Variation in egg weight in the Bengalese finch (*Lonchura striata* var. *domestica*)

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Variation in egg weight was examined in 29 clutches (155 eggs) from 14 pairs of captive Bengalese finches. For clutches of four and seven eggs, egg weight varied more within than among clutches. The opposite was true for clutches of five, six, and eight eggs and when all clutches of four to eight eggs were pooled. Egg weight increased linearly with laying sequence for clutches of four, five, and eight eggs, and for clutches of four to eight eggs combined. Egg weight also varied with clutch size: large clutches contained heavier eggs throughout the clutch than did small clutches. Egg weight was not correlated significantly with the amount of food eaten around the time of egg laying. Furthermore, food consumption did not increase linearly through the laying sequence as did egg weight. These patterns suggest that complex investment allocation decisions underlie egg weight variation in the Bengalese finch.

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Les variations de masse des oeufs ont fait l'objet d'une étude au sein de 29 couvées (155 oeufs) de 14 couples de Capucins dominos en captivité. Dans les portées de quatre et de sept oeufs, la masse varie plus d'un oeuf à l'autre que d'une portée à l'autre. Le contraire est vrai au sein des portées de cinq, six et huit oeufs et vrai aussi lorsque toutes les portées de quatre à huit oeufs sont considérées dans leur ensemble. La masse des oeufs varie aussi en fonction de leur nombre dans la portée : dans les grosses portées, tous les oeufs sont plus lourds que dans les petites portées. La masse des oeufs n'est pas en corrélation significative avec la quantité de nourriture consommée au moment de la ponte. De plus, la consommation de nourriture ne suit pas une courbe d'augmentation linéaire au cours de la ponte comme le fait la masse des oeufs. Ces phénomènes semblent indiquer qu'un système complexe d'allocation de l'énergie est responsable de la variation de la masse des oeufs chez la forme domestique du Capucin domino.

[Traduit par la revue]

Introduction

General models of egg-size allocation (e.g., Smith and Fretwell 1974) assume that there is a single optimal egg size for all individuals of a species that maximizes rate of return per unit investment into the egg. They predict that a female should fix egg size at this optimum and vary her clutch size according to the resources she has available for egg laying. Such models assume either that all eggs will be subject to the same biotic and abiotic factors during development or, at least, that the female cannot adjust egg size to match variations in these parameters.

In contrast, both theoretical analyses and empirical studies conclude that the amount of investment a female puts into an egg has important ramifications for both parent and offspring (e.g., Smith and Fretwell 1974; Birkhead and Nettleship 1982; Slagsvold *et al.* 1984; Rofstad and Sandvik 1987; Sargent *et al.* 1987). For the parent, it determines how much of its resources will be available for other investments, and for the offspring, it will strongly affect its size and chances of survival.

Recent investigations of egg-size allocation suggest that females of some taxa can recognize differences in factors that will influence size-specific egg survival, such as laying-site quality and variation in parental care, and adjust their egg size to match these conditions (e.g., van den Berghe and Gross 1989). In avian-type systems, where clutch size is small and each egg is laid discretely, the eggs are amenable to individual treatment before and after laying. Therefore, we might expect to find patterns in egg-size variation within clutches that reflect differential investment strategies by the female (Howe 1978).

Herein, we report on the variation in egg weight observed in clutches of Bengalese finches (*Lonchura striata* var. *domestica*). Because egg weight is a good predictor of energy content (Muma and Ankney 1987), we used it as an estimate of egg quality and the amount of parental investment into the egg. We examine variation in egg size within and between clutches, trends in egg size with laying sequence, and changes in egg size with clutch size. Using food-intake data, we also relate food intake to egg size and examine trends in food intake during the laying sequence.

Materials and methods

The Bengalese finch

The Bengalese finch is a domesticated descendent of the wild sharp-tailed munia (*L. striata acuticauda*) (Eisner 1957). Adults are approximately 12 cm long, and breed readily and consistently in captivity in commercially available finch nests. The breeding biology of the Bengalese finch is described in Eisner (1957, 1960*a*, 1960*b*, 1961, 1963, 1969), Slater (1970), and Henry (1971). Eggs are laid every day in the early morning, although females occasionally skip a day.

Data collection

The study was conducted in a controlled-environment laboratory. The room was lit with fluorescent lighting from 07:00 to 17:00, and temperature averaged 24°C. Fourteen pairs of finches were each housed in a wood and wire-mesh cage (34 × 30 × 30 cm), visually separated from all other pairs. Birds were fed a standard diet (Coleman and Whittall 1988). Data were collected on 121 consecutive days from

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March through June 1985 and nests were examined every morning between 07:00 and 08:00. New eggs were removed, numbered with a pencil, weighed on a balance ($\pm$ 0.001 g), and returned to the nest within a few minutes. At this time, the food dishes were removed and any remaining food was weighed. The dishes were cleaned and the birds were given their new day's supply of food (25 g). Daily food intake was calculated as the difference between the 25 g and the weight of the remaining food.

The data were analyzed with all clutches pooled and by individual clutch sizes to determine if trends observed in the pooled data were supported within clutch sizes or were merely the consequence of combining clutches of different sizes. Three cracked eggs and single clutches of one, two, and three eggs were excluded from the analyses.

Statistics

To test for the presence of linear regressions, we used regressions of more than one Y per x as described in Sokal and Rohlf (1981; p. 477) when the data consisted of multiple values for each position in the laying sequence. This is a stringent test for linear regression, but allows us to separate deviations from regression and error among Y's for a given value of x. As a conservative measure, pooling of mean squares was not employed (Sokal and Rohlf, 1981; p. 284).

Results and discussion

Twenty nine clutches totalling 155 eggs were laid. Mean clutch size was 5.3 eggs (SD = 1.7; n = 29), with clutches ranging from one to eight eggs. The mean egg weight was 1.148 g (SD = 0.101; n = 152; range = 0.945–1.463 g). These data agree with Eisner's (1960a) data on captive finches, but differ from those of Avery (1978), who found a significantly smaller mean clutch size in a wild population in West Malaysia (Table 1). Avery's modal clutch size was the same as ours, so it is premature to suggest that captive finches lay larger clutches than their wild counterparts.

In clutches of four and seven eggs, variation in egg weight within clutches was greater than that among clutches (Table 2). The opposite was true for clutches of five, six, and eight eggs, and when all clutches of four to eight eggs were combined. The latter finding is in accordance with several other studies (Ojanen *et al.* 1981; Ricklefs 1984; Alisauskas 1986; Redmond 1986; Hepp *et al.* 1987). In contrast, greater variation within clutches than between clutches as we found for clutches of four and seven eggs is unusual, though the result for seven-egg clutches is highly suspect because of the small sample size.

Egg weight increased linearly with laying sequence when all the eggs from clutches of four to eight eggs were pooled (Table 3 and Fig. 1). Egg weight increased linearly in clutches of four, five, and eight eggs. The trend was similar in clutches of six eggs, but the increase was nonlinear. Egg weight decreased in clutches of seven eggs, but this may have been an artifact of the small sample size (n = 2 clutches).

Slagsvold *et al.* (1984) presented an alternative means of examining patterns in egg size using the relative weight of the last egg, calculated as: (last egg weight − mean egg weight)/ (mean egg weight) $\times$ 100. For clutches of four, five, six, and eight eggs and for all clutches combined, the relative weight of the last egg was positive (4.0, 3.8, 4.3, 3.9, and 3.2%, respectively). Only for the two clutches of seven eggs was the value negative (−5.0%), indicating small last eggs.

Jefferies (1969), in a study of the effects of DDT on egg weight in the Bengalese finch, also noted that egg weight tends to increase with the order of laying for data pooled from various clutch sizes. Linear regressions through the means he presents produce regression equations similar to ours (untreated eggs: Y

TABLE 1. Clutch size in the Bengalese finch in three studies[a]

	This study	Eisner (1960a)	Avery (1978)
Population	Captive	Captive	Wild
Mean	5.3	5.6	4.4
SE	0.31	0.13	0.29
N	29	99	13
Range	1–8	2–9	2–5
Mode	5	6	5

[a]Analysis of variance (ANOVA) reveals significant differences in clutch size ($F_{2,138}$ = 4.98, $P < 0.01$) among the three samples. Fisher's least significant difference tests show Avery's results to differ from the other two, which do not differ from each other.

TABLE 2. Comparison of variation in egg weight within and among clutches

Clutch size	No. of clutches	F	df	P	Percentage of variation: among clutches	Percentage of variation: within clutches
4	4	2.11	3, 12	0.15	22.0	78.0
5	9	8.65	8, 36	<0.001	60.5	39.5
6	6	22.56	5, 30	<0.001	78.2	21.8
7	2	0.36	1, 12	0.56	8.4	91.6
8	3	16.78	2, 21	<0.001	66.4	33.6
All	24	11.59	23, 111	<0.001	65.5	34.5

NOTE: The percentage of variation was calculated according to Sokal and Rohlf (1981; p. 216). Note that percentage of variation among clutches divided by 100 is known as the coefficient of intraclass correlation, r_1.

TABLE 3. Regressions of egg weight on position in laying sequence for clutches of four to eight eggs

Clutch size	F	df	P	Regression equation[a]
4	76.4	1, 2	0.01	$Y = 0.03x + 1.02$
5	30.3	1, 3	0.02	$Y = 0.01x + 1.09$
6	6.2	1, 4	0.07	$(Y = 0.02x + 1.13)$
7	6.9	1, 5	0.05	$Y = -0.02x + 1.27$
8	36.4	1, 6	<0.01	$Y = 0.01x + 1.15$
All	17.2	1, 6	<0.01	$Y = 0.01x + 1.11$

[a]The x in the regression equation is the position of the egg in the laying sequence; the regression equation in parentheses is not significant at $P < 0.05$.

$= 0.02x + 1.12$, $r^2 = 0.92$, and $P = 0.01$; DDT-dosed eggs: $Y = 0.02x + 1.08$, $r^2 = 0.92$, and $P = 0.01$; where x is the position in the laying sequence).

Mean egg weight also changed with clutch size (Fig. 2). This relationship is not merely the result of the large size of the last eggs in large clutches (owing to the increase in egg weight through the laying sequence). Rather, the same change in egg weight is seen when only the first four eggs in each clutch size are considered. Thus birds that were going to lay large clutches laid large eggs throughout the clutch. This suggests that females in this species determine both the size of their clutch and the investment into each egg prior to laying the first egg in order to produce a first egg of the appropriate weight for the clutch size.

There was no relationship between egg weight and the amount of food eaten by the pair either the day after the egg was laid, the day before laying, or for any of the 3 preceding days (in all cases, $r^2 \le 0.01$; $n = 128$, $P = 0.17$; $n = 116$, $P = 0.26$; $n =$
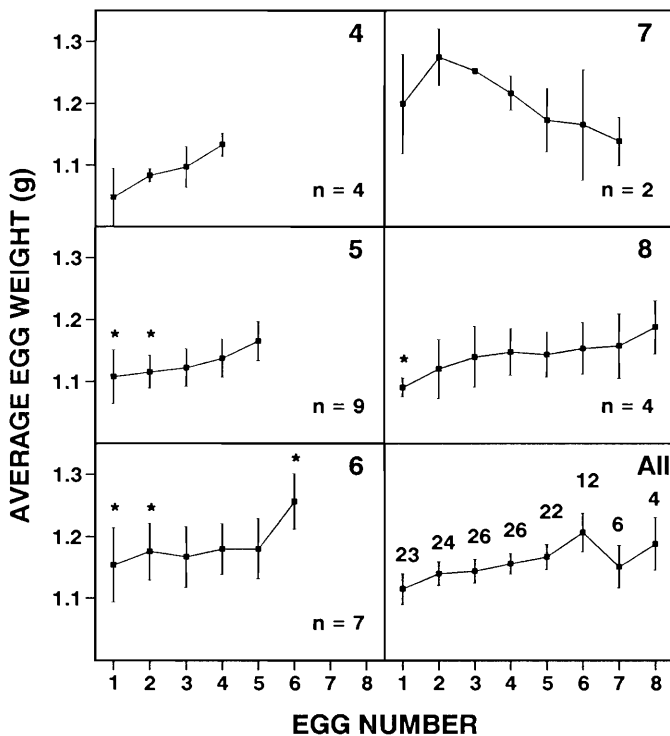
FIG. 1. Egg weight versus laying sequence for clutches of four, five, six, seven, and eight eggs, and for clutches of four to eight eggs combined (All). Data are means ± SE. Numbers indicate sample sizes and an asterisk indicates a missing egg.

FIG. 2. Egg weight and clutch size. ANOVA's on all eggs (———) and on the first four eggs (- - -) of each clutch reveal significant differences in average egg weight with clutch size (all eggs: $F_{4,142} = 4.54$, and $P = 0.002$; first four eggs: $F_{4,98} = 4.46$ and $P = 0.002$). Means are shown with one-sided error bars (SE). Numbers indicate sample sizes.

106, $P = 0.89$; $n = 93$, $P = 0.80$; and $n = 84$, $P = 0.62$, respectively). Furthermore, food consumption did not increase linearly through the laying sequence like egg weight for clutches of four, five, six, or eight eggs, or for all clutch sizes pooled. For clutches of seven eggs, food consumption increased ($F_{1,5} = 18.3$, $P < 0.01$, $Y = 0.33x + 14.60$ g, where x is position in the laying sequence), although egg weight decreased through the laying sequence for this clutch size.

The patterns within the data set, particularly the increase in egg weight with order in the laying sequence and changes in egg weight with clutch size, suggest that complex investment allocation decisions underlie egg weight variation in the Bengalese finch. The fact that food intake was not correlated with egg weight strengthens this hypothesis by showing that investment into each egg is not determined directly by the food resources available around the time of egg laying.

Clark and Wilson (1981, 1985) discussed at length the interactions of egg size variation, onset of incubation, hatching asynchrony, and patterns of mortality. They concluded from a survey of 87 altricial bird species that egg weight often increases with laying order for birds that hatch asynchronously, but not for birds that hatch synchronously. Bengalese finches hatch asynchronously (Eisner 1960a), therefore the pattern of egg weight variation found in our study matches Clark and Wilson's findings for other species. Clark and Wilson (1985) speculated that "the larger size of the last egg(s) partially compensates for its delayed hatching." This explanation may not apply to the Bengalese finch. Their hypothesis predicts that all eggs should be of equal size except for those laid after the onset of incubation, which should be larger. Bengalese finches start incubating with the penultimate egg (Eisner 1960a), yet the data in Fig. 1 do not support the prediction, except perhaps in the clutches of six
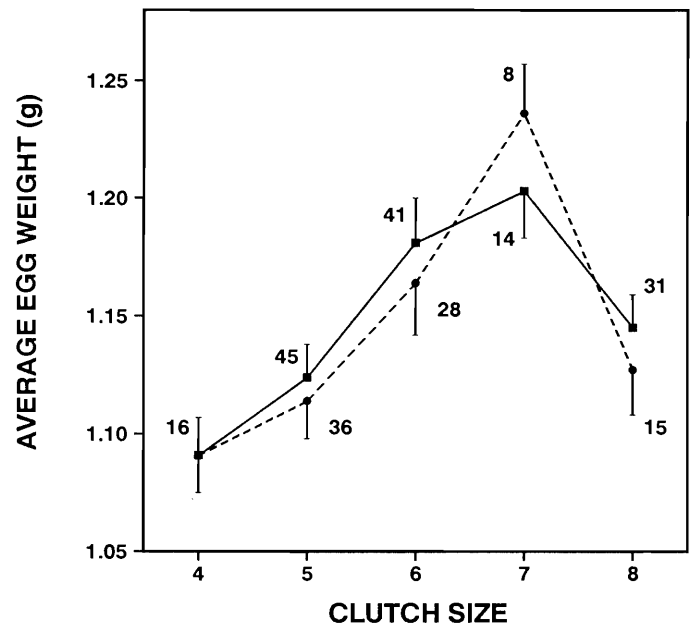
eggs; in other clutch sizes the increase in egg weight is linear prior to incubation. Thus, the reasons for the observed patterns remain elusive.

These data highlight the need for a general robust model of egg size allocation that allows individual treatment of eggs by considering such factors as the onset of incubation, differential hatching times, and differential survivorship probabilities for each egg in the laying sequence. To test this model, detailed data on each of these parameters will be needed if we are to understand egg size variation within clutches.

Acknowledgements

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