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Egg Size and Parental Quality Influence Nestling Growth in the Shag

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Within any avian population, egg size can vary considerably. For most species, this is due primarily to differences in egg size among clutches laid by different females (e.g. Ojanen et al. 1979, Grant 1982, Bancroft 1984, Greig-Smith et al. 1988), but egg size within individual clutches may also vary (see Slagsvold et al. 1984, and references therein). Nestlings hatched from large eggs grow faster (Schifferli 1973, Williams 1980), achieve higher fledgling mass (Howe 1976; but see Greig-Smith et al. 1988), or have higher survival rates (e.g. Davis 1975, Howe 1976, Thomas 1983; but see O'Connor 1979, Moss et al. 1981, Bancroft 1984) than those hatched from small eggs. Within clutches, large eggs may also be less vulnerable to predation (Montevecchi 1976, Verbeek 1988). Because previous studies of nestling growth and survival have been descriptive, it cannot be concluded that there is a specific effect of egg size. For several species, the age (e.g. Coulson et al. 1969, Nisbet 1978, Thomas 1983; but see Davis 1975, Ojanen et al. 1979), and body mass (DeSteven 1978) or condition (Murphy 1986) of the female have a positive correlation with egg size. Similarly, reproductive success, expressed as the number of offspring fledged successfully, generally

increases with parental age (e.g. Thomas 1983, Nisbet et al. 1984). The apparent positive effect of egg size on nestling growth and survival may thus not be a causal relationship, but could exist because better females lay larger eggs (Davis 1975, Birkhead and Nettleship 1982). Although some experimental evidence for an effect of egg size on nestling survival (Parsons 1970, 1975; Nisbet 1973, 1978) exists, experimental data on effects on the growth of nestlings are scarce (Schifferli 1973, Ricklefs 1984). Ricklefs (1984) argued that, for passerines, there is a lack of compelling evidence for a positive effect of egg size on postnatal development.

We performed an experiment to test the relative importance of egg size and parental quality on nestling growth in the Shag (*Phalacrocorax aristotelis*). The study was conducted during May–August 1985, in the Røst archipelago (67°28'N, 11°57'E), northern Norway. In 1985, the mean egg volume of three-egg first clutches of Røst shags was 48.0 ± 0.14 cm³ (range 34.5–63.4, n = 618 eggs). Volumes were calculated from the formula: 0.51 × length × breadth² (Hoyt 1979). Although Shag egg size varies considerably within broods (Coulson et al. 1969, Stokland and Amundsen 1988), the among-brood component accounted for 82.4% of the variation in egg volume in a sample of 381 eggs from 127 three-egg clutches for which the laying sequence was known. The volumes of eggs used in the experiment varied over a range of 40.0–61.0 cm³. Eggs with a volume of 48.0 cm³ or less were designated *small*, and those larger than 48.0 cm³ were designated *large*. The difference between the mean volumes for small and large eggs was 5.4 cm³. That is, large eggs were on average 12% bigger than small eggs. Females that laid clutches with a mean egg volume of 48.0 cm³ or less were *small-egg females*, and those laying larger eggs were *large-egg females*. The original clutch sizes of all the foster parents were three eggs (the modal clutch size; Amundsen and Stokland 1988), with the exception of one female that laid two eggs, and one that laid four. Newly hatched nestlings (mean age: 4.6 days) were interchanged among nests in such a manner that some nestlings hatched from small eggs were reared by large-egg females, and others reared by small-egg females. Nestlings hatched from large eggs were interchanged similarly. After manipulation, each brood comprised one nestling that had hatched in that particular nest, and two nestlings from other nests. We separated data for young reared by their biological parents from data for those reared by foster parents. Most broods contained nestlings hatched from both large and small eggs. Because the same series of experiments was also used to test hypotheses concerning hatching patterns, different degrees of simulated hatching asynchrony were established among the broods: synchronous, normally asynchronous, and double-asynchronous (Amundsen and Stokland 1988). Data for the third-hatched nestlings of the double-

TABLE 1. Body mass and wing length of Shag nestlings reared in their natal nests but hatched from different-size eggs. See text for categorical and analytical details. * = P < 0.05, one-tailed t-test.

Age (days)	Nestling			
	Small-egg[a]		Large-egg[b]	
	$\bar{x} \pm$ SD	n	$\bar{x} \pm$ SD	n
Body mass (g)				
7	162 ± 21	13	178 ± 22*	16
17	667 ± 102	15	723 ± 57*	21
37	1,665 ± 144	15	1,760 ± 99*	17
Wing length (mm)				
7	27 ± 2	12	28 ± 1*	13
17	68 ± 6	14	70 ± 5	21
37	198 ± 9	14	202 ± 6	17

[a] Small-egg nestlings hatched from eggs with a mean volume (cm³) of 44.4 ± 3.0; their female parents laid eggs with a mean volume of 45.5 ± 2.1; n = 17.

[b] Large-egg nestlings hatched from eggs with a mean volume (cm³) of 51.5 ± 2.3; their female parents laid eggs with a mean volume of 51.0 ± 2.2; n = 22.

asynchronous broods were excluded from analysis, since these nestlings were the only ones that suffered markedly depressed growth rates (Amundsen and Stokland 1988). Nestlings hatched from large and small eggs were assigned randomly to broods with different degrees of asynchrony, and to different positions in the simulated hatching sequence. Body mass and wing length of each nestling were recorded at 7, 17, and 37 days post-hatch. The mortality rate of the nestlings involved in the experiment was 11.1%, compared with 17.3% in nonexperimental broods (Amundsen and Stokland 1988). This mortality rate was too low for any detailed analysis to be made in regard to a possible effect of egg size on nestling survival.

Among the nestlings reared in their natal nests, those hatched from large eggs were significantly heavier at all ages than those hatched from small eggs. Wing lengths were significantly different only at seven days (Table 1). Among the nestlings reared by foster parents, small-egg nestlings reared by small-egg females generally had lower body masses and shorter wings than large-egg nestlings reared by large-egg females. This pattern was consistent at all ages (7, 17, and 37 days). The mean values for the two groups were significantly different only for body mass at 17 days, and for wing length at 17 and 37 days (Table 2). We surmize that egg size or other aspects of parental quality influence nestling growth positively, but the data do not allow an evaluation of the relative importance of these two factors.

We separated the two potential determinants of nestling growth by ANOVA, and found significant effects of both factors. Egg size had a significant influence on nestling body mass (F = 14.6, df = 2, 44, P < 0.001) and wing length (F = 7.4, df = 2, 43, P <

TABLE 2. Body mass and wing length of Shag nestlings reared by foster parents. See text for categorical and analytical details. Identical letters indicate that the means are significantly different in comparisons at equal nestling ages; levels of significance: $P < 0.05$ (A), $P < 0.01$ (B), $P < 0.005$ (C); two-tailed t-tests.

Age (days)	Small-egg nestling				Large-egg nestling			
	Small-egg foster female[a]		Large-egg foster female[a]		Small-egg foster female[b]		Large-egg foster female[b]	
	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n
Body mass (g)								
7	161 ± 14	7	164 ± 22	17	169 ± 24	11	176 ± 23	9
17	653 ± 73B	8	667 ± 50C	19	712 ± 86	10	752 ± 58BC	10
37	1,563 ± 200	6	1,691 ± 176	14	1,638 ± 168	9	1,691 ± 129	8
Wing length (mm)								
7	27 ± 1	6	28 ± 1	15	28 ± 2	10	28 ± 1	8
17	64 ± 5C	8	66 ± 5B	19	67 ± 8	10	72 ± 5BC	10
37	193 ± 8A	6	198 ± 8	14	194 ± 14	8	202 ± 5A	8

[a] Small-egg nestlings reared by small-egg foster females hatched from eggs with a mean volume (cm³) of 45.6 ± 1.9 (9), those reared by large-egg foster females, 45.3 ± 2.0 (19); mean foster female egg volume 45.7 ± 1.9 (small-egg) and 50.7 ± 2.1 (large-egg).

[b] Large-egg nestlings reared by small-egg foster females hatched from eggs with a mean volume (cm³) of 51.7 ± 3.9 (11), those reared by large-egg foster females, 50.2 ± 1.3 (10); mean foster female egg volume 45.7 ± 1.7 (small-egg) and 50.4 ± 0.9 (large-egg).

0.01) at 17 days post-hatch. No significant effect of egg size was found at 7 days or at 37 days. We found a significant effect of parental quality (as assessed by the mean size of eggs laid) on the wing lengths of nestlings at 17 ($F = 5.2$, df = 2, 43, $P < 0.05$) and 37 days ($F = 4.2$, df = 2, 33, $P < 0.05$). We saw no significant effect of parental quality on wing length at 7 days. Nestling body mass was not influenced significantly by parental quality at any age.

Small-egg nestlings reared by large-egg females and large-egg nestlings reared by small-egg females were, in general, intermediate in size between those of the small-small and of the large-large group (Table 2). Most differences were not statistically different. There was a tendency for large-egg nestlings reared by small-egg females to become heavier than small-egg nestlings reared by large-egg females, at the ages of 7 and 17 days (Table 2). This indicates that egg size is the more influential of the two factors during the initial third of the Shag nestling period. This was supported further by the analysis of variance that showed a significant effect of egg size only at an age of 17 days. The tendency for an opposite difference in body mass, as well as in wing length, to exist at the age of 37 days, compared with that at 17 days of age, indicates a possible growth advantage to small-egg nestlings reared by large-egg females over large-egg nestlings reared by small-egg females during the later nestling period (Table 2). Parental quality seems to become increasingly important, relative to egg size, during nestling development, and may be the more important of the two factors in determining fledgling size.

Our findings agree with Nisbet's (1973) conclusion that egg-size in the Common Tern (*Sterna hirundo*) is important for nestling development shortly after hatching. For the Shag, however, we found a growth advantage and not a survival advantage as reported by Nisbet (1973). Nisbet (1978) later found that in the Common Tern and Roseate Tern (*S. dougallii*), egg size is also more important than parental quality for nestling growth during later stages of development, and for fledging success. Contrary to this, we found that parental quality tended to be more important in the Shag at this stage. This difference between the Shag and the terns studied by Nisbet (1978) is reasonable, because the fledging period of the Shag (48–58 days; Snow 1960) is approximately twice as long as those of Common and Roseate terns (22–30 days; Nisbet and Drury 1972). In contrast to the lack of compelling evidence for an influence of egg size on growth rate in passerines, as emphasized by Ricklefs (1984), we present evidence for such a relationship in the non-passerine Shag.

Egg size may reflect the quality not only of the female parent but also that of the male. This is because the degree of paternal investment (e.g. courtship feeding) may influence the amount of resources available for egg production (Nisbet 1973). The females of many species tend to choose mates of similar age and hence probably of similar quality (e.g. Coulson and Horobin 1976, Nisbet et al. 1984).

A positive correlation between egg size and nestling growth, or survival, has been found for most avian species studied. Based on our results for the Shag, we hypothesize that for many species this is partly a direct effect of egg size per se, and not merely a reflection of other aspects of parental quality.

during the fieldwork, and Philip A. Tallantire who improved the English.

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