The Condor 93:1026–1028

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 size in Wood Ducks. Because foraging time is limited, clutch size represents a compromise between competing requirements for lipids and protein. Variations in foraging efficiency resulting from experience or changes in invertebrate abundance are therefore plausible explanations for individual, seasonal and annual differences in clutch size.

Two misinterpretations of statements in Drobney and Fredrickson (1985) require clarification. First, Ankney and Afton (1988) state that, according to Drobney and Fredrickson (1985), the PLH "applied to prairie nesting waterfowl generally." It should be clear from the title (Protein acquisition: a possible proximate factor limiting clutch size in Wood Ducks), the statement of objectives, and supporting data in the text that this hypothesis was developed specifically for Wood Ducks. The only reference to other species was in the final paragraph where we stated that detailed studies of how resources are allocated for reproduction were not available (at that time) for most species, but that given the similarity between nutritional strategies for Wood Ducks and for Mallards (*Anas platyrhynchos*) (Krapu 1981), protein might also influence clutch size in prairie nesting ducks. Our intent was to encourage investigators of prairie nesting ducks to examine the potential limiting effects of nutrients and not to generalize the applicability of this hypothesis to other species.

Second, Afton and Ankney (1991) inaccurately assert that the PLH, "suggests that females utilize lipid reserves while foraging inefficiently on aquatic invertebrates to meet protein requirements for egg production." As stated earlier and in Drobney and Fredrickson (1985), females are not "using lipids while foraging," but rather that foraging time devoted to obtaining invertebrates (protein) reduces the amount of time available for acquiring substrates for the lipid fraction of the egg, thereby influencing fat storage and the rate of fat reserve use during laying. Characterizing foraging as "inefficient" is also inappropriate. On the basis of the relative quality and quantity of protein in plant and animal foods (Drobney 1980), foraging on invertebrates is not only the most efficient way to obtain protein, but it is probably the only way to secure essential amino acids at a rate sufficient to sustain protein synthesis during egg production.

In two recent papers (Ankney and Afton 1988, Afton and Ankney 1991) the authors allegedly tested the PLH using data from Northern Shovelers (*Anas clypeata*) and Lesser Scaup (*Aythya affinis*). They consider these species as ideal subjects for examining the predictions of the PLH because they are invertebrate specialists and therefore must forage efficiently on such prey. Because an herbivore (Wood Duck) stores fat and relies on dietary sources of protein, they suggested that the PLH predicts that carnivorous species should require small lipid reserves during egg formation. It is unclear why one would use an herbivore-derived hypothesis to predict how carnivores should satisfy their nutritional requirements for reproduction. However, the authors' conclusions are consistent with what one might intuitively predict; namely, that carnivorous species are not limited by the main constituent of their diet (protein) and that satisfying lipid requirements represents a more formidable and potentially limiting problem. I do not disagree with their conclusions for scaup and shovelers, but contend that the tests neither negate nor appropriately test the PLH as it applies to Wood Ducks. Furthermore, I believe that tests of predictions based solely upon general characteristics of a species' diet and endogenous reserves (Afton and Ankney 1991: 89) are inadequate. The underlying premise of both the PLH and LLH is that food resources proximately influence reproductive output. Hence, these hypotheses cannot be meaningfully verified without also considering the fundamental interrelationships between food availability, foraging efficiency and egg production. Lacking definitive tests, they have only provided evidence to support lipid-limitation as a new hypothesis for scaup and shovelers.

Afton and Ankney (1991) have suggested that most temperate-nesting waterfowl, including Wood Ducks, are lipid- rather than protein-limited in part because waterfowl use highly productive wetlands where "protein is easier to obtain than lipids." This argument presumes that there is some level of equivalence in the relative abundance and availability of plant and animal foods in the wide array of habitats exploited by temperate nesting waterfowl and that interspecific differences in food selection, feeding modes, and foraging efficiency do not appreciably influence the relative ability of females to secure the lipid and protein resources needed for reproduction. Their attempts to broadly generalize the applicability of the LLH without adequate supportive data are, in my opinion, premature and have created unwarranted controversy.

Despite the lack of data, I concur that invertebrates may be more abundant than plant foods in habitats used by many northern nesting ducks because reproduction occurs in advance of seed production by wetland plants and normally corresponds with spring increases in invertebrate populations. However, I do not believe that this relationship applies to habitats used by Wood Ducks in southern portions of their range. In southern bottomland hardwood habitats, the spring seeds of elm (*Ulmus* spp.), maple (*Acer* spp.), and ash (*Fraxinus* spp.) are readily available in windrowed masses along the margins of foraging habitats throughout most of the breeding season. These low fiber, highly nutritious seeds constitute the bulk of the plant food diet of breeding females (Drobney and Fredrickson 1979). Therefore, the availability of plant foods as a substrate for lipid synthesis prior to and during laying does not seem to be limiting. The ability of females to store 60% of their fat reserves for reproduction during a brief 6–7 day period lends support to this conclusion.

My contention that invertebrates are less available and that protein is a more likely limiting nutrient is supported by several lines of evidence. First, I found that invertebrate abundance was low at sites where foraging Wood Ducks were collected, averaging only nine individuals per 1 m sweep sample (Drobney, unpublished data). Furthermore, most of these invertebrates were benthic or nectonic species that are generally unavailable to Wood Ducks, which forage predominantly on the surface (Drobney and Fredrickson 1979). Secondly, if Wood Ducks are lipid-limited as Ankney and Afton suggest, one must question why a female would select an invertebrate diet during laying when windrowed plant seeds, which provide better substrates for lipid synthesis than invertebrates, are abundant and easily obtainable throughout their foraging habitats. The most reasonable explanation is that acquiring protein from invertebrates is both critical and time-consuming, and therefore hens must devote virtually all of their foraging time during laying to satisfying protein requirements for egg synthesis.

The most substantive argument raised by Ankney and Afton (1988) is that protein-limited species should store and use endogenous protein. As discussed in Drobney and Fredrickson (1985), the benefits accrued from using endogenous protein may not outweigh the cost of storing, transporting, and maintaining this metabolically active tissue or the potential risk associated with using digestive organ and muscle tissue as sources of protein for eggs. Given that the ultimate measure of reproductive success is not clutch size, but the number of surviving young produced, I would expect that even a protein-limited individual would forego the expenditure of endogenous protein if use of that tissue posed a threat of sufficient magnitude to either her survival or her ability to successfully carry out incubation or brood rearing. Although some waterfowl use endogenous protein during reproduction, it has yet to be demonstrated that this is a viable tactic for all species.

In conclusion, recent studies have identified protein and lipid as probable proximate factors influencing intraspecific clutch size variation in temperate-nesting ducks. Neither hypothesis provides a universally acceptable explanation for clutch size limitation in all temperate-nesting species. Because of the range of food availability in the diverse wetlands used by breeding ducks as well as interspecific differences in feeding ecology, the lack of a universal hypothesis is not surprising. As more species are studied, new theories or variations of existing hypotheses will probably be generated. Long-term studies could demonstrate that limiting nutrients vary between breeding seasons in response to changes in food resources. In species with extensive breeding ranges such as Wood Ducks, the proximate influences of food might differ between northern and southern breeding habitats. Unfortunately, controversies regarding nutrient limitation of clutch size cannot be resolved until methodologies are developed for measuring food availability and its concomitant effect on egg production.

I wish to thank D. L. Galat, D. B. Noltie, M. R. Petrie and J. E. Thompson for their many helpful comments on earlier drafts of this manuscript. This is a contribution from the Missouri Cooperative Fish and Wildlife Research Unit (U.S. Fish and Wildlife Service; Missouri Department of Conservation; The School of Natural Resources, University of Missouri; and Wildlife Management Institute, cooperating).

LITERATURE CITED

Afton, A. D., and C. D. Ankney. 1991. Nutrient-reserve dynamics of breeding Lesser Scaup: a test of competing hypotheses. Condor 93:89–97.

Ankney, C. D., and A. D. Afton. 1988. Bioenergetics of breeding Northern Shovelers: diet, nutrient reserves, clutch size, and incubation. Condor 90:459–472.

Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

Drobney, R. D. 1980. Reproductive bioenergetics of Wood Ducks. Auk 97:480–490.

Drobney, R. D., and L. H. Fredrickson. 1979. Food selection by Wood Ducks in relation to breeding status. J. Wildl. Manage. 43:109–120.

Drobney, R. D., and L. H. Fredrickson. 1985. Protein acquisition: a possible proximate factor limiting clutch size in Wood Ducks. Wildfowl 36:122–128.

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

Krapu, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29–38.

Lack, D. 1967. The significance of clutch size in waterfowl. Wildfowl 18:125–128.

Raveling, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96:234–252.

Rohwer, F. C. In press. The evolution of reproductive patterns in waterfowl. *In* B.D.J. Batt et al. [eds.], The ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

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