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INVITED ESSAYS

THE ROLES OF NUTRIENT RESERVES IN LIMITING REPRODUCTION IN WATERFOWL

As Editor, I intend to occasionally solicit alternative views of interesting and potentially important issues in avian biology. One such exchange of views is contained in the following essays. These deal with the unresolved controversy regarding the importance of various nutrient reserves during reproduction in waterfowl and, perhaps, other groups of birds.

I would welcome suggestions from readers of other topics that might be profitably addressed in future collections of essays.—Glenn Walsberg

NUTRIENT LIMITATION OF CLUTCH SIZE IN WATERFOWL: IS THERE A UNIVERSAL HYPOTHESIS?

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Lack's (1967) paper on the potential limiting effects of food on clutch size in precocial species has stimulated considerable debate among waterfowl biologists about the types of nutrients that may be limiting and the time in the annual cycle when the limitation occurs. There is general agreement that waterfowl, which feed little during egg synthesis, are limited by the endogenous nutrient reserves of females (Ryder 1970, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979). Considerably more controversy, however, has surrounded hypotheses generated for species that use both dietary and endogenous sources of nutrients to satisfy requirements for reproduction. In this group, which includes most temperate-nesting waterfowl, the problem is more complex and requires an understanding of how food resource availability, food selection, foraging efficiency, and endogenous nutrient reserves collectively influence egg production.

Hypotheses currently proposed to explain how nutrients influence intraspecific variation in clutch size include the protein-limitation hypothesis (PLH) (Drobney and Fredrickson 1985), the lipid-limitation hypothesis (LLH) (Ankney and Afton 1988), and the migrational-uncertainty hypothesis (MUH) (Rohwer, in press). Because the MUH does not apply to Wood Ducks (*Aix sponsa*), my comments will be confined to the relative merits of the LLH and PLH as explanations for clutch size limitation in Wood Ducks and issues raised by Ankney and Afton (1988) and Afton and Ankney (1991) regarding these hypotheses.

Both hypotheses acknowledge that clutch size is dictated by lipid reserves. The main distinctions between them are the mechanism that limits lipid reserves and the species to which they allegedly apply. The LLH argues that fat reserves are limited by the ability to store fat and, according to the authors, applies to most temperate nesting waterfowl (including Wood Ducks). By contrast, the PLH was developed specifically for Wood Ducks and states that protein requirements influence lipid storage prior to laying and the rate at which lipid reserves are expended during laying.

The PLH as it applies to Wood Ducks has been detailed in Drobney and Fredrickson (1985) and, therefore, I will provide only the following brief synopsis of it in this paper. Wood Ducks incur high costs for reproduction because they produce large clutches of relatively large eggs that have a high caloric density (Drobney 1980). To satisfy these costs while maintaining a laying rate of one egg per day requires both dietary and endogenous sources of nutrients. Lipid and energy requirements are satisfied primarily by endogenous fat reserves that are stored prior to laying, from a diet consisting largely of plant foods. Females satisfy protein and mineral requirements from dietary sources by foraging on invertebrates during egg synthesis. Because laying ceases when fat reserves are depleted, any factor that impedes fat storage before laying or increases the use of endogenous lipids during laying can potentially influence clutch size.

Wood Ducks store 60% of their fat reserves during the 6–7 day period of rapid follicular growth (RFG) that immediately precedes laying. Protein requirements for synthesis of reproductive organs also increase during this period, reaching a maximum just before laying. To satisfy these elevated protein requirements, females increase consumption of invertebrates during RFG. Because time devoted to foraging for invertebrates can potentially reduce lipid reserve storage before laying, protein can have a limiting effect on clutch size during RFG.

During laying, 82% of the diet consists of invertebrates, suggesting that foraging effort is devoted almost exclusively to protein acquisition. Based upon the average mass and protein content of the principal invertebrates consumed, a female would need to ingest in excess of 5,200 invertebrates to satisfy the daily protein requirements for an egg at a protein conversion efficiency of 100%. Although conservative, I believe that this estimate illustrates the magnitude of the problem of protein acquisition. The large amount of time allocated to meeting protein needs during laying undoubtedly impairs the ability of females to meet concurrent requirements for the lipid fraction of eggs from dietary sources and, as a consequence, clutch lipid requirements must be satisfied almost entirely from endogenous fat reserves. Protein requirements, therefore, also affect the number of eggs produced, by influencing the rate at which lipid reserves are expended during laying.

I believe that the preceding evidence implicates protein as a potential proximate factor influencing clutch