INTER- AND INTRASPECIFIC RELATIONSHIPS BETWEEN EGG SIZE AND CLUTCH SIZE IN WATERFOWL

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ABSTRACT.—Lack (1967, 1968a) proposed that clutch size of waterfowl and other birds with self-feeding young was limited by females' ability to produce eggs. Lack supported this egg-production hypothesis by showing a strong inverse relationship between egg size and clutch size within and among species of waterfowl. A reanalysis using updated data and more appropriate statistics failed to confirm Lack's results. Grouping all the waterfowl produced a weak ($r^2 = 0.13$) inverse relationship between relative egg size and relative clutch size. This relationship was due mainly to a handful of ducks that nest on oceanic islands. Analyses by tribes showed that relative egg size and relative clutch size were inversely related in only 2 of the 8 major tribes of waterfowl. Finally, intraspecific analyses failed to reveal a trade-off between egg size and clutch size in Blue-winged Teal (*Anas discors*) and Northern Shovelers (*A. clypeata*). Similar intraspecific analyses for 12 other waterfowl have failed to show the predicted inverse relationship between egg size and clutch size. These results suggest that the widely accepted egg-production hypothesis may be considerably overemphasized. *Received 19 December 1986, accepted 13 July 1987.*

A CENTRAL question concerning life-history adaptation is how many young to have in any breeding event. Field studies of this problem have largely dealt with birds. Much of this literature was inspired by the work of David Lack (1947, 1948, 1954a, 1968a). Lack's thesis was that clutch size in most birds has evolved to correspond to the maximum number of young the parents can feed. Lack suggested that females that laid larger than normal clutches would leave fewer descendants because the brood would be undernourished and suffer greater nestling or fledgling mortality. Lack's (1954a, 1968a) conclusions that parents' ability to feed young is more likely to constrain clutch size than their ability to lay or incubate eggs are widely accepted (Klomp 1970, Ricklefs 1977, Högstedt 1980).

Waterfowl (Anatidae) have highly precocious young that leave the nest shortly after hatching and secure their own food. Parental duties consist of leading the brood to feeding areas, warming chilled young, watching for predators, and, in the larger species, defending the brood from predators. With such forms of parental care, it seems unlikely that survival of young would be affected by brood size. Manipulations of brood size in Blue-winged Teal (*Anas discors*) and Canada Geese (*Branta canadensis*) have shown no relationship between survival of young and brood size (Rohwer 1985, Lessells 1986). Brood size alterations brought about by intraspecific nest parasitism also failed to affect duckling survival in Wood Ducks (*Aix sponsa*) and Common Goldeneyes (*Bucephala clangula*) (Heusmann 1972, Clawson et al. 1979, Rothbart 1979, Dow and Fredga 1984; but see Andersson and Eriksson 1982). Likewise, clutches enlarged either experimentally or through intraspecific nest parasitism have shown ducks to be capable of hatching greatly enlarged clutches with little or no reduction in the percentage of eggs that hatch (Leopold 1951, Hori 1969, Morse and Wight 1969, Heusmann 1972, Clawson et al. 1979, Eriksson 1979, Dow and Fredga 1984, Rohwer 1985).

Waterfowl lay large eggs relative to their body size (Lack 1968a, King 1973, Rahn et al. 1975), and they lay large clutches (Johnsgard 1978, Bellrose 1980). In many species the total clutch mass approaches the mass of the female (Appendix). Such a large commitment to egg nutrients suggests that the production of eggs could constrain reproductive output. Lack (1967) proposed that "the average clutch of each species (of waterfowl) has been evolved in relation to the average availability of food for the female around the time of laying, modified by the relative size of the egg." Lack suggested that species laying eggs that were small relative to their

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body size would be able to lay many eggs, whereas species laying large eggs would lay fewer eggs. As a test of this hypothesis Lack (1967, 1968a) related egg size to clutch size, and concluded that the two were inversely related.

Lack's description of a trade-off between egg size and clutch size has been widely accepted as strong support for the hypothesis that clutch size in waterfowl is limited by egg production. Lack, however, employed an inappropriate correction for the allometry of egg size to body size, made relatively arbitrary categories of egg sizes in his analyses, and was forced to use questionable data for some species (Lack 1968a: appendix 15). I re-examined the relationship between egg size and clutch size on inter- and intraspecific levels in an effort to reassess the hypothesis that egg production limits clutch size in waterfowl.

METHODS

Interspecific analyses of egg size and clutch size.—The interspecific analyses required information on female body mass, the mass of unincubated eggs, and clutch size (Appendix). Because egg size and clutch size are presumed to covary negatively, I tried to use sources reporting data for the same population in the same years. At the minimum I used data for the same subspecies. I used female masses taken at the beginning of incubation when such detailed data were available.

For some species egg mass was calculated from egg dimensions using the equation:

$$\text{egg mass} = \text{constant} \cdot \text{length} \cdot \text{breadth}^2$$

(Hoyt 1979). The constant of 0.555 (g/cm^3) was used; this was calculated from a variety of waterfowl data (Young 1972; Laughlin 1976; Mackenzie and Kear 1976; Riggert 1977; Norman 1982; Summers 1983; Rohwer 1986a, unpubl. data) and is unaffected by egg size.

I used Livezey's (1986) tribal classification. The main way this classification differs from others (Delacour and Mayr 1945; Delacour 1954, 1956, 1959; Johnsgard 1978; Bellrose 1980; A.O.U. 1983; Scott 1985) is to eliminate the tribe of perching ducks (previously: Cairinini) and split the swans and geese into two tribes. The former change had been suggested previously based on skeletal characters, behavior, and hybridization studies (Johnsgard 1960, 1979; Woolfenden 1961). Names for North American species are those of the American Ornithologists' Union (1983). Specific and subspecific nomenclature for other waterfowl follow Johnsgard (1978).

Several times in this paper I report the relationship between two sets of data each with natural variability, such as egg mass and female mass. Standard regression techniques, though commonly applied, are not appropriate for such data because standard regression creates a line of best fit by minimizing only the deviations of the presumed dependent variable from the regression line (Kidwell and Chase 1967, Harvey and Mace 1982, Ricker 1984). In relating egg size and clutch size, neither has logical primacy as the causal agent of the variation in the other. For this reason, I used principal axis analysis (Sokal and Rohlf 1981) to provide a line of relationship between variables that demonstrated a significant Pearson correlation. The strength of the principal axis is indexed by the correlation coefficient.

Intraspecific analyses of egg size and clutch size.—I gathered data on Blue-winged Teal and Northern Shovelers (*Anas clypeata*) breeding in southwestern Manitoba in pothole habitat (for a description of the study area see Evans et al. 1952). For both species I located active nests and weighed eggs (or measured length and breadth of incubated eggs) and repeatedly checked nests to determine the number of eggs laid. Frequent nest checks during the egg-laying period have never revealed cases of intraspecific nest parasitism for either species. I also measured wing, bill, tarsus, keel, and body lengths (bill tip to the end of the tail) for females that were nest trapped (Weller 1957a) or collected (for energetics studies) at their nest. Blue-winged Teal data were collected in 1978–1983 and shoveler data in 1980–1983.

I used egg mass as an index to the cost of an egg. Egg mass is a good index to the cost of an egg in terms of energy or lean dry content for Blue-winged Teal (Rohwer 1986a), Northern Shoveler (unpubl. data on 213 eggs), and several other waterfowl (Manning 1978; Ankney 1980; Birkhead 1984, 1985). Likewise, the proportion of yolk and the composition of yolk and albumen are similar for the eggs of most waterfowl (Lack 1968b, Rohwer unpubl. data), suggesting that egg size is an adequate index of egg cost in comparisons between species.

RESULTS

Interspecific relationships between egg size and clutch size.—In waterfowl, egg mass increases with body size, but egg mass as a proportion of adult body mass decreases with body size, as is typical of avian groups (e.g. Rahn et al. 1975). This relationship is best demonstrated as a logarithmic plot of egg mass vs. body mass (Fig. 1; $r = 0.92$, $n = 152$, $P < 0.0001$). The slope of the principal axis of this log-log plot measures the exponent in the power function that relates egg mass (E) to female body mass (B):

$$E = 0.47B^{0.72}. \quad (1)$$

The constant, 0.47 (g/g body mass), is the intercept from the same log-log plot (Fig. 1), and

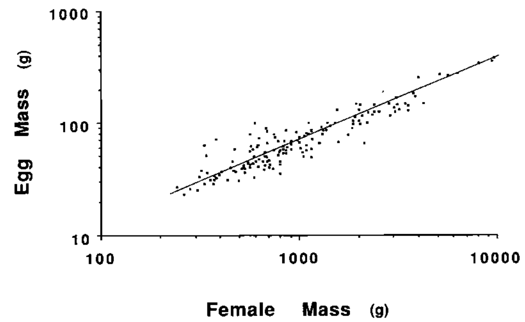

Fig. 1. Relationship of egg mass and female mass among waterfowl.

represents the extrapolated egg mass of a 1-g female.

Relative egg size can be estimated from Eq. (1) by subtracting predicted egg mass from actual egg mass. By the egg-production hypothesis, species that lay relatively large eggs (points above the line in Fig. 1) should lay fewer eggs per clutch than species that lay relatively small eggs (points below the line in Fig. 1). A correlation of relative egg size and clutch size shows a highly significant ($r = -0.34$, $n = 151$, $P < 0.0001$) but weak inverse correlation ($r^2 = 0.11$). This analysis suffers two problems. First, large-bodied species that lay large eggs show much greater absolute differences between actual and predicted egg mass than do species that lay small eggs. Thus, the largest species dominate the analysis, making it mostly an analysis of swans and geese. Second, the analysis ignores the substantial differences between tribes in clutch size and in the relationship between egg mass and female mass.

To overcome these problems, I analyzed the relationship between egg mass and body mass separately for each of the eight most diverse tribes of waterfowl (Table 1). Surprisingly, egg mass and female mass were uncorrelated in whistling ducks (Dendrocygnini, $r = 0.51$, $n = 8$, $P > 0.10$). In all other groups the exponent that relates body mass to egg mass was less than one (Table 1), but there was heterogeneity in these exponents between tribes (analysis of covariance, interaction $F = 16.2$, $P < 0.0001$). New measures of relative egg mass were calculated using these within-tribe principal axis analyses (Table 1). Relative egg size for the Dendrocygnini was simply the species average for egg mass minus the tribal average for egg mass. To standardize clutch size among the diverse tribes of

TABLE 1. Statistics for the relationship of log egg mass and log female mass.

Tribe	Correlation coefficient	n	P	Slope[a]	Intercept[b]
Anatini	0.85	53	<0.0001	0.67	0.63
Anserini	0.88	18	<0.0001	0.56	1.68
Aythyini	0.77	15	<0.001	0.85	0.18
Cygnini	0.93	8	<0.001	0.62	1.24
Dendrocygnini	0.51	8	>0.10	—	—
Mergini	0.86	16	<0.0001	0.54	1.58
Oxyurini	0.87	8	<0.005	0.63	1.35
Tadornini	0.90	21	<0.0001	0.48	2.71

[a] b in the equation egg mass = a(female mass)^b.
[b] a in the equation egg mass = a(female mass)^b.

waterfowl, I calculated a relative clutch size by subtracting the tribal mean clutch size from the clutch size of each species. For two tribes, the Anserini and Mergini, clutch size was a power function of body mass. Therefore, for these two tribes relative clutch size was the log deviation from the principal axis line relating log clutch size to log female body mass (Anserini: $r = 0.53$, $n = 18$, $P < 0.05$, log clutch size = 0.02 + 0.20 [log body mass]; Mergini: $r = -0.56$, $n = 16$, $P < 0.05$, log clutch size = 2.26 − 0.48 [log female mass]). No other tribes showed significant relationships between clutch size and female body mass, thus alleviating any need to control statistically for the influence of body size on clutch size.

Relative egg size and relative clutch size remained inversely related ($r = -0.36$, $n = 146$, $P < 0.0001$) in this more refined analysis, but, as is obvious (Fig. 2), the relationship is weak ($r^2 = 0.13$). Furthermore, the relationship would have a slope of −1.0 if the relationship between egg size and clutch size was a perfect gram-for-gram trade-off. To elaborate, relative egg size and relative clutch size (Figs. 2–4) are expressed in logarithmic units; therefore, a relative egg size of 0.3 logarithmic units would be eggs that are about twice as large as predicted, so we expect clutch size to be only half of normal (i.e. show a deviation of −0.3 logarithmic units). The principal axis of this refined analysis of relative egg size and relative clutch size had a slope of −3.39 (95% confidence intervals −5.86 to −2.33), much greater than the predicted slope (−1.0). The negative slope suggests some allocational trade-off between egg size and clutch size; however, the magnitude of the slope can

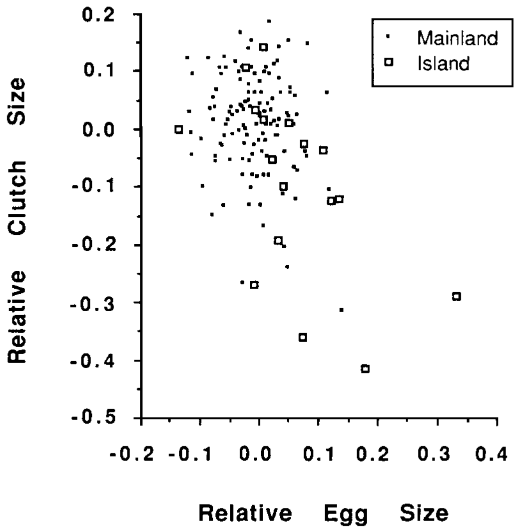

Fig. 2. Relationship of relative egg size and relative clutch size for the 8 most diverse tribes of waterfowl. Relative egg size and relative clutch size are defined in the text. Values are in logarithmic units. The slope of the principal axis is −3.39.

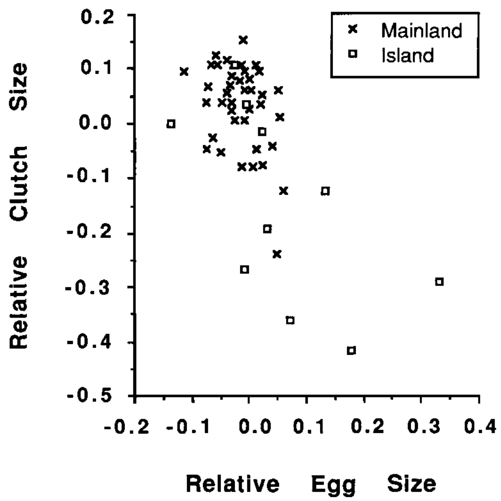

Fig. 3. Relationship of relative egg size and relative clutch size for the Anatini. Relative egg size and relative clutch size are defined in the text. Values are in logarithmic units. The slope of the principal axis with all species = −2.38 and without the island species = −4.10.

have two seemingly different interpretations. Note that altering clutch size has relatively little influence on egg size. The converse interpretation is also appropriate, namely, that a relatively slight change in egg size has a dramatic effect on clutch size (Fig. 2).

Even more troubling is the possibility that the inverse relationship between egg size and clutch size is entirely a consequence of the few waterfowl that breed on oceanic islands. Island waterfowl are exceptional in laying large eggs and small clutches (Lack 1970, Weller 1980; Fig. 2). Reanalysis excluding the 17 island species or subspecies of waterfowl yielded a nonsignificant correlation between relative egg size and relative clutch size ($r = -0.10$, $n = 129$, $P > 0.10$).

Tribal analyses of egg size and clutch size.—Pooling such diverse waterfowl as small tropical ducks and large, arctic-breeding swans and geese in a single comparison of clutch size and egg size may introduce unexpected biases. Therefore, I examined the relationship between egg size and clutch size for each of the eight largest tribes of waterfowl (Table 1). Relative egg and clutch sizes were calculated as before. Only the Anatini and Aythyini (Figs. 3 and 4) showed significant negative relationships between relative clutch size and relative egg size (Anatini: $r = -0.62$, $n = 53$, $P < 0.0001$; Aythyini: $r = -0.69$, $n = 15$, $P < 0.005$). Exclusion of the island-breeding members of these two tribes considerably reduced the strength of the relationship between relative egg mass and relative clutch size (Anatini: $r = -0.39$, $n = 43$, $P < 0.01$; Aythyini: $r = -0.43$, $n = 14$, $P > 0.10$). The exclusion of the ducks restricted to islands also changed the slope of the relationship between egg size deviations and clutch size deviations (Figs. 3 and 4).

Intraspecific relationships between egg size and clutch size.—Lack (1954b) advocated intraspecific studies of clutch size, because interspecific analyses are plagued by the complexities of differing biologies for the different species. The preceding interspecific analyses, which revealed a low correspondence between egg size and clutch size, were based on species averages. Both egg size and clutch size show considerable intraspecific variation (Ankney and Bisset 1976, Bellrose 1980, Rohwer 1986a). If clutch size is limited by the ability to produce eggs (Lack 1967, Ryder 1970, Ankney and MacInnes 1978, Raveling 1979, Drobney 1980, Krapu 1981), then we would predict an inverse relationship between egg size and clutch size within species.

Intraspecific analyses of egg size and clutch size for Blue-winged Teal and Northern Shov-

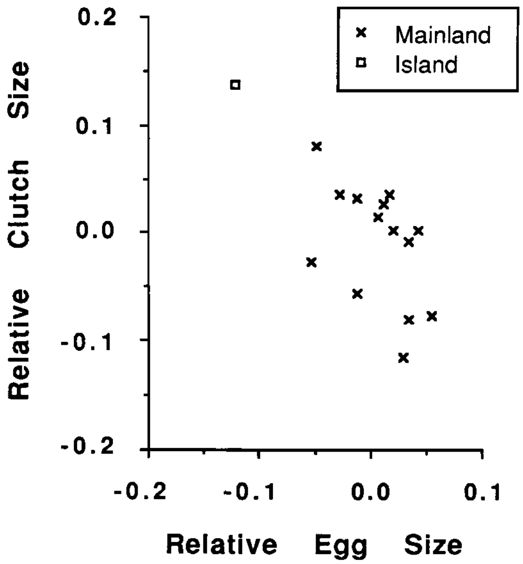

Fig. 4. Relationship of relative egg size and relative clutch size for the Aythyini. Relative egg size and relative clutch size are defined in the text. Values are in logarithmic units. The slope of the principal axis with all species = −0.59 and without the single island species = −0.33.

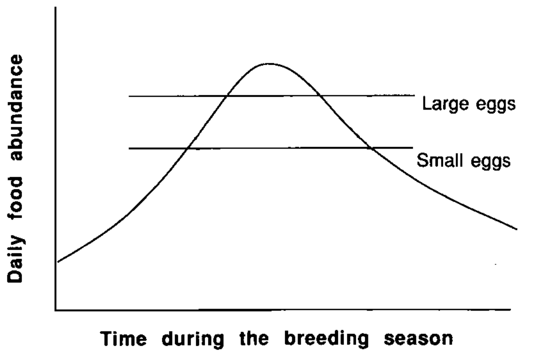

Fig. 5. Model of seasonal increase in food abundance. Horizontal lines represent threshold of food abundance needed to meet the nutritional requirements to produce eggs of different sizes.

elers were simplified by the lack of association between a female's body size and the average size of her eggs. Neither Blue-winged Teal nor Northern Shovelers showed a significant correlation between egg mass and the length of the wing, bill, tarsus, keel, or total body (Blue-winged Teal: n = 157, 161, 164, 136, 131, and Northern Shoveler: n = 55, 52, 52, 51, 51, for respective body measurements; $P > 0.05$ for all Pearson correlations). To gain a composite index of structural size for Blue-winged Teal and Northern Shovelers, I performed a principal components analysis (PCA) based on the covariance matrices of the five log-transformed measures of body dimensions. The first combination of variables, which explained 48% of the variation in Blue-winged Teal size and 66% of the variation in Northern Shoveler size, can be related to overall body size because all loadings had positive signs of the same relative magnitude. The correlation between egg size and the PCA body size index was not significant for Northern Shovelers ($r = 0.05$, $n = 45$, $P > 0.10$). The correlation was significant for Blue-winged Teal ($r = 0.24$, $n = 107$, $P < 0.05$), but the PCA index of body size explained a trivial amount (6%) of the variation in egg size. Neither Blue-winged Teal nor Northern Shovelers showed the expected inverse correlation between egg size and clutch size (shoveler: $r = 0.02$, $n = 136$, $P > 0.10$; teal: $r = 0.09$, $n = 427$, $P > 0.05$). For Blue-winged Teal and Northern Shovelers a considerable amount (r^2 = 0.39 and 0.28, respectively) of the variation in clutch size can be explained by laying date. Adding egg size as an additional independent variable to regressions of clutch size and laying dates, however, did not reduce the unexplained variation in clutch size (egg size partial regression coefficient $F = 0.00$; $n = 136$ for Northern Shovelers, and $F = 1.23$; $P > 0.10$; $n = 424$ for Blue-winged Teal).

Discussion

Lack (1967) did not suggest an explicit mechanism when he proposed that egg production limits clutch size in waterfowl. Apparently, Lack (1968a) thought food availability peaked during the laying season and species that laid small eggs could commence laying earlier and sustain laying for a longer period because of their lower food requirements for egg production (Fig. 5). Species that lay relatively large and costly eggs would be able to lay only at the peak of food availability and would produce smaller clutches. This mechanism seems improbable because laying in many waterfowl spans 2–3 months and because many females renest if their first clutch is destroyed (Bellrose 1980, Doty et al. 1984). Renestings usually have reduced clutch sizes (reviewed by Bellrose 1980), but egg size shows little or no change (Rohwer 1986a). Lack's mechanism also assumes that females could not reduce their laying rate (typically 1 egg/day, but longer for swans and geese [Bellrose 1980]) to reduce daily intake requirements and extend laying.

A more widely accepted mechanism for the egg-production hypothesis suggests that females quit laying when their body condition drops to some threshold (Ryder 1970, Reynolds 1972, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Drobney 1980, Krapu 1981). Females use a combination of stored reserves and exogenous nutrients to meet the demands of laying an egg each day. Large eggs would deplete nutrient reserves at a greater rate and cause the termination of laying at smaller clutch sizes. This mechanism and the hypothesis are reinforced by several studies that document a large net mass reduction by females during the egg-laying period (Ryder 1970, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Drobney 1980, Krapu 1981, Ankney 1984, Hohman 1986). This mechanism, like Lack's, assumes that laying rates are fixed (presumably adaptive) and that females could not lay at intervals of two or more days to reduce or eliminate the requirements for stored reserves.

The most dramatic cases of utilization of stored nutrients for egg production occur in large-bodied waterfowl, particularly arctic geese. Short nesting seasons require that these birds begin breeding before a substantial amount of new vegetation is available for grazing (Newton 1977). Nutritional requirements for egg production and a large part of incubation are met by the use of stored lipids and some catabolism of muscle (Ryder 1970, Newton 1977, Ankney and MacInnes 1978, Raveling 1979, Ankney 1984, Mainguy and Thomas 1985). The nutrient reserves are acquired on staging areas during northward migration (Hobaugh 1985), and the condition of females as they leave such staging areas has a substantial impact on their breeding success (Ebbinge et al. 1982, Davies and Cooke 1983). Because geese and swans show a strong reliance on stored nutrients for breeding, I expected that these would be the most likely groups of waterfowl to show an inverse relationship between egg size and clutch size. The tribal analyses, however, showed no such allocational trade-offs.

When Smith and Fretwell (1974) formalized the idea of an optimal balance between size and number of offspring (see also Brockelman 1975), they suggested that the trade-off between size and number was "intuitively obvious," so they concentrated on the less obvious relationship between parental fitness and effort per offspring. They felt that trade-offs between offspring size and number would be difficult to measure in birds because of extensive postlaying reproductive effort. Smith and Fretwell (1974) suggested that trade-offs would be most apparent in organisms with large clutch size and no parental care. Plants seem likely candidates, and an inverse relationship exists between seed size and seed set (reviewed by Harper 1977). Vertebrate taxa seem to have received relatively little study (Svärdson 1949, Stearns 1976, Wootton 1984), though groups such as fish, reptiles, and amphibians would seem ideal. Among birds, the waterfowl are the obvious group for such study. Studies that examined offspring survival in waterfowl (Heusmann 1972, Clawson et al. 1979, Dow and Fredga 1984, Rohwer 1985, Lessells 1986, Rockwell et al. 1987) or parental investment (Lazarus and Inglis 1978, Afton 1983, Guinn and Batt 1985, Lessells 1987) found little or no relationship to brood size, thus partially alleviating the complexities of postlaying reproductive effort. More to the point, the foundation of the egg-production hypothesis is that clutch size is limited by the availability of nutrients for making eggs. Thus, the hypothesis is a restatement of the major assumption concerning trade-offs, namely that parents have a limited supply (optimal apportionment) of energy for any one reproductive event (Smith and Fretwell 1974, Brockelman 1975). Failure to detect a convincing trade-off may indicate that this assumption is inappropriate.

Interpretation of the interspecific analyses is open to question. Failure to detect an inverse relationship between egg size and clutch size may be due to inappropriate assumptions of the egg-production hypothesis. Species experience different feeding conditions during laying or accumulate different amounts of stored reserves. This effect of body condition, however, should introduce unexplained variation only in clutch sizes. Furthermore, some environments may favor the survival of young from large eggs more than other environments, thus selecting for relatively large eggs. Conditions that select for a particular relative egg size also may influence the nutritional condition of laying females, so the predicted inverse relation of egg size and clutch size might be obscured. For example, birds in excellent nutritional condition might lay both large clutches and large eggs, whereas species in poor nutritional condition might lay small eggs and small clutches. This would be most likely if large clutches imposed some cost to nest or brood success (but see Rohwer 1985, Lessells 1986, Rockwell et al. 1987), thereby causing selection for females to place extra nutrients into each egg to increase juvenile survival (Ankney 1980). This argument was not supported by a direct relationship between egg size and clutch size, but less extreme cases may simply lead to weak or nonsignificant relationships between egg size and clutch size, as was generally the case in my interspecific analyses.

Interpretation of an inverse relationship between egg size and clutch size may also be problematic, particularly in the dabbling ducks (Anatini). In this group the inverse relationship was largely due to the island-breeding species, which lay large eggs but small clutches (Lack 1970, Weller 1980). This could be a nutrient allocation problem, but an alternative hypothesis is that small clutches and large eggs both represent independent adaptations to an unproductive or nonseasonal environment (cf. Ricklefs 1980).

Intraspecific (intrapopulational) analyses of egg size and clutch size are more easily interpreted than are interspecific analyses. Individual differences in nutritional status and environmental food conditions are much less pronounced than are differences between species. Members of a single population will have a similar payoff for relatively large young, which hatch from large eggs. Likewise, the optimal amount of reserves to allocate to a single reproductive event will be more similar within a population than between species that differ ecologically and demographically. The failure to detect an inverse relationship between egg size and clutch size for either Blue-winged Teal or Northern Shovelers challenges the egg-production hypothesis. This lack of relationship is consistent with every other intraspecific (intrapopulational) examination of egg size and clutch size in waterfowl of which I am aware (Table 2). Most surprising are the geese (Table 2), because their use of stored nutrients for egg production would strongly suggest an inverse relationship between size and numbers of eggs laid.

Studies of other precocial birds with self-feeding young, such as Red Grouse (*Lagopus lagopus scoticus*) and Willow Ptarmigan (*L. l. lagopus*) (Moss et al. 1981, Erikstad et al. 1985), have not found a trade-off between egg size and number, even though these birds are also suspected of having clutch sizes limited by their ability to lay eggs (Lack 1968a).

One might ask why the results and subsequent conclusion of my study differ so much from those of Lack (1967, 1968a). To answer this question, I used Lack's data (1968a: appendix 15), reassigned species according to Livezey's (1986) classification, and repeated the analyses. The results were, to my surprise, similar to those based on the data in the Appendix. For instance, Lack's data also showed a weak inverse relationship between relative egg size and relative clutch size ($r = -0.30$, $n = 142$, $P < 0.005$); in fact, this relationship had a lower coefficient of determination than shown by the revised data (9% vs. 13%). The tribe-by-tribe analyses of Lack's data produced very similar results to those using data from the Appendix; the Anatini and Aythyini were the only two tribes to show significant negative relationships between egg size and number. Interestingly, Lack's data produced a significant egg size and clutch size relationship for Mergini (sea ducks), but the relationship was positive ($r = 0.51$, $n = 16$, $P < 0.05$).

There was a slightly "improved" fit to the predicted trade-off when the analyses were based on the updated data (Appendix) as compared with Lack's data. This suggested that some relatively poor data may have obscured a stronger relationship between egg size and number. Accordingly, I categorized the data for each species or subspecies as "good" or "poor." Species had poor data if samples were based on few observations (about 10 or less).

Eliminating poor data reduced the sample to 89 species, of which only 7 were island endemics. The pooled analysis for all species did not show a significant inverse relationship ($r = -0.01$, $n = 89$, $P > 0.10$) between relative clutch size and relative egg size. Tribal analyses showed only the Anatini with a significant inverse relationship ($r = -0.42$, $n = 26$, $P < 0.05$) when analyses utilized only good data. As earlier, this relationship was weakened when reanalyzed without the island species ($r = -0.36$, $n = 23$, $P = 0.09$). These analyses show that inclusion of some suspect data is not obscuring the relationship between egg size and clutch size.

TABLE 2. Intraspecific relationships of egg mass to clutch size in waterfowl.

Species	Relationship	No. of nests checked	Source
Blue-winged Teal (*Anas discors*)	None	427	This study
Northern Shoveler (*Anas clypeata*)	None	136	This study
Mallard (*Anas platyrhynchos*)	None[a]	336	Batt and Prince 1979
	None	56	Hill 1984
Northern Pintail (*Anas acuta*)	None	147	Duncan 1987a
Black Swan (*Cygnus atratus*)	None	304	Braithwaite 1977
Mute Swan (*Cygnus olor*)	None	100+	Birkhead et al. 1983
Pacific White-fronted Goose (*Anser albifrons frontalis*)	None	~75	Ely and Raveling 1984
Graylag Goose (*Anser anser*)	None	201	Witkowski 1983
Lesser Snow Goose (*Chen caerulescens caerulescens*)	None	366	Ankney and Bisset 1976
Pink-footed Goose (*Anser brachyrhynchus*)	None	20	Nyholm 1965
Giant Canada Goose (*Branta canadensis maxima*)	None[b]	188	Cooper 1978
Interior Canada Goose (*Branta canadensis interior*)	None[c]	66	Manning 1978
Atlantic Canada Goose (*Branta canadensis canadensis*)	None[d]	447	Lessells 1982
Tufted Duck (*Aythya fuligula*)	None	31	Hill 1984
White-winged Scoter (*Melanitta fusca fusca*)	None	82	Koskimies 1957
Spectacled Eider (*Somateria fischeri*)	None	66	Dau 1974

[a] Captive birds.
[b] Slight trend of increasing egg size with increasing clutch size; not statistically examined.
[c] Significant negative correlation for one subpopulation in mid-May, $n = 31$.
[d] No significant relation when corrected for locality and laying date. Uncorrected data had significant positive relationship ($n = 572$, $P < 0.05$).

The general correspondence between analyses with Lack's data and data I compiled suggests that analytical results are unlikely to be much affected by further revisions of the data. In more general terms, the correspondence of similar methods of analysis suggests that the comparative method is robust enough to handle some poor data, but quite sensitive to analytical technique (see also Harvey and Mace 1982).

In summary, I found little evidence for the predicted inverse relationship between waterfowl egg sizes and clutch sizes. The analysis failed to show either a consistent or a strong negative relationship between egg size (adjusted for body size) and clutch size (Fig. 2). Only 2 of 8 tribes of waterfowl showed the expected inverse relationship of egg size and clutch size (Figs. 3 and 4), and a few island populations of waterfowl were responsible for much of the observed egg size and clutch size relationships in these groups (Table 2). Based on Lack's (1967) egg-production hypothesis, I would expect a trade-off between egg number and size because most, if not all, of these species use stored nutrient reserves for laying eggs (Kistchinski and Flint 1974, Newton and Kerbes 1974, Laughlin 1976, Ankney and MacInnes 1978, Raveling 1979, Owen 1980, Krapu 1981, Mainguy and Thomas 1985, Rohwer 1986b). The lack of a strong inverse relationship between egg size and clutch size suggests that the widely accepted hypothesis that clutch size is limited by egg production (Lack 1967, 1968a; Ryder 1970; Ankney and MacInnes 1978; Raveling 1979; Drobney 1980; Krapu 1981) may not be generally correct, or at the very least, has been overstated.

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APPENDIX. Female body mass (g), egg mass (g), and clutch size of waterfowl.

Tribe (family/subfamily) Species	Female mass	Egg mass	Clutch size	Source[a] Body	Egg	Clutch
Anseranatidae						
Anseranas semipalmata	2,070	112.2	8.6	51	51	51
Dendrocygninae						
Dendrocygna guttata	800	41.7	11.0	66	66	66
D. eytoni	792	34.5	11.0	51	51	51
D. arcuata australis	732	38.7	10.0	51	51	51
D. bicolor	675	49.1	9.7	11	15	30
D. arborea	1,150	48.8	10.0	75	66	66
D. javanica	525	35.3	10.0	3	3	3
D. viduata	662	38.0	10.5	66	26	26
D. autumnalis fulgens	716	44.3	13.0	23	17	87
Thalassorninae						
Thalassornis leuconotus leuconotus	680	82.6	8.0	18	24	24
Anserinae						
Anserini						
Cereopsis novaehollandiae	3,560	126.9	4.1	36	54	54
Anser cygnoides	3,150	142.7	5.5	66	66	66
A. anser anser	3,100	165.0	5.9	85	132	132
A. albifrons frontalis	2,000	128.0	4.9	74	44	44
A. erythropus	1,875	103.0	5.0	32	32	32
A. fabalis fabilis	2,843	146.2	5.0	32	32	32
A. brachyrhynchus	2,381	122.5	4.3	92	92	92
A. indicus	2,400	142.2	5.0	66	3	3
Chen canagica	2,233	120.4	4.8	121	43	43
C. rossii	1,430	91.5	3.8	107	108	107
C. caerulescens caerulescens	2,530	122.0	4.0	6	5	5
C. caerulescens atlanticus	3,080	128.5	5.1	94	78	78
Branta sandvicensis	1,930	144.0	4.2	71	71	71
B. canadensis maxima	3,868	169.0	5.6	59	29	29
B. canadensis minima	1,387	97.0	4.8	100	100	100
B. leucopsis	2,020	104.0	4.5	80	32	32
B. ruficollis	1,100	78.2	4.5	32	34	34
B. bernicla hrota	1,143	84.0	3.9	7	7	7
Cygnini						
Coscoroba coscoroba	3,800	178.4	6.8	110	110	110
Cygnus atratus	5,100	267.0	5.5	51	51	51
C. olor	9,650	353.0	7.5	102	102	102
C. melanocoryphus	4,000	247.4	4.6	110	110	110
C. cygnus	8,100	333.9	5.2	110	110	110
C. buccinator	9,639	366.5	5.2	58	58	58
C. columbianus	6,300	273.2	4.3	11	94	11
C. bewickii	5,642	257.9	5.1	47	110	110
Stictonettinae						
Stictonetta naevosa	744	77.2	7.4	50	50	50
Plectropterinae						
Plectropterus gambensis niger	3,560	138.8	9.4	57	68	27
Tadorninae						
Sarkidiornini						
Sarkidiornis melanotos melanotos	2,125	64.3	9.5	3	3	75
Tadornini						
Tadorna tadornoides	1,290	90.0	10.4	51	51	51
T. variegata	1,300	88.1	9.4	79	127	127
T. cana	1,100	97.1	9.5	52	66	66
T. ferruginea	1,140	83.4	8.5	32	32	32
T. radjah rufitergum	839	57.8	9.0	51	51	51
T. tadorna	960	80.9	8.9	97	32	97
Malacorhynchus membranaceus	344	35.2	6.7	51	51	51
Neochen jubata	1,250	64.5	9.0	75	68	68
Alopochen aegyptiacus	1,872	95.7	8.5	56	32	32
Chloephaga melanoptera	2,900	113.5	7.0	66	67	66
C. poliocephala	2,200	97.1	5.0	75	66	66
C. rubidiceps	2,000	102.8	5.0	75	67	68

APPENDIX. Continued.

Tribe (family/subfamily) Species	Female mass	Egg mass	Clutch size	Source[a] Body	Egg	Clutch
C. picta leucoptera	3,072	128.0	6.1	119	119	119
C. hybrida hybrida	2,041	141.5	5.3	66	53	53
Cyanochen cyanopterus	1,520	97.1	7.5	75	68	68
Hymenolaimus malacorhynchus	810	73.0	5.4	134	69	69
Merganetta armata leucogenis	330	62.0	3.3	66	67	67
Tachyeres pteneres	4,228	146.5	6.6	81	65	65
T. brachypterus	3,450	145.4	6.0	81	65	65
T. patachonicus	2,346	116.6	6.2	81	65	65
T. leucocephalus	3,013	132.4	4.6	81	65	65
Anatanae						
Anatini						
Pteronetta hartlaubii	790	53.8	8.3	75	67	66
Cairina moschata	1,300	78.7	8.8	79	79	131
C. scutulata	1,860	89.0	10.0	83	83	83
Aix sponsa	580	42.6	11.1	39	38	28
A. galericulata	512	38.7	9.3	34	32	22
Nettapus pulchellus	304	25.0	10.0	51	51	51
N. coromandelianus albipennis	380	32.0	10.0	51	51	51
N. auritus	260	22.9	8.5	75	84	84
Anas waigiuensis	469	57.0	3.0	70	70	70
A. sparsa sparsa	909	67.7	5.9	116	113	113
A. penelope	625	46.4	9.0	32	32	13
A. americana	649	44.1	8.5	130	105	129
A. sibilatrix	828	57.2	6.5	124	67	67
A. falcata	585	49.7	8.0	111	67	34
A. strepera strepera	697	45.9	9.5	16	105	16
A. formosa	431	30.9	7.3	111	34	34
A. crecca carolinensis	280	25.2	8.6	9	105	11
A. flavirostris flavirostris	395	34.3	6.5	124	67	67
A. capensis	402	35.9	8.4	128	128	128
A. gibberifrons gracilis	474	36.0	7.9	51	51	51
A. castanea	550	44.0	9.7	91	91	91
A. aucklandica aucklandica	380	70.5	4.0	126	126	126
A. aucklandica chlorotis	614	61.7	5.9	126	101	101
A. platyrhynchos platyrhynchos	1,047	49.9	9.7	73	105	73
A. wyvilliana	585	32.1	7.8	126	126	126
A. laysanensis	461	44.1	3.4	89	48	89
A. fulvigula	860	50.0	10.0	98	11	11
A. rubripes	1,080	61.5	9.5	93	31	31
A. undulata undulata	823	52.4	7.8	33	106	106
A. poecilorhyncha poecilorhyncha	1,075	55.6	8.5	3	3	3
A. pelewensis	670	54.0	8.0	75	75	75
A. superciliosa	1,025	54.1	9.1	51	51	51
A. luzonica	779	50.4	10.0	99	67	75
A. specularis	975	69.0	4.5	75	67	67
A. specularioides specularioides	900	56.9	6.5	75	67	67
A. acuta acuta	612	40.3	6.9	40	40	41
A. acuta eatoni	450	39.6	5.0	76	126	126
A. georgica georgica	465	37.0	4.2	75	75	126
A. georgica spinicauda	706	42.0	7.0	124	75	66
A. bahamensis bahamensis	530	40.5	8.4	55	55	55
A. erythrorhyncha	523	40.1	9.0	35	84	24
A. versicolor versicolor	373	30.6	8.5	124	67	67
A. hottentota	240	26.6	7.1	18	84	25
A. querquedula	330	28.0	8.5	32	32	32
A. discors	380	28.1	10.4	104	103	105
A. cyanoptera septentrionalium	353	30.8	9.7	11	117	117
A. platalea	523	41.3	6.5	124	67	67
A. smithi	598	44.7	9.4	112	112	112
A. rhynchotis rhynchotis	665	41.0	10.0	51	51	51
A. clypeata	563	39.1	10.2	105	105	105
Callonetta leucophrys	310	32.4	9.0	124	68	68
Chenonetta jubata	800	55.8	10.0	51	51	51
Amazonetta brasiliensis brasiliensis	370	33.3	7.0	66	67	67
Aythyini						
Marmaronetta angustirostris	490	30.2	10.5	3	3	3
Netta rufina	1,146	56.8	9.9	75	32	4

APPENDIX. Continued.

Tribe (family/subfamily) Species	Female mass	Egg mass	Clutch size	Source[a]		
				Body	Egg	Clutch
N. erythrophthalma brunnea	822	60.3	9.0	88	88	88
N. peposaca	1,004	58.3	9.0	124	124	68
Aythya valisineria	1,157	70.5	8.2	10	105	118
A. ferina	830	68.0	8.3	32	32	60
A. americana	907	62.9	9.4	123	82	82
A. collaris	666	49.9	9.5	64	63	62
A. australis australis	838	55.8	10.0	51	51	51
A. baeri	708	40.9	10.0	95	35	35
A. nyroca	547	42.5	9.0	32	32	32
A. fuligula	739	55.5	9.6	77	77	77
A. novaeseelandiae	610	59.7	7.0	66	101	101
A. marila marila	991	66.1	9.7	13	15	12
A. affinis	685	48.2	10.2	2	105	1
Mergini						
Polysticta stelleri	836	55.1	8.0	95	95	95
Somateria mollissima mollissima	1,916	111.0	4.3	8	8	8
S. spectabilis	1,567	66.7	5.0	120	96	96
S. fischeri	1,767	77.1	3.7	72	72	72
Histrionicus histrionicus	558	54.4	5.7	95	95	14
Clangula hyemalis	687	44.1	7.9	13	95	12
Melanitta nigra nigra	1,049	74.2	8.7	13	32	12
M. perspicillata	906	63.2	6.0	90	15	95
M. fusca deglandi	1,316	82.4	9.2	19	21	20
Bucephala albeola	320	36.7	8.8	46	46	46
B. islandica	777	67.7	7.9	42	42	42
B. clangula clangula	687	64.1	8.7	133	95	37
Lophodytes cucullatus	579	57.6	10.2	49	95	49
Mergellus albellus	560	41.7	8.0	32	32	32
Mergus serrator serrator	998	73.3	9.5	13	95	12
M. merganser americanus	1,076	79.2	9.4	45	95	61
Oxyurini						
Heteronetta atricapilla	565	60.2	—	125	125	—
Oxyura dominica	339	50.5	6.0	66	95	66
O. jamaicensis jamaicensis	619	71.3	7.6	122	105	122
O. leucocephala	593	97.0	6.0	109	86	68
O. maccoa	677	88.0	6.0	115	114	115
O. vittata	560	78.7	4.0	124	67	67
O. australis	852	84.4	5.5	51	51	51
Biziura lobata	1,551	127.9	2.8	51	51	51

[a] (1) Afton 1984, (2) A. Afton pers. comm., (3) Ali and Ripley 1968, (4) Amat 1982, (5) Ankney and Bisset 1976, (6) Ankney and MacInnes 1978, (7) Ankney 1984, (8) Baillie and Milne 1982, (9) Baldassarre et al. 1986, (10) J. Barzen and J. Serie pers. comm., (11) Bellrose 1980, (12) Bengtson 1971, (13) Bengtson 1972a, (14) Bengtson 1972b, (15) Bent 1923, (16) Blohm 1979, pers. comm., (17) Bolen and Rylander 1983, (18) Britton 1970, (19) Brown 1981, (20) Brown and Brown 1981, (21) Brown and Fredrickson 1983, (22) Bruggers 1979, (23) Chronister 1985, (24) Clancey 1967, (25) Clark 1969, (26) Clark 1976, (27) Clark 1980, (28) Clawson 1975, (29) Cooper 1978, (30) Cottam and Glazener 1959, (31) Coulter and Miller 1968, (32) Cramp and Simmons 1977, (33) Dean and Skead 1979, (34) Dement'ev and Gladkov 1967, (35) Douthwaite 1976, (36) Dorward et al. 1980, (37) Dow and Fredga 1984, (38) Drobney 1980, (39) Drobney 1982, (40) Duncan 1987a, (41) Duncan 1987b, (42) J. Eadie pers. comm., (43) Eisenhauer and Kirkpatrick 1977, (44) Ely and Raveling 1984, (45) Erskine 1971, (46) Erskine 1972, (47) Evans and Kear 1978, (48) Fisher 1903 *in* Weller 1980, (49) L. H. Fredrickson pers. comm., (50) Frith 1965, (51) Frith 1967, (52) Geldenhuys 1983, (53) Gladstone and Martell 1968, (54) Guiler 1967, (55) L. Guiminski pers. comm., (56) Halse and Skead 1982, (57) Halse and Skead 1983, Halse pers. comm., (58) Hansen et al. 1971, (59) Hanson 1965, (60) Havlín 1966, (61) Hildén 1964, (62) Hohman 1984, (63) Hohman pers. comm., (64) Hohman 1986, (65) Humphrey and Livezey 1985, (66) Johnsgard 1978, (67) Johnson 1965, (68) Johnstone 1970, (69) Kear 1972, (70) Kear 1975, (71) Kear and Berger 1980, (72) Kistchinski and Flint 1974, (73) Krapu 1981, (74) Krogman 1979, (75) Lack 1968a, (76) Lack 1970, (77) Laughlin 1976, (78) Lemieux 1959, (79) Leopold 1959, (80) Lessells et al. 1979, (81) Livezey and Humphrey 1986, (82) Low 1945, (83) Mackenzie and Kear 1976, (84) Mackworth-Praed and Grant 1962, (85) Matthews and Campbell 1969, (86) Matthews and Evans 1974, (87) McCamant and Bolen 1979, (88) Middlemiss 1958, (89) Moulton and Weller 1984, (90) Nelson and Martin 1953, (91) Norman 1982, (92) Nyholm 1965, (93) Owen and Reinecke 1979, (94) Palmer 1976a, (95) Palmer 1976b, (96) Parmelee et al. 1967, (97) Patterson 1982, (98) S. Paulus pers. comm., (99) Rand and Rabor 1960, (100) Raveling 1979, (101) Reid and Roderick 1973, (102) Reynolds 1972, (103) Rohwer 1986a, (104) Rohwer 1986b, (105) Rohwer unpubl. data, (106) Rowan 1963, (107) Ryder 1967, (108) Ryder 1971, (109) Savage 1965, (110) Scott and the Wildfowl Trust 1972, (111) Shaw 1936, (112) Siegfried 1965, (113) Siegfried 1968, (114) Siegfried 1969, (115) Siegfried et al. 1976, (116) Siegfried et al. 1977, (117) Spencer 1953, (118) Stoudt 1982, (119) Summers 1983, (120) Thompson and Person 1963, (121) Thompson and Raveling 1987, (122) Tome 1984, (123) Weller 1957b, (124) Weller 1968a, (125) Weller 1968b, (126) Weller 1980, (127) Williams 1979, (128) Winterbottom 1974, (129) Wishart 1983, (130) Wishart pers. comm., (131) Woodyard and Bolen 1984, (132) Young 1972, (133) M. Zicus pers. comm., (134) M. Williams pers. comm.