Protein acquisition: a possible proximate factor limiting clutch size in Wood Ducks[1]

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Introduction

An extensive review of waterfowl clutch and egg sizes for a number of waterfowl species indicated that clutch size and relative egg size were inversely related (Lack 1967). On the basis of this relationship, Lack hypothesized that the average clutch of each species has evolved in relation to the average availability of food for the female around the time of laying and is modified by the relative size of the egg. The high energy requirement for laying in waterfowl as compared to other major groups of birds lends credence to this hypothesis, but it must be further demonstrated that laying puts the female into nutrient or energy deficit (Ricklefs 1974). Therefore, fully to understand the relationship between nutrients and clutch size, those foods or nutrients that are limiting and the time during the reproductive cycle when the effects of the limitation occur must be identified.

Studies of Arctic nesting geese (Ryder 1970; Ankney & Mac Innes 1978; Raveling 1979) and of American Eiders *Somateria mollissima dresseri* (Korschgen 1977) have provided some of the best evidence for the limiting effects of nutrients on clutch size. In these species, little or no feeding occurs during laying and incubation and therefore, clutch size is limited by the endogenous nutrient reserves of females as proposed by Ryder (1970).

In contrast to eiders and Arctic nesting geese, most waterfowl continue to feed during nesting. In these species, females can utilize both dietary and endogenous sources of nutrients during egg production and incubation. As a result, the problem of identifying the potential limiting effects of food or nutrients on clutch size is more complex.

The results of our studies of the feeding ecology, nutrition, and reproductive bioenergetics of Wood Ducks *Aix sponsa* (Drobney 1977, 1980, 1982, 1984; Drobney & Fredrickson 1979) provided evidence for a hypothesis relating to limiting effects of nutrients on clutch size in this species. We propose that dietary requirements for protein during the time of egg synthesis provides an important proximate regulatory mechanism that influences clutch size.

Clutch size and resource allocation for the clutch

Wood Duck females incur high costs for reproduction because they produce large clutches of relatively large eggs. Reported clutch sizes for non-parasitized nests average 12.2 eggs, but range from 10.4 to 14.7 in different areas (Bellrose 1976). In our study area on the Duck Creek Wildlife Management Area in south-eastern Missouri, the clutch size of box-nesting females with non-parasitized nests averaged 11.0 eggs (N=447) over an 18-year period (Fredrickson, unpublished data). A five-year average for non-parasitized nests on an adjacent study area (Mingo National Wildlife Refuge) was 11.8 eggs (Hansen 1971).

Eggs average 42.6 g and therefore a female must deposit 511.2 g of materials into the eggs to produce a 12-egg clutch. Total clutch weight is equivalent to about 84% of the average body weight of a prebreeding female (Drobney 1977). However, water comprises a large proportion of egg weight (61%) and therefore only about 39% of the materials in eggs represent potentially limiting nutrients (Drobney 1977). Nevertheless, the daily costs for egg production are quite high and, at maximum, can exceed 210% of the basal metabolic rate (Drobney 1980).

Nutritional requirements are sufficiently high that a female would probably be unable to produce a normal sized clutch at a laying rate of one egg per day if requirements had to be satisfied entirely from dietary sources during laying. However, there are several ways that females can distribute nutrient requirements over a longer time interval

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and thereby lessen the effect of high daily requirements during laying.

By depositing materials in developing follicles during the period of rapid follicular growth for 6 days before laying, lipid and protein requirements for eggs are extended over an 18-day period rather than the 12 days of laying (Fig. 1). This mechanism also reduces requirements during the latter stages of laying and as a result, requirements equivalent to an entire egg are incurred for only 6 days (Drobney 1980).

Females are able substantially to reduce dietary requirements during laying by expending endogenous lipid reserves. Non-protein requirements (carbohydrates, lipids, and energy costs for biosynthesis) comprise nearly three-quarters of the total costs for reproduction in Wood Ducks (Drobney 1980). However, the fat reserves expended by females during laying are sufficient to account for more than 88% of these requirements (Drobney 1982). Assuming that all of the endogenous fat expended by females during laying is allocated to egg production, the principal remaining requirement for the clutch is protein. Because the protein content of females does not change significantly ($P>0.05$) during laying, protein represents a dietary requirement (Drobney 1982).

Females meet their requirements for protein by shifting to an invertebrate diet during the period of egg synthesis (Drobney & Fredrickson 1979). Similar dietary modifications are common in some breeding

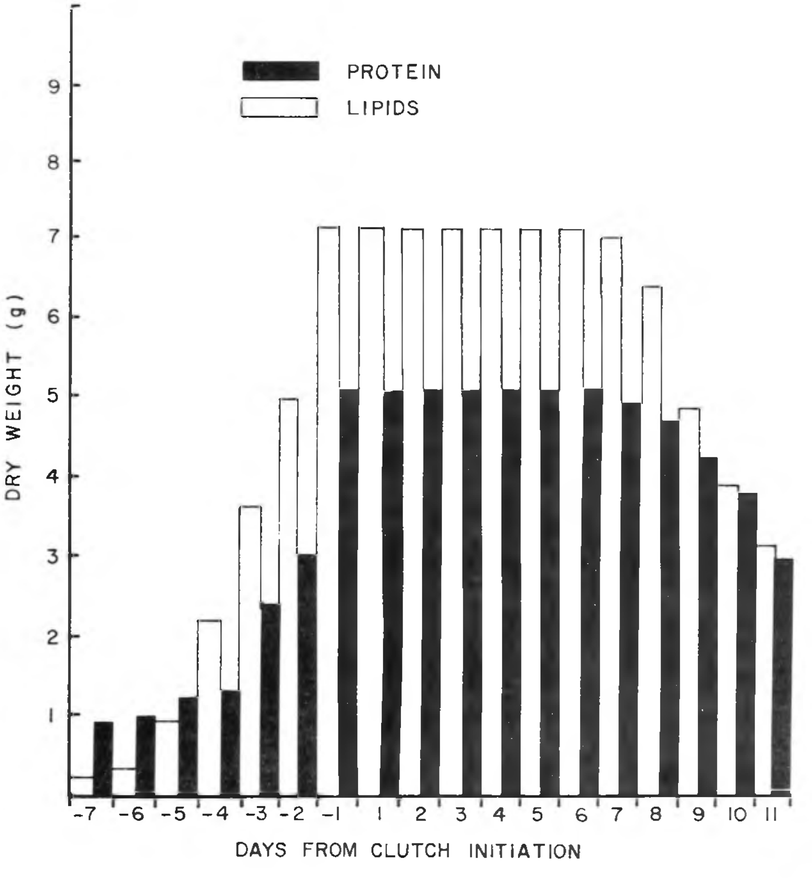

Figure 1. Estimated daily protein and lipid requirements during gonadal recrudence and laying for a Wood Duck female producing a 12-egg clutch (adapted from Drobney (1980)).

Anas including Mallard *A. platyrhynchos* (Krapu 1974), Blue-winged Teal *A. discors* (Swanson *et al.* 1974), and Gadwall *A. strepera* (Serie & Swanson 1976). In Wood Ducks, invertebrate consumption increases during laying, but the proportion of invertebrates in the diet (Fig. 2) corresponds closely with changes in protein requirements during various stages of the reproductive cycle (Fig. 1).

Landers *et al.* (1977) have suggested that the increased intake of animal foods by Wood Ducks during spring might be the result of greater availability relative to plant foods. However, our results (Drobney & Fredrickson 1979) show that the change in diet is nutritionally motivated and is not the result of changes in the relative availability of plant and animal foods.

The nutritional basis for the change in diet has been established through chemical analysis of foods and laboratory experiments. Our findings (Drobney 1977; Drobney & Fredrickson 1979) and those of Krapu and Swanson (1975) show that invertebrate foods contain a higher proportion of protein and a better balance of essential amino acids relative to egg composition than plant foods and are therefore needed in the diet to meet protein requirements for normal egg production.

The effects of protein limitation on reproduction have been demonstrated in experiments with captive mallards (Krapu 1979). Females fed a protein deficient diet (14% protein) produced half as many eggs as controls on a 29% protein diet and ovulated at irregular intervals.

Limiting effects of nutrients

The physiological mechanism that causes females to cease laying is currently poorly understood, but the available evidence indicates that the mechanism differs interspecifically. In Cackling Geese *Branta canadensis minima* (Raveling 1979) and the Red-billed Quela *Quela quela* (Jones & Ward 1979) the depletion of reserve protein is thought to be responsible, whereas in the Ring-necked Pheasant *Phasianus colchicus* a depletion of fat reserves has been implicated (Breitenbach & Meyer 1959). Evidence from our studies indicates that fat depletion is more likely to terminate laying in Wood Ducks because females do not use significant amounts of endogenous protein

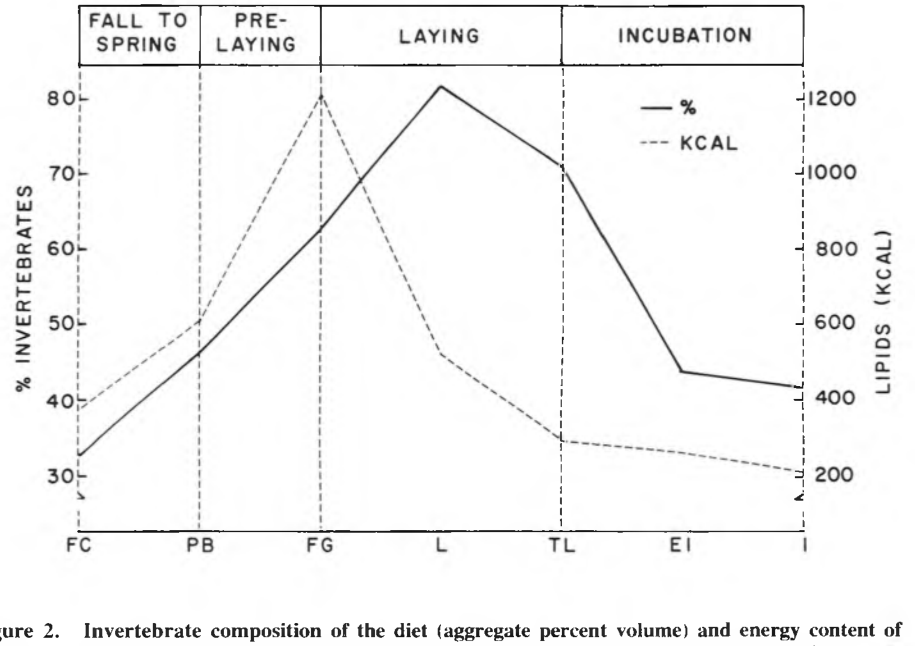

Figure 2. Invertebrate composition of the diet (aggregate percent volume) and energy content of carcass fat of Wood Duck females during the reproduction cycle. FC = Fall Courtship; PB = Prebreeding; FG = Follicle Growth; L = Laying; TL = Terminal Laying; EI = Early Incubation; I = Incubation. Data from Drobney (1980).

during laying (Drobney 1982) and females with depleted fat reserves cease laying prematurely (after 3 to 4 eggs) (Drobney 1977).

Assuming that fat depletion is responsible for the determination of laying and that the number of eggs produced is dependent upon the size of the endogenous lipid reserve, the argument that clutch size is limited by the ability of females to store fat seems plausible. However, the mechanism that controls the cessation of laying is not necessarily the factor that limits clutch size.

On the basis of nutrient requirements for the clutch, the most probable candidates for limiting clutch size are protein and lipids. Because foraging time is limited, clutch size probably represents an optimal compromise between competing requirements for these two nutrients. The basic nutritive strategy used by Wood Ducks is storage of lipids before laying, but during laying lipids are provided by endogenous fat reserves, and proteins are required from dietary sources. Therefore, any factor that would; 1) reduce the ability of females to store fat before laying, 2) increase the use of endogenous lipids during laying, or 3) impede protein acquisition are potential candidates to limit clutch size.

We propose that protein requirements which are met primarily by foraging for invertebrates, can influence both fat deposition in prelaying females and utlization of endogenous fat reserves during laying. Dietary protein requirements thereby provide a proximate mechanism that can affect the number of eggs that are produced.

On the basis of the estimated daily requirements (Fig. 1), protein would not appear to be an important limiting nutrient because at maximum, protein requirements amount to only 5.1 g/day. However, the invertebrate foods that provide the principal source of protein are small and have a high water content. Therefore, the potential limiting effect of protein becomes apparent only when protein requirements are evaluated in the context of foraging effort.

Chemical analyses of the principal invertebrate taxa consumed by Wood Ducks females showed that they contained an average of 79.4% water and 12.4% protein (Drobney 1980). On the basis of these proportions, a female would need to ingest about 41 g of invertebrates to obtain 5.1 g of protein. Females are probably not 100% efficient in converting dietary protein to egg protein and therefore the actual biomass of invertebrates needed would be greater than the preceding estimate. If the protein conversion efficiency is similar to that of domestic chickens (55%) (Scott *et al.* 1976), 75 g of invertebrates would be needed to produce an egg.

To provide a more realistic assessment of dietary protein requirements in relation to foraging effort by laying females, we determined daily consumption in terms of the number of individuals of several important invertebrate taxa required to meet protein demands for an egg at conversion efficiencies of 100% and 55% (Table 1). Assuming that the foods listed in Table 1 represent an average diet, a female would have to consume 5211 invertebrates to produce an egg at a protein conversion efficiency of 100%. This would require an ingestion rate of one organism every 5.5 seconds if a female foraged continuously for 8 hours per day. Although the preceding estimate is probably conservative, the requirement illustrates the magnitude of the problem of protein acquisition for Wood Duck females and provides support for our hypothesis that protein requirements can potentially influence clutch size.

Table 1. Invertebrate intake needed to meet daily protein requirements for a Wood Duck egg at conversion efficiencies of 100% and 55%. Estimates derived on the basis of the average weight and percent protein content of each organism listed (Drobney 1977).

Invertebrate food	No. of individuals needed at consumption rates of: 100% PCE*	55% PCE
Midge larvae (Chironomidae)	14,342	26,076
Scuds *(Gammarus)*	5,711	10,384
Aquatic sow bugs *(Asellus* sp.)	4,724	8,589
Water striders *(Gerris* sp.)	2,610	4,745
Predaceous diving beetles (Dytiscidae)	2,056	3,738
Damselfly larvae (Zygoptera)	1,823	3,315
Mean rate	5,211	9,474

*PCE = Protein Conversion Efficiency

Both eiders and Arctic nesting geese mobilize significant amounts of endogenous protein for egg production (Ryder 1970; Korschgen 1977; Ankney & MacInnes 1978; Raveling 1979). Therefore, if protein represents a potentially limiting nutrient as we propose, one might question why Wood Ducks do not also use endogenous protein to supplement dietary requirements.

Producing and incubating a clutch entirely from endogenous reserves represents an extreme strategy which would be imposed by high predation on unattended nests and/or low food availability on the breeding grounds. The consequence of this strategy is a relatively small clutch size. There is little doubt that Wood Ducks can produce more eggs by foraging during laying and incubation than if they relied solely on endogenous reserves.

Furthermore, the primary sources of endogenous protein are the pectoralis muscle and organs of digestion (Raveling 1979). Because protein is not a specialized storage product (Fisher 1954), withdrawal of protein from these organs is at the expense of organ function. Such use of gut and pectoralis protein would seem highly adaptive in those species that produce and incubate a clutch with little or no feeding, because these organs are used little during the nesting period and size reduction lowers costs for supporting these metabolically active tissues (Raveling 1979). Wood Duck females, however, must be able to digest foods consumed during laying and incubation and fly between foraging sites and their nesting cavities. Therefore, impairment of the functioning of flight muscles or organs of digestion would be maladaptive, and would undoubtedly reduce their reproductive capacity.

Timing of the nutrient limitation

Nutrient requirements for the clutch are greatest during the period of rapid follicular growth and laying. Therefore, the limiting effects of nutrients would most likely occur during one or both of these periods.

Carcass analyses showed that on the average, females begin laying with enough fat to produce a clutch of about 12 eggs, but that fat reserves vary among individuals (Drobney 1982). Therefore, some females could produce more and others fewer than 12 eggs. Because nest initiations occur throughout a 3–4 month period in southeastern Missouri, the smaller fat reserves of some individuals are probably not the result of insufficient time for fat deposition. In fact smaller clutches are most common late in the season at a time when females should have adequate time to forage and deposit fat (Fredrickson, unpublished data). Some of these late nests represent second clutches or renests but others are the only known nest for that year.

For reasons that are currently unclear, most of the fat accumulated during spring (60%) is deposited during the 6–7 day period of rapid follicular growth (Fig. 2). Protein requirements also increase during this period reaching a maximum just before laying (Fig. 1). The corresponding increase in invertebrate consumption (Fig. 2) presumably reflects a dietary adjustment to meet the increased protein requirements for gonadal recrudescence.

If the increased amount of time spent foraging for invertebrates reduces a female's ability to store lipids before laying, protein requirements could have a limiting effect on clutch size during the period of rapid follicular growth. Variations in foraging efficiency resulting from experience or changes in invertebrate availability thus provide plausible explanations for individual, regional, seasonal, and annual differences in clutch size.

After laying has commenced, females must be able to sustain the output of large quantities of both protein and lipids if the egg production is to occur at the normal sequence of one egg per day. The diet of laying females consists chiefly of invertebrates (Fig. 2) suggesting that foraging efforts are being concentrated almost exclusively on protein acquisition. The large amount of foraging time required for protein acquisition during laying undoubtedly impairs the ability of females to meet concurrent requirements for the lipid fraction of the egg from dietary sources. Dietary requirements for protein thereby restrict the fat available for egg formation primarily to the endogenous reserves that are deposited before clutch initiation. Therefore, if fat depletion is responsible for the cessation of laying as Breitenbach and Meyer (1959) suggest, and protein requirements limit the amount of food that can be allocated for lipid synthesis during laying, then protein also has a regulatory effect on clutch size during the laying period.

The preceding evidence supports Lack's

(1967) hypothesis that clutch size is limited by food for the female. Although Lack primarily was concerned with ultimate factors, we believe that proximate factors also influence waterfowl clutch sizes as suggested by Johnsgard (1973) and that protein represents an important proximate limiting nutrient.

Detailed studies of how resources are allocated for reproduction are not available for most waterfowl species. However, intensive work on Mallard by Krapu (1981) indicates that females of this species utilize dietary sources of protein and endogenous lipids for egg production in a manner very similar to that of Wood Ducks. It seems likely, therefore, that protein might also influence clutch size in North American prairie nesting ducks.

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Summary

The limiting effect of food on clutch size in Wood Ducks *Aix sponsa* was examined on the basis of nutritional requirements and allocation of nutrients for reproduction. The principal requirements for egg production are protein and lipids. Lipid requirements are satisfied largely from endogenous fat reserves deposited before laying. The depletion of lipid reserves is responsible for the cessation of laying. Protein is a dietary requirement and is obtained primarily by foraging for invertebrates. The invertebrates consumed by Wood Duck females are small and have a high water content. As a consequence, much foraging time is needed to obtain a sufficient amount of protein for egg synthesis. The amount of time that females must devote to foraging for invertebrates can affect both fat deposition before laying and the use of endogenous reserves during laying. Hence, protein influences clutch size via its effects on the lipid dynamics of breeding females. Differences in foraging efficiency resulting from experience or availability of invertebrate foods provides an explanation for observed regional, temporal and individual variation in Wood Duck clutch size.

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