

INTRACLUTCH VARIATION IN EGG WEIGHTS OF PIED-BILLED GREBES¹

M.R.L. FORBES² AND C. D. ANKNEY

Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada

Key words: *Pied-billed Grebes*; *Podilymbus podiceps*; egg weights; hatching asynchrony.

Much discussion has recently focused on the effects that quality of eggs, and hatching order of chicks, have on chick survival within avian broods. Chicks which hatch from larger eggs are heavier (e.g., Howe 1976), grow faster (e.g., Ankney 1980), and survive better (e.g., Lundberg and Väisänen 1979). Chicks which hatch later, however, generally have poorer survivorship (e.g., Parsons 1975). Thus there potentially exists either additive or opposing influences of egg quality and hatching order of chicks on chick survival. One rationale for examining whether or not such effects are additive has been an attempt to resolve controversy concerning the adaptiveness of hatching asynchrony (review by Clark and Wilson 1981).

The only work on intraclutch variation in egg quality for grebes has been Fugle and Rothstein's (1979) examination of the effects of egg removal, from two clutches of Pied-billed Grebes (*Podilymbus podiceps*), on clutch size and egg-size determination. Grebe broods, however, show considerable hatching asynchrony (Cramp and Simmons 1977). For example, Forbes and Ankney (1987) found that broods of *P. podiceps* from clutches of five to eight eggs hatched over 3 to 7 days. Thus chicks within grebe broods may exhibit considerable differences in size at hatch completion due to hatching order (Nuechterlein 1981, Forbes and Ankney 1987).

Our objective was to determine whether or not variation in egg weights within clutches of Pied-billed Grebes was related to laying order of eggs. For both altricial (e.g., Richter 1984) and semiprecocial species (e.g., Horsfall 1984), laying order of eggs was a good predictor of hatching order of chicks and thus may be used for comparisons with egg quality (review by Slagsvold et al. 1984).

MATERIALS AND METHODS

Fieldwork was done from 28 April to 15 July 1984. Egg data were obtained from 28 nests found in the emergent vegetation of 26 ponds. These semipermanent ponds ranged from 0.1 to 1.2 ha and were roughly 10 km southeast of Minnedosa, Manitoba (55°16'N, 99°50'W).

Nests were visited daily during the egg-laying period because Pied-billed Grebes generally lay eggs daily (Glover 1953). Eggs were numbered serially with a pencil, measured for length and maximum breadth (to the nearest 0.1 mm) with Vernier calipers, and, if fresh, weighed (estimated to the nearest 0.1 g) with a 50-g Pesola spring balance. We removed any adhering vegetation and gently dried the eggs before weighing. Fresh egg weight, or the weight of an egg weighed within 24 hr of being laid, is an accurate index of egg quality, i.e., the absolute amount of protein and/or lipid available to the developing chick (Nisbet 1978, Ankney 1980, Alisauskas 1986; but see Ricklefs 1984).

For 13 nests first discovered with two or more eggs present, i.e., nests >2 days old, it was possible to determine only the last-laid egg. Pied-billed Grebe eggs are blue-white when freshly laid, but become faded and stained by emergent vegetation within a few days (Palmer 1962). Only the unstained egg was weighed at nests, but linear measurements were taken for all eggs. When nest visits were made on rainy and/or windy mornings, no eggs were weighed. During such visits, it was too difficult to get accurate egg weights because the weighing bag became wet or moved too much in the wind. Thus only 67 of 165 eggs were weighed.

After clutch completion, nests were visited at 5- to 8-day intervals until the expected date of onset of hatch (based on a 23-day incubation period for Pied-billed Grebe eggs, Palmer 1962) to check that nests were still active. Once hatching started, nests were again visited daily to determine the sequence of hatching for remaining eggs.

We regressed egg weights against egg volumes (after Hoyt 1979) to determine the following linear equation:

$$y = 0.92 + 0.52LB^2, \quad r^2 = 0.94, \quad n = 67$$

where y = fresh weight (g) of eggs, L = length (mm), and B = maximum breadth (mm). This equation was used to estimate weights of eggs for which only linear measurements were known. A simple correlation test (Zar 1984) was used to examine the relationship between laying order of eggs and hatching order of chicks from those eggs.

We did a one-way ANOVA (Goodnight et al. 1982) on egg weight with respect to females (or different clutches). Only those females ($n = 23$) which laid complete clutches were included in the above analysis. The analysis was unbalanced as seven of 23 females laid six eggs, 11 laid seven eggs, and five laid eight eggs.

To further investigate intraclutch differences in egg weights, we performed a one-way ANOVA of unbalanced design on egg-weight residuals with respect to laying order. An egg weight residual was the difference

¹ Received 23 September 1987. Final acceptance 22 February 1988.

² Present address: Department of Zoology, Erindale Campus, University of Toronto, Mississauga, Ontario L5L 1C6, Canada.

TABLE 1. Results of Student-Neumann-Keuls test for pairwise comparisons between mean egg weight residuals.^a

Egg no.	n	\bar{x}	SD	Range	Code ^b
1	6	-1.51	1.14	-2.85, -0.29	A
2	6	-0.09	0.79	-0.85, 0.83	B
3	6	0.31	0.55	-0.17, 1.25	B
4	6	0.68	0.49	0.09, 1.24	B
5	6	-0.03	0.56	-0.98, 0.66	B
6	6	0.46	0.40	-0.03, 0.95	B
7	5	0.31	0.74	-0.63, 1.37	B
8	1	-0.17	—	—	B

^a Mean refers to the mean of residuals where a residual is the difference between an egg's weight and the mean egg weight of the clutch to which that egg belongs.

^b All means coded with the same letter were not significantly different from each other at $\alpha = 0.05$.

between an egg's weight and the mean egg weight of the clutch to which that egg belonged. Thus between-clutch variation in egg weight was removed. We then used a Student-Neumann-Keuls test (Goodnight et al. 1982) to make pairwise comparisons between mean residual weights with respect to laying order. Unfortunately, we could only use six clutches for the second analysis as the other 17 nests were first discovered with three or more eggs. For those 17 clutches we could not assign all eggs to a specific laying order.

RESULTS

We found that female (or clutch) accounted for 76.4% of the total variation ($F = 20.1$; $df = 22, 136$; $P < 0.0001$) in egg weights of Pied-billed Grebes. After removing the effect of each female on egg weight, we found that laying order accounted for 52% of the residual variation ($F = 5.44$; $df = 7, 34$; $P < 0.003$) in egg weights. This result was due solely to first eggs being 8% lighter than subsequent eggs within clutches (Table 1). The difference between the mean residual (i.e., -1.51 g) of first eggs ($n = 6$) and the mean residual (i.e., 0.15 g) of all other eggs combined ($n = 36$) was 1.65 g. The mean egg weight for that sample of six clutches was 20.4 g.

DISCUSSION

Slagsvold et al. (1984) suggested that size of the last egg, relative to all other eggs in avian clutches, could provide information as to the adaptive significance of hatching asynchrony, i.e., either to reduce the probability of total nest failure or to promote brood reduction. Emphasis has been placed on the last egg because many species of birds begin full incubation with the penultimate egg (Clark and Wilson 1985). Thus, chicks from last-laid eggs are usually the only chicks at a disadvantage due to hatch position. Pied-billed Grebes, however, like other grebes (Cramp and Simmons 1977), begin incubation before laying the penultimate egg (Forbes 1986) and thus the overall pattern of intra-clutch variation in egg weight warrants investigation for this group of birds.

Variation in quality of Pied-billed Grebe eggs was largely due to female (or clutch) effects as has been

shown for other species of birds (e.g., Blue-winged Teal, *Anas discors*; Rohwer 1986 and references cited therein). Thus it was necessary to remove female effects before examining variation in egg weights due to laying order. We found that laying order also accounted for significant variation in fresh egg weights, largely because the first egg was lighter (by approximately 8%) than subsequent eggs. Intraclutch differences of egg quality of <10% have been partly responsible for differential hatching success (e.g., *Apus apus*, O'Connor 1979), and differential growth (e.g., *Quiscalus quiscula*, Howe 1976) or survival (e.g., *Sterna hirundo*, Nisbet 1978) of chicks.

Only four eggs in our sample failed to hatch due to causes other than egg loss or predation. The egg-weight residuals of those eggs (i.e., +0.81, +0.70, -0.42, -0.58) revealed no association with hatching failure. We also did not determine whether an 8% difference in egg quality between the first egg and subsequent eggs in the clutch could have translated into differential survival among Pied-billed Grebe chicks.

Nevertheless, the pattern of a smaller first egg for Pied-billed Grebe clutches is noteworthy inasmuch as there is no a priori reason to separate the first egg from all other eggs in the clutch based on existing hypotheses concerning the adaptive significance of intraclutch variation in egg quality. We note elsewhere (Forbes and Ankney 1987) that two to four Pied-billed Grebe eggs generally hatched on the first day of hatching with remaining eggs hatching at daily intervals. Chicks from the first two to four eggs, therefore, comprise one group based on hatch position. Thus we might expect the first two to four eggs to be similar to each other in terms of egg quality, but dissimilar in this regard from eggs laid subsequently, irrespective of the particular pattern of intraclutch variation in egg weight.

As noted above, we knew laying order for all eggs in only six clutches. Unfortunately, we could not determine the hatching order of eggs which hatched on the first day of hatching because of daily nest visits. However, we found that laying order of eggs was highly correlated with hatching order of chicks from eggs 3 to 8 ($r = 0.957$, $n = 18$, $P < 0.05$) in those six clutches. Hatching order of eggs remaining after the first day of hatching likely results in size disparities among chicks from those eggs. However, no trends in mean weight residuals were found with respect to laying order of those eggs (Table 1). Although patterns of initial investment in eggs may depend on clutch size or the particular female (e.g., Howe 1976) and, therefore, grouping of clutches may obscure information, it is clear that differential investment in eggs within clutches of Pied-billed Grebes was not based on hatching patterns observed in this species.

In conclusion, we found intraclutch differences in egg weights of Pied-billed Grebes. These differences were due solely to lighter first eggs which was unexpected based on patterns of hatching known for this species. Our results emphasize the importance of examining overall intraclutch variation to ensure that differences in egg quality are related to hatching patterns rather than a possible artifact of grouping eggs.

Funds for this study were provided through an operating grant from the Natural Sciences and Engineer-

ing Research Council of Canada to C. D. Ankney and through grants-in-aid-of-research from the Sigma-Xi foundation to M.R.L. Forbes. We are especially indebted to the Delta Waterfowl and Wetlands Research Station for providing space and logistic support and to many landowners in the Minnedosa area for allowing us to visit their ponds. We are also grateful for the field assistance of T.O.M. Thomas, and to R. L. Baker and two anonymous reviewers for providing helpful comments on an earlier version of this paper.

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