

## COMMENTARY

### FOOD ADDITION, CLUTCH SIZE, AND THE TIMING OF LAYING IN AMERICAN COOTS

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Hill (1988) has recently published a study showing that supplemental feeding increased egg mass but did not affect laying date or clutch size in American Coots (*Fulica americana*). She added food (protein content 26%) to coot breeding territories in 1982, from the last week of March until the end of June. The coots in her study area started laying around the end of April in 1982, with median hatch date 13 June. Thus Hill added food from approximately 1 month before laying commenced to hatching.

Alisauskas and Ankney (1985) found that 85% of the lipids required for egg production in coots came from stored reserves. Although Hill (1988) stated otherwise, Alisauskas and Ankney (1985) determined that these energy reserves were acquired prior to arrival at the breeding site. They found that, unlike fat, most protein (72% of requirements) for egg formation is acquired exogenously on the breeding grounds. Thus, adding food to coot breeding territories provides extra protein for eggs but not extra fat.

Supplementary food has been shown to enlarge or advance all, some, or none of clutch size, egg size, and laying date in several species of birds (Davies and Lundberg 1985, Hochachka and Boag 1987, Hochachka 1988, and references therein). Consistent, between-species effects of added food on egg production should not be expected. In particular, the impact of added food on laying date, clutch size, and egg mass will depend on four factors: when food is added relative to when it is obtained from the environment, relative contributions of endogenous and exogenous resources to egg formation, whether food is naturally limiting, and whether laying date and clutch characteristics are plastic, i.e., indeterminate.

Assuming that laying date, clutch size, and egg mass are plastic, then the following relations should occur. Additional food during the time of reserve acquisition should advance laying date in species that use endogenous reserves and need to reach a condition threshold for breeding (Drent and Daan 1980), because the reserves are acquired sooner. Adding food during this time will increase clutch size and egg mass in such species only if naturally available food is limiting. (Species, like coots, that accumulate fat reserves for breeding before or during migration [Alisauskas and Ankney 1985], may be constrained in when they commence breeding by migration itself. Weather may determine migration, and hence laying date, irrespective of nutritional conditions.) Supplementary food during

the breeding period will enlarge clutch size, egg mass, and/or advance laying, only in species that rely on exogenous resources, and only if naturally available food is limiting. Consequently, food added to the breeding territory will affect neither clutch size, nor egg mass, nor laying date if these are determined by endogenous reserves stored prior to arrival on the territory, or naturally present in quantities in excess of their needs.

These generalizations can be checked by determining effects of food supplementation on laying date, clutch size, and egg mass, in relation to timing of nutrient acquisition for egg production in individual species. Such food experiments should include separate treatments of food added prior to, and during, egg laying. Nonmigratory species should be used where possible. Simultaneous monitoring of nutrient reserves, food resources, and egg production is required. This is currently difficult if not impossible (Ankney and Afton 1988), and some of the methodology is controversial (Murphy 1986, Alisauskas et al. 1987, Murphy 1987).

Effects of food supplementation could also be tested on species whose relative use of endogenous and exogenous resources for egg laying is known. For example, Eurasian Kestrels (*Falco tinnunculus*) provide support for these postulated relationships between sources of nutrient for egg production and effects of food addition. Food supplied prior to laying increased clutch size and advanced laying date in this species in poor food years, but did not affect laying date (no data for clutch size) in good food years (Dijkstra et al. 1982). Kestrels form eggs from endogenous reserves (Drent and Daan 1980). Sources of nutrients for clutch formation in species for which results of food provisioning experiments are known (Davies and Lundberg 1985, Hochachka and Boag 1987, and references therein) could also be ascertained. Determining sources of nutrients for egg formation should be done with care because species may vary in their use of endogenous and exogenous resources for laying depending on their environment (Batt and Prince 1978, Krapu 1981, Hohman 1986).

These interpretations and the results of Hill's (1988) experiment strongly suggest the following. Firstly, clutch size and laying date in American Coots are largely determined by endogenous lipid and protein reserves acquired prior to laying. Secondly, natural protein resources in the breeding territories are in excess of their needs, and do not determine clutch size or laying date. Thirdly, egg mass is controlled by, and probably limited by, protein levels in the breeding territories. This third conclusion is supported by Hill's findings that larger eggs were produced by coots in the food-enhanced territories, and that larger eggs generally had relatively more albumen (mostly protein solids) than yolk (solids mostly lipid, with some protein [Alisauskas 1986]). The data of Hill (1988) demonstrate that protein availability in the breeding territory has little or

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, re-nesting 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