal metabolic rate (*BMR*) (King 1973, Ricklefs 1974). *BMR* calculations for Wood Ducks were based on the summer night equation for nonpasserines ($BMR = 0.5675\ W^{0.7282}$; $W$ = weight in g and $BMR$ = kcal/day) (Kendeigh et al. 1977). Assuming an average weight of 665 g, the *BMR* of hens was 270 kJ/day. Energy requirements for laying as a percentage of *BMR* ranged from 1.1% 7 days prior to laying to 177.6% on the day before clutch initiation (Fig. 1).

## NUTRIENT SOURCES FOR THE CLUTCH

An increase in the percentage of invertebrates in the diet (Krapu 1974, Swanson et al. 1974, Landers et al. 1977) and large decreases in the body weight of hens during laying (Weller 1957, Falk et al. 1966, Harris 1970, Korschgen 1977) have been found to occur in a number of species of ducks. Specific relationships between these changes and the requirements for egg production are only poorly understood.

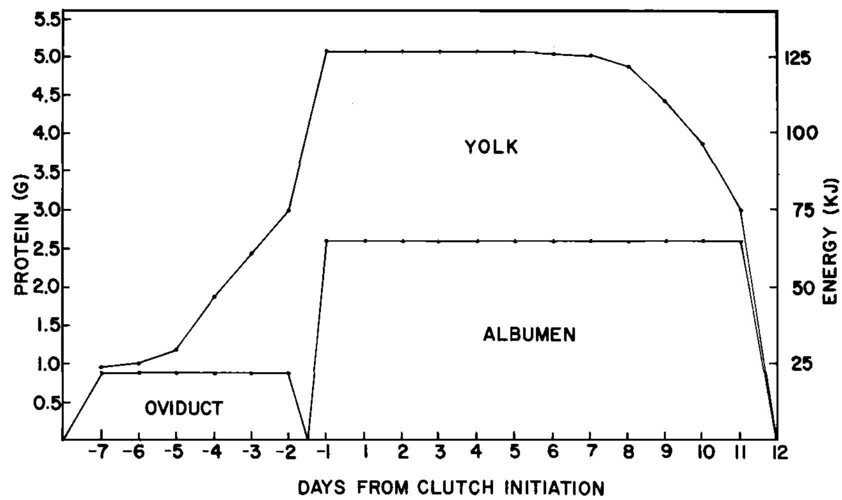


Fig. 3. Estimated daily protein requirements (in g and kJ) during the period of follicular growth and laying for the synthesis of yolk, albumen, and an oviduct. Estimates based upon the protein composition of the materials produced (derived by proximate analysis) and an energy equivalent of 23.86 kJ/g for protein.

Species that feed during laying have two potential sources of nutrients for the clutch (dietary and stored).

Changes in the food habits (Drobney and Fredrickson 1979) and carcass composition (Drobney 1977) of Wood Ducks collected during this study provide insight into how these sources are apportioned to meet reproductive requirements. Carcass composition analyses for water, protein, lipid, and ash showed significant changes ($P < 0.05$) only in the lipid and ash content of hens. A small 3-g increase in the ash content during laying presumably resulted from the development of medullary bone that can be used to supplement absorbed minerals during eggshell formation (Sturkie 1965). Large decreases in the fat content of hens during laying suggest that fat deposits provide an important source of energy and lipid substrates for the synthesis of eggs (Fig. 2).

*Nonprotein requirements.*—To illustrate the degree to which fat deposits could potentially supplement dietary sources of nutrients, Table 1 provides a summary of the energy available from fat reserves expended during laying and the energy requirements for biosynthesis and the nonprotein fraction of the oviduct and clutch. The average fat content of hens decreased 103.0 g between the period of rapid follicular growth (133.9 g ± 8.4) and the end of laying (30.9 g ± 5.2). The energy content of these expended lipids (3,880.0 kJ) is sufficient to account for 88.2% of the total energy requirements for biosynthesis (1,432.5 kJ) and the nonprotein fraction of the oviduct and clutch (2,968.5 kJ).

It should be noted that the 103-g decrease in body fat represents the difference in the average fat content of hens between the period of rapid follicular growth and the end of laying. The ovaries of hens in the former category already contained from two to seven developing follicles. If the lipids and energy expended in producing these follicles is considered, it seems probable that all nonprotein and biosynthetic energy requirements would be accounted for.

*Protein requirements.*—The results of this study indicate that protein for the oviduct and clutch is acquired in the diet rather than from endogenous sources. Supporting evidence for this contention includes the lack of significant ($P > 0.05$) changes in the average protein content of the carcasses of hens during laying and the large increase in the percentage of invertebrates in the diets of laying hens (Fig. 2). The fact that the proportion of invertebrates in the diets of breeding males collected at the same feeding sites as females did not increase during spring (Drobney and Fredrickson 1979) shows that hens were foraging selectively for invertebrates and that the increase was not just the result of a seasonal increase in the abundance of invertebrates.

Proximate analyses of the oviduct and eggs of Wood Ducks showed that they contained 22.4% and 13.5% protein, respectively. On the basis of these proportions, the average weight of materials in the egg (38.0 g), and the increase in the weight of the oviduct (23.6 g), hens would require 66.9 g of protein for the oviduct and a 12-egg clutch.

The daily protein requirements for reproduction range from 0.9 g to 5.1 g (Fig. 3). Requirements are lowest during the early stages of follicular development but increase rapidly as the period of laying is approached due to the growth and greater number of developing follicles. Requirements become maximal (5.1 g) on the day prior to the beginning of laying and remain at that level for 6 days. During this 6-day period, protein requirements are allocated almost equally for the synthesis of yolk (2.6 g) and albumen (2.5 g). The amount of protein needed for albumen remains the same throughout laying, but requirements for the synthesis of yolk decrease during the latter stages of laying because the number of developing follicles in the ovary decreases.

## DISCUSSION

High costs per egg, large clutches, and long incubation periods collectively result in a high total cost for reproduction in many species of waterfowl. Because of these high costs, it has been suggested that egg production places a tremendous energetic strain on the female (Ricklefs 1974) and may, under certain circumstances, predispose hens to stress-associated mortality (Harris 1970, Korschgen 1977).

High reproductive requirements, however, need not automatically imply stress or high parental risk for all species of waterfowl. Because waterfowl are relatively long-lived, it would seem that their breeding strategies should reflect adaptations that would, under normal conditions, reduce stress and mortality associated with reproductive effort.

The results of this study provide an example of how Wood Ducks, and possibly other species of waterfowl, have adapted to meet the requirements associated with reproduction. The energy density of Wood Duck eggs (8.7 kJ/g) is high and only slightly lower than the values of 9.3 and 10.2 kJ/g reported for the Maccoa Duck (Siegfried et al. 1976) and Black-Bellied Whistling-Ducks (*Dendrocygna autumnalis*) (Cain 1976). Furthermore, Wood Ducks produce large clutches and incubate their eggs for 28–30 days. Even though requirements for reproduction in Wood Ducks are large, the temporal distribution of costs, use of fat reserves, and changes in food habits enable hens to meet them in such a way that, under normal conditions, they would probably not be adversely affected.

*Egg production.*—Wood Ducks normally lay one egg per day during a 12-day laying cycle. As a consequence, sufficient nutrients and energy to produce an egg must be available each day during laying. Even though these requirements are fixed, they are not restricted to or uniformly distributed throughout the laying period (Fig. 1). Because materials are deposited in the developing ova prior to the beginning of laying, requirements are distributed over an 18-day period rather than the 12 days of laying. Furthermore, costs are progressively reduced during the last 6 days of laying, and, as a result, daily costs equivalent to an entire egg are incurred for only 6 days.

The use of stored fat is another mechanism that enables hens to distribute the costs incurred during laying over a longer time interval. During spring, Wood Duck hens undergo a period of hyperphagia that facilitates the deposition of large quantities of fat (Drobney 1977). These fat reserves, which are stored prior to laying, can be used to supplement dietary sources of nutrients at the time that eggs are being produced.

Energy requirements for lipids, carbohydrates, and biosynthesis comprise nearly three-fourths (73.4%) of the total estimated costs for reproduction. More than 88% of these costs, however, can be accounted for by the body fat that is expended by hens during laying. Hence, a large proportion of the requirements for reproduction are available in the form of body fat before laying begins.

Assuming that all expended lipids are used for reproductive processes, the principal remaining requirement would be a source of protein. The lack of significant changes in the protein content of the carcasses of hens during laying (Drobney 1977) indicated that protein requirements for the clutch are obtained in the diet rather than from internal sources. The change in the food habits of females during laying (Fig. 2) supports this contention and suggests that hens obtain the protein needed for the synthesis of eggs by foraging for invertebrates. Chemical analyses of the principal foods consumed by breeding hens showed that invertebrates provide both a higher percentage of protein and a better balance of essential amino acids relative to egg composition than plant foods and are probably needed in the diet to meet protein requirements (Drobney 1977). On the basis of the preceding evidence, the correspondence between changes in protein requirements (Fig. 3) and the percentage of invertebrates consumed by hens (Fig. 2) during comparable stages of the egg production cycle may therefore reflect dietary adjustments in response to changing protein needs.

The relatively low daily requirement for protein (Fig. 3) seems to indicate that hens could meet their needs for this nutrient with little difficulty. These protein requirements appear deceptively low, however, because they are dry weight estimates. Under natural conditions, protein is not consumed in a purified state or on a dry matter basis. The eight most important animal foods found in the diet of laying hens contained an average of 79.4% water and 12.4% (wet weight) protein. On the basis of these proportions, hens would need to consume 41.4 g of invertebrates to acquire enough protein to meet the 5.1 g maximum daily requirement.

The actual amount of time that Wood Duck hens spend feeding is unknown. If it were assumed for the purpose of illustration that hens spend 8 h per day feeding, however, they would need to ingest 5.2 g of invertebrates per hour. Using data on the average weights and the percent water and protein composition of the principal invertebrate foods consumed by Wood Duck hens, it was estimated that they would need to ingest in excess of 300 individuals per hour to produce an egg (Drobney 1977).

The preceding estimates are based upon an efficiency of protein utilization of 100%. Birds, however, are not able to utilize all of their dietary protein. For example, laying chickens have been found to be only about 55% efficient in converting dietary protein into the protein of eggs and body tissue (Scott et al. 1976). At this level of efficiency, Wood Duck hens would need to consume 75 g of invertebrates to obtain enough protein to produce an egg.

Even if Wood Duck hens are considerably more efficient in utilizing dietary protein than chickens, they must still allocate a substantial fraction of their daily time budget to foraging to obtain enough protein to produce eggs. The ability to meet most lipid and biosynthetic energy requirements with stored fat reserves may therefore be essential to ensure that hens have sufficient time to forage for invertebrates.

*Incubation.*—No attempt was made to estimate the energy requirements for incubation in Wood Ducks; however, the results of carcass composition analyses did provide an indication of the extent to which hens rely upon stored fat to meet energy requirements during incubation. Estimates for American Eiders (*Somateria mollissima dresseri*) (Korschgen 1977) and Maccoa Ducks (Siegfried et al. 1976) indicate that these species expend 300 and 104 g of fat, respectively, during incubation. The average fat content of Wood Duck hens, by contrast, decreased only 17 g between the beginning (31 g ± 5.2) and end (14 g ± 2.3) of incubation. On a per unit of body weight basis, the amount of fat utilized by Wood Ducks is considerably lower than either of the preceding species.

The amount of stored fat needed for incubation is important because it can affect clutch size and nest success. Eiders (Korschgen 1977) and Arctic-nesting geese (Ryder 1970, MacInnes et al. 1974, Ankney 1977) feed little during incubation and therefore must cease laying with enough stored reserves to carry them through incubation. The high endogenous requirement for incubation in these waterfowl reduces the amount of stored fat that can be used for egg production and can result in abandonment of the nest if reserves become depleted during incubation.

The fat expended by Wood Duck hens would probably provide only a small fraction of the total energy needed during incubation. Even at a basal level of metabolism (270.0 kJ/day), the energy derived from these expended lipids (39.8 kJ/g × 17 g = 676.6 kJ) would not be sufficient to maintain a hen through the third day of incubation. The entire 31 g of fat that was available at the beginning of incubation would provide enough energy for only about 5 days at a basal level of metabolism. Because Wood Ducks incubate for 28–30 days, hens must be able to obtain enough energy by foraging during inattentive periods to meet most of the energy requirements for incubation.

The ability of hens to obtain the energy needed for incubation seems to be due, at least in part, to changes in the kinds of foods consumed. Food-habits data show that hens shifted from a diet consisting primarily of invertebrates (81.8%) during laying to one predominated by plant foods (58.5%) during incubation. The seeds of elm (*Ulmus* spp.) and maple (*Acer* spp.) were consumed in greater volume by incubating hens than any of the 25 genera of plant foods used in the spring. These two foods were lowest in crude fiber (elm 17.4%, maple 13.8%) of all foods analyzed and comprised 88% (by volume) of all plant foods consumed during incubation. It is not known whether these foods were being selected on the basis of their nutritional quality; however, the fact that they were available and readily consumed is important. The low fiber (presumably indigestible) content indicates that a large proportion of the energy content of these seeds could be used to meet the requirements for incubation. By using these foods, incubating females are able to obtain more energy per unit of food consumed. High foraging efficiency is particularly important during incubation because the amount of time available for feeding is reduced as a result of nest attentiveness.

These results indicate that large quantities of stored reserves are not needed by incubating Wood Ducks, because they are able to meet most of their requirements by foraging during incubation. The adaptive significance of this strategy is that the low endogenous energy requirement for incubation allows Wood Ducks to expend a greater proportion of their stored reserves in the production of eggs and thereby to increase the number of eggs that can be laid. It could also reduce the likelihood of desertion of the nest due to energy depletion during incubation.

## Acknowledgments

I thank J. E. Savage for chemical analysis of the specimens; V. C. Cravens, T. S. Taylor, and C. Duren for technical, laboratory, and clerical assistance; and L. H. Fredrickson, J. R. Karr, and S. C. Kendeigh for reviewing earlier drafts of this manuscript.

## Literature Cited

Ankney, C. D. 1977. Feeding and digestive organ size in breeding Lesser Snow Geese. Auk 94: 275–282.

Brisbin, I. L., Jr. 1969. Bioenergetics of the breeding cycle of the Ring Dove. Auk 86: 54–74.

Brody, S. 1945. Bioenergetics and growth. New York, Reinholt Publishing Corp.

Cain, B. W. 1976. Energetics of growth for Black-bellied Tree Ducks. Condor 78: 124–128.

Drobney, R. D. 1977. The feeding ecology, nutrition, and reproductive bioenergetics of Wood Ducks. Unpublished Ph.D. dissertion, Columbia, Missouri, Univ. Missouri.

———, & L. H. Fredrickson. 1979. Food selection by Wood Ducks in relation to breeding status. J. Wildl. Mgmt. 43: 355–363.

El-Wailly, A. J. 1966. Energy requirements for egg-laying and incubation in the Zebra Finch (*Taeniophygia castanotis*). Condor 68: 582– 594.

Falk, C., J. Hudec, & J. Toufar. 1966. The weight of the Mallard, (*Anas platyrhynchos*), and its changes in the course of the year. Zool. Listy 15: 249–260.

Hansen, J. L. 1971. The role of nest boxes in management of the Wood Duck on Mingo National Wildlife Refuge. Unpublished M. A. thesis, Columbia, Missouri, Univ. Missouri.

Harris, J. H., Jr. 1970. Evidence of stress response in breeding Blue-winged Teal. J. Wildl. Mgmt. 34: 747–755.

Horwitz, W. (Ed.). 1970. Official methods of analysis, 11th Ed. Washington, D. C., Assoc. Off. Anal. Chem.

Kendeigh, S. C., V. R. Dol'nick, & V. M. Gavrilov. 1977. Avian energetics. Pp. 127–204 *in* Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). New York, Cambridge Univ. Press.

King, J. R. 1973. Energetics of reproduction in birds. Pp. 78–107 *In* Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.

Kleiber, M. 1961. The fire of life. New York, John Wiley and Sons, Inc.

———, & J. E. Dougherty. 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. J. Gen. Physiol. 17: 701–726.

Korschgen, C. E. 1977. Breeding stress of female Eiders in Maine. J. Wildl. Mgmt. 41: 360–373.

Krapu, G. L. 1974. Foods of breeding Pintails in North Dakota. J. Wildl. Mgmt. 38: 408–417.

Landers, J. L., T. T. Fendley, & A. S. Johnson. 1977. Feeding ecology of Wood Ducks in South Carolina. J. Wildl. Mgmt. 41: 118–127.

Leopold, F. 1951. A study of nesting Wood Ducks in Iowa. Condor 53: 209–220.

MacInnes, C. D., R. A. Davis, R. N. Jones, B. C. Lieff, & A. J. Pakulak. 1974. Reproductive efficiency of McConnell River small Canada Geese. J. Wildl. Mgmt. 38: 686–707.

Pullar, J. D., & A. J. F. Webster. 1977. The energy cost of fat and protein deposition in the rat. Brit. J. Nutrition 37: 355–363.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152–292 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Cambridge, Massachusetts, Nuttall Ornithol. Club.

ROMANOFF, A. L., & A. J. ROMANOFF. 1949. The avian egg. New York, John Wiley and Sons, Inc.

RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. Wilson Bull. 82: 5–13.

SCOTT, M. L., M. C. NESHEIM, & R. J. YOUNG. 1976. Nutrition of the chicken, 2nd Ed. Ithaca, New York, M. L. Scott and Associates.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw Hill Book Co.

SIEGFRIED, W. R., A. E. BURGER, & P. G. H. FROST. 1976. Energy requirements for breeding in the Maccoa Duck. Ardea 64: 171–191.

STURKIE, P. D. 1965. Avian physiology, 2nd Ed. Ithaca, New York, Comstock Publishing Associates, Cornell Univ. Press.

SWANSON, G. A., M. I. MEYER, & J. R. SERIE. 1974. Feeding ecology of breeding Blue-winged Teals. J. Wildl. Mgmt. 38: 396–407.

WELLER, M. W. 1957. Growth, weights, and plumages of the Redhead, (*Aythya americana*). Wilson Bull. 69: 5–38.