no effect on clutch size of coots. They thus support the conclusions of Ankney and Afton (1988) that the role of protein in regulating clutch size of temperate nesting waterfowl has been overstated. Perhaps this is the case also for other wetland birds, such as coots.

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REPLY TO BRIGGS: THE ROLES OF ENDOGENOUS AND EXOGENOUS NUTRIENT SUPPLIES

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Briggs has presented some interesting interpretations concerning the importance of nutrient reserves and intake on reproduction. Her alternative explanations of my work are, for the most part, consistent with my results and do not negate nor exclude the conclusions reached in my original paper. However, there are a few points raised by Briggs to which I feel compelled to respond.

One crucial assumption of Briggs' interpretations is that coots arrive on the breeding grounds with enough endogenous fat stores for breeding and therefore the influence of exogenous intake is minimal. She cites the work of Alisauskas and Ankney (1985) as the basis for this point. Alisauskas and Ankney demonstrated that coots finish migration with sufficient endogenous lipids to lay a clutch of seven or eight eggs. An extension of this is that a female producing a larger clutch would need exogenous nutrient resources. Alisauskas and Ankney's effort also implies that females would be unable to produce renests. However, both of these reproductive events were typical for coots from my study population. Approximately 40% of the completed clutches contained more than nine eggs. Furthermore, renesting was frequent; for example, in 1982 over one-third of the nests found were second breeding attempts. These subsequent clutches were begun even when the first clutch had been destroyed by a predator during the latter part of incubation. Thus, many females were going well beyond the breeding effort that would be predicted solely from Alisauskas and Ankney's reproductive criteria. These results suggest that there may be far greater flexibility in the use of exogenous resources toward reproduction than has previously been noted in coots. Consequently, the influence of endogenous and exogenous resources are probably more intertwined than Briggs' commentary would suggest.

In her final paragraph, Briggs' conclusions are inconsistent. She first states that protein resources in the territories of coots are in *excess of needs,* and in the following sentence concludes that egg mass is *limited by* protein levels in the territories. If protein levels are superabundant then they are not likely to be limiting. Proceeding under the premise that protein levels in coot breeding territories are excessive, Briggs then suggests that the extra intake of protein caused females to "add" greater amounts of albumen to eggs. This reasoning assumes a direct relationship between nutrient intake and the physiological components of eggs. However, most of the research conducted to date has shown that diet has minimal effects on egg components (Romanoff and Romanoff 1949, Fisher 1969), except for

a relationship between calcium levels in diets and eggshell characteristics (Jackson et al. 1987, Makled and Charles 1987). Unfortunately, the majority of this work has been conducted on domestic chickens and therefore generalization to wild birds should be done with caution. Recent work on Black-billed Magpies, *Pica pica* (Hochachka 1988), however, showed that supplemental feeding only altered the water content and did not affect the nutrient composition of eggs. Given the profound effects that variations in yolk and albumen levels are likely to have on the developmental characteristics of the young it is quite possible that nature has buffered these physiological relations from the effects of dietary compositions. Thus albumen variations across egg size may result from the specific metabolic needs of the developing embryo and reflect biological constraints inherent to the developmental characteristics of the young (Warham 1983).

A conclusion one reaches from Briggs' commentary is that we need more refined experimental methods of supplementing food. Briggs has suggested varying the time period over which supplementation occurs (this point has also been addressed by Hochachka 1988). However, given the plaguing question of the importance of protein intake to reproduction, I would suggest that we should not only manipulate *when* food is added, but also *what* food is added. To determine the relative importance of protein and lipid requirements, food-enrichment studies should be conducted in which the supplemented food varies in the overall percentage of these two macronutrients. Although the experimental design would be "cleaner" if purified diets were added, unfortunately, animals typically find these single-nutrient foods unpalatable. Thus, for practical purposes, "mixed" diets should be used. For instance, one experimental group could be given a high-fat/low-protein diet whereas the other is given a high-protein/low-fat diet. Comparing the breeding characteristics of these two groups would demonstrate the separate influence of each of these nutrients. In this manner, the relative importance of protein vs. fat for reproduction would become clear.

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