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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-

sauskas et al. 1990). We refer to all hypotheses that deal with classes of nutrients (lipid, protein, or minerals) as the "nutrient-limitation hypothesis." The debate over the merits of the contrasting hypotheses is interesting, but secondary to the question of whether any stored nutrients constrain clutch size.

We believe that the nutrient-limitation hypothesis has been prematurely accepted, especially for waterfowl that do not nest in the Arctic. We suggest that testing the nutrient-limitation hypothesis should involve a three-step process. The first step is to see if stored nutrients are used during egg formation. Ryder (1970) first did that, and since his study the use of nutrient reserves during laying has been well documented. We have no contention with this point. The next important step in testing the nutrient-limitation hypothesis is to show that stored nutrients are required for egg laying. We believe that tests of this aspect of the nutrient-limitation hypothesis have been uncommon and their results equivocal. A third phase of testing the egg-formation hypothesis is to determine whether the level of stored nutrients limits clutch size. This critical phase of testing the nutrient-limitation hypothesis has been virtually ignored.

We suspect that the plausibility of the nutrient-limitation hypothesis has led to its uncritical acceptance. For instance, the use of nutrient reserves by laying females has been considered evidence that nutrient reserves limit clutch size. Imagine instead that cause and effect are the reverse of how most people interpret nutrient use. Under this scenario, clutch size is limited to 10 eggs by some unknown factor, yet ducks store the amount of nutrients that allow them to lay their 10 egg clutches. To dismiss such an idea as implausible is, we believe, an indication of how entranced we are with the idea that energetics dictate life history. It is even less appropriate to support the nutrient-limitation hypothesis because we have rejected most of the other hypotheses concerning clutch size in waterfowl.

In this essay we examine the nutrient-limitation hypothesis with the intent of determining whether waterfowl require stored nutrients for egg laying, and, if so, whether the level of stored nutrients actually limits clutch size. We raise nine general points that cast considerable doubt upon the nutrient-limitation hypothesis.

1. *Variation in nutrient reserves greatly exceeds variation in clutch size.* If the size of a female's nutrient reserve determines her clutch size, then we would expect individuals with large and small prelaying reserves to produce large and small clutches, respectively, such that both groups complete laying with equivalent nutrient reserves. On a population level, such a relationship has been documented among arctic-nesting Lesser Snow Geese (*Chen caerulescens caerulescens*) (Ankney and MacInnes 1978). However, there is little support for such a relationship among temperate-nesting waterfowl. The slope of the regression of somatic nutrients (e.g., FAT, PROT) versus reproductive nutrients (RFAT, RPROT) indicates the rate of stored nutrient use during egg formation (see Alisauskas and Ankney 1985). If we assume that all individuals use stored nutrients at this same rate (b_{fat} , b_{prot}) and that they terminate laying when they have reached the same

minimum reserve level (FAT_{min} , PROT_{min} - set as the minimum level of somatic nutrients observed in each study), and if we further assume that each egg contains the same amount of nutrient (EGGFAT, EGGPROT), then we can generate predicted clutch size (CS) based on nutrient reserves:

$$\text{CS}_{\text{fat}} = [\text{RFAT} + (\text{FAT} - \text{FAT}_{\text{min}}) (-b_{\text{fat}})^{-1}] \text{EGGFAT}^{-1}$$

$$\text{CS}_{\text{prot}} = [\text{RPROT} + (\text{PROT} - \text{PROT}_{\text{min}}) (-b_{\text{prot}})^{-1}] \text{EGGPROT}^{-1}$$

These predicted clutch sizes are, without exception, significantly more variable than actual clutch sizes, often exceeding actual clutch sizes by two to three fold (Table 1).

2. *Variance in nutrient reserves remains high in post-laying birds.* A corollary to the above examination of the differences between females in nutrient reserves is the examination of how variance in nutrient reserves changes during the reproductive cycle. The nutrient-limitation hypothesis predicts that variance in nutrient reserves decreases between pre-laying and post-laying birds. Such a relationship should occur if birds with larger reserves use these additional nutrients to lay more eggs. To test this prediction we extracted data from the literature (available upon request from T.W.A.) to examine patterns of within-population variance in the size of nutrient reserves. Only two of 24 nutrient reserve-by-population comparisons (8.3%) exhibited significant declines in variance among post-laying females. Predictably, these two populations were large arctic-nesting waterfowl. It is surprising that most researchers have not collected post-laying females, an important omission given that the nutrient-limitation hypothesis predicts that termination of laying is related to depletion of reserves to some threshold level.

In American Coots (*Fulica americana*), lipid and protein reserves of post-laying females were positively correlated with total lipids and proteins invested in egg formation (Arnold 1990); a similar relationship existed for lipid reserves of Blue-winged Teal (*Anas discors*) (Rohwer 1986a). These correlations suggest that individuals laying relatively small clutches may have stopped laying due to depletion of their lipid reserves, but individuals laying relatively large clutches stopped laying before reserves became limiting. Ankney and Afton (1988) devised an alternative means of determining whether declining reserve levels influenced a female's decision to stop laying. They found, among late-laying Northern Shovelers (*Anas clypeata*), that variation in fat reserves explained 36% of the variation in number of developing follicles. For Gadwalls (*A. strepera*), variation in protein and lipid reserves accounted for only 27% and 3% of this variation, respectively (Ankney and Alisauskas, in press b). These positive correlations between nutrient reserve levels and clutch size (or potential clutch size) need not imply causation, but even if they do, such data indicate only a modest influence of nutrient reserves on clutch size.

3. *Resting birds lay eggs without using stored reserves.* If birds require stored nutrients for egg production, then females should not be able to produce replacement clutches (re-nests) until they have reacquired their original pre-laying reserve levels (or levels at least approximating these). However, many temperate-nest-

TABLE 1. Predicted clutch size based on nutrient reserves (see text) compared with actual clutch sizes from nesting studies. Nutrient reserve data are from studies that used regression techniques (Alisauskas and Ankney 1985) and found significant declines in fat or protein reserves.

		Number of females/nests with each predicted/observed clutch size:							$\bar{x} \pm SD$ (range)	F_{\max} test	
		1-5	6-10	11-15	16-20	21-25	26-30	31-35			36-45
Mallard	-lipid	—	3	10	5	1	—	—	—	14.2 ± 3.4 (8-21)	**
	-nests	—	39	31	—	—	—	—	—	10.3 ± 1.2 (8-14)	
Gadwall	-lipid	—	6	30	28	12	1	—	—	16.5 ± 4.4 (7-28)	**
	-protein	1	5	24	27	12	5	5	—	18.1 ± 6.4 (4-35)	**
American Wigeon	-nests	1	100	34	5 ^a	—	—	—	—	9.7 ± 2.3 (5-20 ^a)	
	-protein	—	1	5	2	7	4	—	—	19.5 ± 6.0 (8-30)	**
Northern Shoveler	-nests	1	28	—	—	—	—	—	—	8.5 ± 1.2 (5-10)	
	-lipid	2	28	14	7	3	—	—	—	11.3 ± 4.6 (5-25)	**
Blue-winged Teal	-nests	—	11	14	—	—	—	—	—	10.6 ± 1.0 (8-12)	
	-lipid	—	3	8	11	15	4	2	3	20.7 ± 8.0 (7-44)	**
Canvasback	-nests	—	71	65	—	—	—	—	—	10.1 ± 1.6 (6-13)	
	-lipid	1	5	9	8	6	2	—	—	16.0 ± 6.1 (4-30)	**
Ring-necked Duck	-nests	—	11	1	—	—	—	—	—	9.5 ± 1.2 (7-12)	
	-lipid	1	3	3	5	5	1	—	—	16.6 ± 6.6 (3-27)	**
Lesser Scaup	-nests	—	—	—	—	—	—	—	—	8.2 ± 1.5	
	-lipid	2	4	5	6	2	—	—	—	13.1 ± 5.8 (0-24)	**
American Coot	-nests	—	43	13	5 ^a	—	—	—	—	10.3 ± 2.6 (7-19 ^a)	
	-lipid	—	4	6	3	—	—	—	—	12.6 ± 3.6 (8-20)	*
	-protein	1	5	9	8	6	2	—	—	16.0 ± 6.1 (4-30)	**
	-nests	13	49	2	—	—	—	—	—	7.2 ± 2.0 (2-14)	

^a Island nesting populations; large clutches likely represent conspecific nest parasitism (Rohwer and Freeman 1989).

References (top to bottom): Krapu in Alisauskas and Ankney, in press; Krapu and Doty 1979; Ankney and Alisauskas, in press b (yearlings and adults combined); *ibid*; Duebbert 1966; Wishart in Alisauskas and Ankney, in press; Wishart 1983; Ankney and Afton 1988; T. Arnold, unpubl. data; Rohwer 1986a (first nests only); Dane 1966 (includes renesters); Barzen and Serie 1990 (yearlings included, renesters excluded); *ibid*; Doty et al. 1984 (first nests only); Alisauskas et al. 1990; McAuley and Longcore 1989; Afton and Ankney 1991; Hines 1977; Alisauskas and Ankney 1985; *ibid*.

ing waterfowl reneest within 10 days of clutch destruction (reviewed in Bellrose 1980), suggesting that ducks do not reacquire reserves before reneesting, or that reserves can be reacquired so quickly that nutrients would not be limiting. Rohwer (1986a) showed that Blue-winged Teal did not reacquire reserves before initiating renesters, nor did they use their remaining reserves for egg production during reneesting. Similar observations have been obtained for small samples of other reneesting ducks (Krapu 1981; Barzen and Serie 1990; but see Ankney and Alisauskas, in press b). We recognize that renesters lay later in the season than first-nesters (when food may be more abundant) and that they lay smaller clutches, yet their apparent lack of use of any nutrient reserves is contradictory to the idea that stored nutrients are required for laying.

4. *Stored energy is a minor fraction of total energy budgets.* When we learn that some ducks store enough lipids for a complete clutch (Ankney and Alisauskas, in press a, in press b), or that peak daily energy expenditure during laying averages 160% of basal metabolic rate for North American waterfowl (Alisauskas and Ankney, in press), it is easy to believe that egg formation costs would limit clutch size. Such statements are misleading, however, because they ignore the total energy budget of the laying female. We estimate that clutch formation averaged $28 \pm 5\%$ (1 SD) of total female energy expenditures during egg formation in 13 temperate-nesting waterfowl, and the

contribution of stored reserves only offsets these total energy demands by an average of 9.5% (Table 2). This is an order of magnitude less than the near-total reliance on nutrient reserves observed among arctic-nesting geese and eiders, and we therefore question whether such an increment in total energy costs can be important enough to limit clutch size.

5. *Variation in clutch size is unexpectedly low.* If clutch size is limited by the ability of parents to provide food for their nestlings (i.e., altricial birds), then we would not expect pronounced annual variation in clutch size because parents cannot predict food abundance for nestlings when they are laying eggs (Lack 1947). In contrast, if clutch size is limited by the ability of females to produce eggs, then clutch size is proximately limited by food supply because reproductive success would be enhanced by laying more eggs (Daan et al. 1988). Thus, we predicted that clutch size in waterfowl should be more variable than clutch size in parentally-fed birds. To test this prediction, we assembled data on among-year variation in clutch size for 30 populations of waterfowl and for 30 populations of birds with parentally-fed young (references available from T.W.A.). In contrast to our prediction, clutch size was not more variable for waterfowl; in fact, annual variation was more pronounced for birds with parentally-fed young ($t = 2.16$, $P = 0.03$).

Bengtson's (1971) study of annual clutch-size variation among ducks nesting at Lake Mývatn, Iceland

TABLE 2. Estimated field metabolic rates (FMR) and energy requirements of laying female waterfowl.

Species	Body mass	Daily FMR	Energy in 1 egg	CS	RFG	Energy required during the period of egg formation			Maximum energy in nutrient stores			Percent of total energy from stored nutrients	
						Existence	Clutch	Total	Lipid slope ^a	Lipid stores	Protein slope ^a		Protein stores
Mallard	1,000	847	513	9	6	12,705	4,617	17,322	-1.04	2,967	0	0	17.1
Gadwall	650	614	417	10	6	9,824	4,170	13,994	-0.78	2,010	-0.16	255	16.2
American Wigeon	708	654	409	9	6	9,810	3,681	13,491	-0.34	773	-0.44	619	10.3
Northern Shoveler	550	541	379	9	5	7,574	3,420	10,994	-0.72	1,522	+0.10	-131	12.5
Blue-winged Teal ^b	355	390	275	11	5	6,240	3,025	9,265	-0.45	841	0	0	9.1
Blue-winged Teal ^c	355	390	275	9	5	5,460	2,475	7,935	-0.01	15	-0.12	113	1.6
Canvasback ^a	1,360	1,067	646	8	7	16,005	5,168	21,173	-1.06	3,385	-0.09	178	16.8
Ring-necked Duck	660	621	484	9	6	9,315	4,356	13,671	-0.47	1,265	+0.06	-100	8.5
Lesser Scaup	650	614	417	9	6	9,210	3,753	12,963	-0.50	1,160	+0.02	-29	8.7
White-winged Scoter	1,420	1,101	876	9	8	18,717	7,884	26,601	+0.06	-292	-0.08	241	-0.2
Ruddy Duck	510	512	696	8	12	10,240	5,568	15,808	-0.61	2,099	-0.13	277	15.0
American Coot ^d	500	504	195	7	7	7,056	1,365	8,421	-0.55	402	-0.24	152	6.6
American Coot ^e	520	519	194	9	5	7,266	1,746	9,012	-0.13	121	0.02	-16	1.2

Calculated from data in Bellrose 1980; Alisauskas and Ankney 1985, in press; Rohwer 1986a; Nagy 1987; Ankney and Afton 1988; Arnold 1990; Afton and Ankney 1991; Ankney and Alisauskas in press a, in press b. Body mass in g, energy equivalents in kJ, clutch size (CS), rapid follicle growth (RFG) in d. FMR is field metabolic rate, estimated from allometric equations derived from doubly-labelled water studies of non-passerine birds (Nagy 1987).

^a Slopes of nutrient reserves used during follicle development (after Alisauskas and Ankney 1985).
^b First nesting attempts.
^c Renesting attempts.
^d Combined sample of pre-layers and layers.
^e Delta, Manitoba (Alisauskas and Ankney 1985).
^f Minnedosa, Manitoba (Arnold 1990).

has been widely cited as evidence supporting the egg-formation hypothesis. Invertebrate prey of several ducks declined by 40–74% in one year, yet clutch size in that year was reduced by only 0.7 eggs, on average (Bengtson 1971). Therefore, we suggest that food availability has a small proximate influence on clutch size.

6. *Captive waterfowl do not lay exceptional clutches.* Wild waterfowl are wide-ranging, active, and reliant on natural food supplies, whereas captive waterfowl are confined, inactive, and provided with high-quality ad libitum foods. If clutch size in waterfowl is proximately limited by food availability, then captive females should be able to produce much larger clutches than wild females. Contrary to this prediction, captive ducks lay only 1–2 more eggs than do their wild counterparts (Batt and Prince 1979, Rohwer 1984, Duncan 1987, Eldridge and Krapu 1988). Likewise, captive geese show little (Owen and West 1988) or no increase in clutch size (Leblanc 1989). Overall, captive waterfowl lay larger clutches than wild birds, but the differences are small given what must be enormous differences in food availability and existence energy expenditures.

7. *Some wild waterfowl lay exceptional clutches.* Continuation nesting occurs when a female loses her nest during laying and goes on to produce a replacement clutch without interrupting her normal laying sequence. Rohwer (1986b) summarized records of continuation nesting in temperate dabbling ducks. The most phenomenal case involved a Gadwall that laid 22 eggs in 22 days, twice as many eggs as are normally laid in succession (Gates 1962). If nutrients limit clutch size, then how can continuation nesters produce more sequential eggs than are ever found in normal unparasitized nests (Rohwer 1986b)? Admittedly, there are few clear cases of continuation nesting; however, continuation nesting has been reported from over half of the re-nesting studies where it could have been detected (Rohwer 1986b). Alisauskas and Ankney (1985) suggested that clutch size in American Coots was limited by the ability of females to produce eggs because these birds use lipid and protein reserves during laying (but see Arnold 1990). However, Arnold (1990) found that most coots that lost clutches during laying could produce an immediate continuation clutch; the most remarkable record involved a coot that laid 35 eggs in 37 days in four different nests. Additional data on the ability/inability of waterfowl to produce continuation nests would be welcomed.

8. *Laying rates are at a physiological maximum.* Most temperate-nesting ducks lay one egg per day (Alisauskas and Ankney, in press). If clutch size of these ducks is limited by the need to supplement daily foraging intake with stored reserves, then this limitation could be removed or relaxed by laying eggs at a slower rate. This could involve a slower constant rate of egg formation or facultative “laying skips” on days when foraging intake failed to meet requirements. Slow laying rates among swans, geese, and eiders are probably related to egg size, rather than nutrient shortfalls, because large waterfowl obtain most of their nutrients for egg production directly from reserves. The rapid laying rate of most prairie ducks suggests that they are rarely nutrient limited during laying, and are instead adopting a “time-minimization strategy.” We presume that wa-

terfowl cannot further increase their laying rates beyond one egg per day because of physiological constraints associated with shell formation and/or because it would greatly interrupt their normal circadian rhythm.

9. *Larger eggs do not mean smaller clutches.* If egg formation in waterfowl is limited by the amount of nutrients available to laying females, then we would expect egg size to have an important modifying influence on clutch size (Lack 1967). With a fixed amount of reserves, a laying female could theoretically produce many small eggs or fewer large eggs (Rohwer 1988, Lessells et al. 1989). In reality, egg size appears to be highly heritable and repeatable in birds (Lessells et al. 1989), and it exhibits little proximate variation with food supply (Arnold 1990), so individual females are probably incapable of appreciably modifying the size of their eggs. However, if reserves limit clutch size, then we should still expect females with an inherent tendency to produce large eggs to be able to lay fewer eggs, on average, than do females that lay small eggs. No such correlations have been observed within 29 populations of waterfowl (reviewed in Rohwer 1988, Arnold 1990). There is, however, a weak inverse correlation among species (Rohwer 1988, Blackburn 1991).

SO WHY DO LAYING FEMALE WATERFOWL USE NUTRIENT RESERVES?

Although our critique casts numerous doubts on the nutrient-limitation hypothesis as a general explanation of clutch-size limitation among waterfowl, our criticisms do not dispute the fact that most female waterfowl use reserves during laying. For arctic-nesting geese and eiders, which appear to be highly reliant on nutrient reserves during egg laying, the nutrient-limitation hypothesis certainly remains the most tenable explanation of clutch-size limitation. However, some of our above criticisms (e.g., #'s 2, 5, 6, and 9) are not easily reconcilable with this hypothesis, even for arctic geese.

Several observations suggest that nutrient reserves may have a small effect on clutch size among temperate-nesting waterfowl: (1) significant positive correlations between nutrient reserves and clutch size among late-laying and post-laying females (point #2 above), (2) somewhat larger clutches among captive waterfowl on ad libitum diets (point #6), and (3) a trade-off between clutch size and egg size across waterfowl taxa (Blackburn 1991). However, the main theme of these observations is that the effect of nutrient limitation on clutch size in temperate waterfowl populations is probably small and limited to a fraction of the population.

We believe that the most important selective factor affecting clutch size in temperate waterfowl has been the amount of time required to complete the clutch (Arnold et al. 1987). If time is limiting, but nutrients are not, then there will be selection on females to produce eggs as rapidly as possible. We suggest that most waterfowl use nutrient reserves to maintain high rates of egg production (that is, one egg per day), despite potential day to day shortfalls in availability of dietary nutrients. We suspect that if such shortfalls occurred, then natural selection would favor the strategy of storing and using nutrient reserves during laying, regardless of whether such shortfalls occurred regularly or irreg-

ularly (e.g., nine out of ten years, or one out of ten years).

Female waterfowl do not reach seasonal minima in nutrient reserve levels at the end of laying. Thus, all species of waterfowl have the capacity for additional egg production, so why do they stop laying? If nutrient reserves are important determinants of a female's ability to incubate successfully (e.g., Ankney and MacInnes 1978; Erikstad 1986; M. L. Gloutney and R. G. Clark, unpubl. MS; but see Hepp et al. 1990), or to renest rapidly following clutch destruction (Milonoff 1989, but see Krapu 1981, Rohwer 1986a), then use of nutrient reserves during egg laying may indeed affect reproductive success via trade-offs with these other important processes, even if nutrient reserves do not determine clutch size per se. We believe that there have been too few tests of these alternative roles for nutrients reserves among breeding waterfowl.

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