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THE ROLE OF NUTRIENT RESERVES IN LIMITING WATERFOWL REPRODUCTION

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There are only two competing hypotheses that attempt to explain, both proximately and ultimately, clutch size in waterfowl (Anatidae). The "Egg Production Hypothesis," developed by Lack (1967, 1968), proposes that average clutch sizes of waterfowl species evolved in relation to average amounts of food available to laying females. The "Egg Viability Hypothesis," advanced by Arnold et al. (1987), argues that because (1) waterfowl eggs lose viability as they sit unincubated, and (2) predation risk is cumulative over that time, the upper limit (about 14 eggs) to clutch size of prairie-nesting ducks is set by the combined effects of these egg-mortality factors. In this essay, we briefly discuss and dismiss the latter hypothesis and summarize data and arguments supporting the former hypothesis. Finally, we argue that lipid generally is the nutrient that limits clutch size in waterfowl.

The "Egg Viability Hypothesis" (EVH) was based on the erroneous assumption that egg viability is genetically fixed within species. The data of Arnold et al. (1987) showed that there was great variability among eggs in the age that they became non-viable (among female variation in egg viability was not presented, but almost certainly was present). It is well known that the length of time that unincubated chicken eggs remain viable can be increased by artificial selection. Thus, we find it remarkable, if egg viability was limiting clutch size of waterfowl, that natural selection would not have produced increased viability. Moreover, other birds show longer time of viability (e.g., Wild Turkeys [*Meleagris gallopavo*] lay a clutch of 12–14 eggs over 18–20 days without loss of viability). At the other extreme, viability of American Coot eggs (*Fulica americana*) begins to decline after four days (Arnold 1990); we doubt that it is merely a coincidence that this is when, on average, coots begin incubating eggs. Arnold et al. (1987) overlooked the alternative explanation for their data on egg viability; that is, duration of egg viability has been selected to correspond to the number of days (eggs) before incubation begins. We conclude that length of time that eggs remain viable is set by the upper limit of clutch size in waterfowl and not vice versa.

Regardless of the foregoing, the EVH lacks explanatory power because it does not address the truly interesting questions regarding waterfowl clutch sizes; that is, "what causes variation in clutch size among females (and annual variation within individuals)?" and "what selects for among-species variation in mean clutch sizes?" The "Egg Production Hypothesis" (EPH), as modified by Ryder (1970) for Arctic-nesting geese, and interpreted and modified by us (Ankney and Afton 1988; Alisauskas et al. 1993; Afton and Ankney 1991; Ankney and Alisauskas 1991a, 1991b) for temperate-nesting ducks, has such explanatory power. Before developing those arguments, we first address Rohwer's (1986, 1988) studies that purportedly refute the EPH.

Lack (1967, 1968) derived the EPH from graphical analyses of clutch- and egg-size data of over 100 waterfowl species. He concluded that there was a *broad* inverse relation between clutch size and egg size. Lack (1968:225) wisely argued that the relation between egg size and clutch size would only be "broad" because "of the great variation in food supply available to the average female among waterfowl species." He interpreted this relation as an evolutionary trade-off whereby, on average, species that laid relatively large eggs were constrained by food availability to lay smaller clutches. Rohwer (1986, 1988) re-surveyed the literature on waterfowl clutch- and egg-size and used powerful (although not entirely appropriate, see below) statistical techniques to analyze these data. Rohwer found that after controlling for potentially confounding variables (e.g., body mass, taxonomy, latitude, etc.), clutch size explained "only" 13% of variation in egg size among species; he dismissed this variation as trivial and concluded that the EPH was incorrect. Ironically, Rohwer (1986:48) faulted Lack for using inappropriate statistics and for "expectational bias"; that is, finding what he had expected to find. Lack was unable to defend against this, but Blackburn (1991) has done so successfully. He correctly pointed out that the 13% of variation in egg size that was explained by clutch size in Rohwer's analysis is anything but "trivial." Moreover, Blackburn showed that Rohwer used inappropriate statistical techniques and that when a more appropriate analysis was done, clutch size explained 29% of variation in egg size among waterfowl species. Thus, the basis for the EPH stands as proposed by Lack and we are unaware of other hypotheses that explain the trade-off between egg size and clutch size among species of waterfowl.

In another study, Rohwer (1986, pers. comm.) destroyed nests of 126 Blue-winged Teal (*Anas discors*) and found that the 42 females that re-nested apparently did not use nutrient reserves. Despite his claim that this refutes the EPH, we disagree that it was even a valid test of the EPH because: (1) re-nests occurred later in spring when more exogenous nutrients are available, (2) clutch sizes of re-nests were smaller than those of first nests and consequently time of peak nutrient requirement was greatly reduced, and (3) Rohwer did not

compare body weights of females that did reneest to those of females that did not (and such a comparison might help explain why *most* females did not reneest). Regardless, Rohwer mistakenly assumed that use of nutrient reserves is a prerequisite of the EPH. Clearly, the females that reneested utilized exogenous nutrients; if their ability to produce eggs was constrained by availability of such nutrients (not measured by Rohwer), then their smaller clutch sizes provide strong support for the EPH.

Lack's EPH has stimulated considerable research. However, few researchers have studied *food* availability to laying females (but see Bengston 1971). Rather, most research has focused on use of nutrient reserves (lipid, protein, and mineral; defined by Ankney 1974). A major reason for this focus was Ryder's (1970) modification of Lack's hypothesis to explain intraspecific variation in clutch size of Arctic-nesting geese. Ryder (1970) assumed that these geese spent little time feeding during egg laying and thus postulated that clutch size had evolved in relation to size of energy reserves that females store before arrival on breeding areas. Subsequent research on use of reserves by breeding geese (Ankney 1974, Ankney and MacInnes 1978, Raveling 1979, Ankney 1984) strongly supported Ryder's hypothesis. Additionally, research showed that Common Eiders (*Somateria mollissima*) relied heavily on nutrient reserves for egg formation (Korschgen 1977).

Perhaps stimulated by goose/eider research, others investigated diets and use of nutrient reserves by temperate-nesting ducks. Drobney (1980) and Krapu (1981) reported that female Wood Ducks (*Aix sponsa*) and Mallards (*Anas platyrhynchos*), respectively, used large amounts of lipid reserves during egg production. Unlike investigators studying geese and eiders, who interpreted such use as a direct commitment to ova, Drobney and Krapu independently proposed that use of lipid reserves was an adaptation enabling females to forage for protein-rich but relatively scarce invertebrates. They further hypothesized that a female's ability to acquire protein limits her clutch size. Drobney and Fredrickson (1985) stated "It seems likely, therefore, that protein might also influence clutch size in North American prairie nesting ducks"; this was termed the "Protein Limitation Hypothesis" by Ankney and Afton (1988).

We initially tested the "Protein Limitation Hypothesis" (PLH) using data from female Northern Shovelers (*Anas clypeata*) and Lesser Scaup (*Aythya affinis*). These species were chosen because, as invertebrate specialists, they should be less constrained than other prairie ducks in obtaining such food; that is, under the PLH, shovelers and scaup should require little or no lipid reserves during egg production. Contrary to the PLH, we found that 72% of lipids deposited in an average clutch of shovelers and 50–92% of lipids in an average clutch of scaup could be accounted for by use of lipid reserves. Remarkably, both species *stored* protein reserves during laying. Furthermore, for female shovelers late in the laying cycle, there was a strong positive correlation between size of lipid reserves and number of developing ova. This suggested that female shovelers terminate laying when they reach a threshold level of lipid reserves.

Ankney and Afton (1988) noted that waterfowl eggs contain approximately equal amounts of lipid and protein. They argued, therefore, that the PLH overemphasized the importance of protein. They further argued that protein is easier to obtain than is lipid in the productive wetlands used by temperate-nesting ducks (see also Alisauskas et al. 1990). Thus, Ankney and Afton hypothesized that size of a female's lipid reserves is more likely to limit clutch size than is rate of protein ingestion; this was termed the "Lipid Limitation Hypothesis" (LLH) by Afton and Ankney (1991).

Rohwer's (1986, in press) "Migrational Uncertainty Hypothesis" states that female ducks simply "dump" left-over lipid reserves, stored for migration, into eggs. Several studies (Barzen and Serie 1990, Alisauskas et al. 1990, Afton and Ankney 1991, Ankney and Alisauskas 1991b) have shown that female ducks store fat after arrival on breeding areas. Therefore, this hypothesis is untenable.

Ankney and Afton (1988) argued that if breeding females *normally* encountered protein shortages, they would store protein for subsequent use during egg production. We believe that this is a critical argument because protein storage and use is well documented in Arctic-nesting geese, Common Eiders and in some nonwaterfowl species. Furthermore, we argue that food-habits data from females during egg production, per se, say nothing about what nutrient(s) may limit clutch size. Food habits data can, at most, provide information about which nutrients are important. In the case of egg production, this can be predicted *a priori* from nutrient composition of eggs. Thus, we conclude that only use of a nutrient store can indicate that this nutrient is normally limiting.

Ankney and Alisauskas (1991b) further tested the LLH and PLH with data from female Gadwalls (*Anas strepera*). Gadwalls were studied because, on an annual basis, they are one of the most herbivorous *Anas* species in North America. That is, Gadwalls provided an excellent opportunity to study nutrient-reserve dynamics of a *potentially* protein-limited prairie duck. Ankney and Alisauskas predicted that under the PLH, female Gadwalls should use lipid reserves at rates higher than do females of other species (because of their inefficiency at foraging for invertebrates). Under the LLH, female Gadwalls should use lipid reserves at a rate similar to that of other species, but should also use protein reserves. The latter prediction was supported by the data (Ankney and Alisauskas 1991b). Ankney and Alisauskas (1991b) also found that female Gadwalls in early stages of rapid follicle growth (RFG) had larger lipid and protein reserves than did females, collected at the same time, that had not yet entered RFG. These data indicated that female Gadwalls must acquire a threshold level of reserves before initiating egg production (see Alisauskas et al. 1990 for similar data from Ring-necked Ducks, *Aythya collaris*). Furthermore, Ankney and Alisauskas (1991b) showed that for female Gadwalls late in the laying cycle, there was a strong positive correlation between size of protein reserves and number of developing follicles. That is, female Gadwalls stop laying when they reach a threshold level of protein reserves.

Use of lipid reserves is ubiquitous among breeding

waterfowl, whereas use of protein reserves is confined to species that feed little during reproduction (Arctic geese, eiders), and to the most herbivorous prairie-nesting ducks (Gadwall, American Wigeon, *Anas americana*) and to Ruddy Ducks (*Oxyura jamaicensis*) (Alisauskas and Ankney, in press; Ankney and Alisauskas 1991a). We previously argued that use of lipid reserves is an evolved mechanism whereby lipids can be supplied to rapidly growing ovarian follicles at a higher rate than could be maintained by dietary intake alone (Alisauskas et al. 1990, Afton and Ankney 1991). We interpret use of protein reserves similarly; that is, those *exceptional* prairie-nesting species that use protein reserves support the general rule that most such species are not protein-limited or they also would use protein reserves. Thus, we conclude that data from prairie-nesting waterfowl, complemented by data from Arctic geese, provide overwhelming support for the LLH and concomitantly refute the PLH.

Because of space limitations, we focused this essay on the role of nutrient reserves in limiting clutch size. Nutrient reserves, however, also are critical for successful incubation in many waterfowl. Catabolism of endogenous reserves, primarily lipid, accounted for, on average, 30% of total energy requirements during incubation in 17 studies of 14 waterfowl species (Afton and Paulus, in press). Heavier female Canada Geese (*Branta canadensis*) were more attentive to nests and had shorter incubation periods than did lighter females (Aldrich and Raveling 1983). Lower attentiveness and longer incubation times result in greater nest loss in geese and probably in eiders and other ducks (see review in Afton and Paulus, in press). Recently, Gloutney and Clark (1991) reported that female Mallards and Northern Shovelers that hatched eggs were heavier than those that were unsuccessful. These results further emphasize the importance of lipid reserves to egg-laying waterfowl. That is, it is otherwise inexplicable why females would use lipid reserves for egg production given their importance during incubation. We encourage further studies of how individuals apportion nutrient reserves to eggs and to incubation and the concomitant effects on reproductive success (see Ankney and Alisauskas 1991b).

To summarize, there are several phenomena that can be explained by Lack's EPH that cannot be explained by competing hypotheses. Among these are (1) the broad negative relation between clutch size and egg size among waterfowl species, (2) the strong reliance on lipid reserves by virtually all species, and reliance on protein reserves by species that, predictably, have trouble acquiring animal protein, (3) the evidence for nutrient-reserve *thresholds* at initiation and at termination of egg production (Ankney and Afton 1988; Alisauskas and Ankney, in press; Ankney and Alisauskas 1991a, 1991b) and (4) the strong correlation, in females late in the laying cycle, between size of reserves and number of developing follicles (Ankney and Afton 1988, Ankney and Alisauskas 1991b). Finally, there is evidence that mean clutch sizes of waterfowl are not the most productive (Rohwer 1985, Rockwell et al. 1987). As argued by Price and Liou (1989), this is easily explained if females in good nutritional condition lay more eggs than do those which are not.

We are unaware of data from waterfowl that are inconsistent with the "Egg Production Hypothesis." Thus, we urge critics of the EPH to attempt to refute it in the "old-fashioned way." That is, obtain data from waterfowl; according to the AOU checklist, coots do not qualify!

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DO EGG FORMATION COSTS LIMIT CLUTCH SIZE IN WATERFOWL? A SKEPTICAL VIEW

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North-temperate ducks lay about 8–12 eggs. The explanation for these 10 egg clutches remains a controversial topic. Lack (1967) initiated the controversy when he suggested that, among waterfowl, “clutch size and [egg size] . . . have evolved in relation to average availability of food for the female at the time of laying.” As stated, this hypothesis is logically flawed because eggs are produced sequentially at a constant rate, so larger clutches do not require a greater rate of energy expenditure, they simply require a longer period of constant energy flow. This assumes that the time required to lay a full clutch is longer than the time it takes to mature one follicle, a condition met by most temperate-nesting waterfowl (Alisauskas and Ankney, in press). If ducks can obtain enough food per day to produce eggs for 8–12 consecutive days, then what would stop them from obtaining a similar food allotment for 15–30 days and thereby producing larger clutches? One answer is that ducks cannot meet the daily costs of egg formation solely through foraging, so

they rely on stored nutrients to produce eggs. Accordingly, clutch size will be limited by the size and rate of use of these stored nutrients.

Ryder (1970) was the first person to formalize this modification of Lack's hypothesis. Ryder observed that Ross' Geese (*Chen rossii*) lay eggs in the Arctic well before local food becomes available, so the nutrients for eggs must be derived from nutrient stores acquired prior to arriving in the Arctic. These stored nutrients can not be replenished in the compressed arctic breeding season, so the size of reserves presumably limits the size of the clutch. Ryder's (1970) suggestion that arctic geese rely on stored reserves has been confirmed for geese and eiders (reviewed in Parker and Holm 1990).

Drobney (1980) recognized that utilization of stored reserves to produce eggs was not unique to arctic-nesting waterfowl. He hypothesized that stored nutrients were needed to produce normal clutches even in temperate-nesting waterfowl that forage extensively during egg laying. Drobney (1980) further modified the egg-formation hypothesis by suggesting that Wood Ducks (*Aix sponsa*) had special difficulty meeting the protein requirements for egg production, so they relied on large stores of lipid to allow them to direct their foraging toward protein rich foods (see also Krapu 1981). Ankney and Afton (1988) call this the “protein-limitation hypothesis.” The “lipid-limitation hypothesis” also is based on the idea that stored nutrients are essential for egg production, but it proposes that lipid requirements for eggs cannot be met from the diet, therefore clutch size is limited by the lipid stores that can be called upon to produce eggs (Ankney and Afton 1988, Ali-