INITIAL SIZE HIERARCHY IN BROODS OF THE SHAG: RELATIVE SIGNIFICANCE OF EGG SIZE AND HATCHING ASYNCHRONY

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ABSTRACT.—We studied the relative importance of hatching asynchrony and intraclutch egg-size variation in the establishment of a size hierarchy in broods of the Shag (*Phalacrocorax aristotelis*). In 3-egg clutches (87% of all clutches), the second egg averaged 3.0% larger than the first and 2.3% larger than the third. Mean hatching intervals were 11.7 h between the first and second chicks, and 48.3 h between the second and third chicks. In broods of three, the first chick weighed on average 1.9 times more than the last chick at the time the last one hatched. This difference was almost entirely a result of hatching asynchrony. For the last two chicks, hatching asynchrony accounted for 95% of mass difference and the variation in egg size for the remaining 5%. We conclude that variation in egg size has little influence in determining the initial size differences within broods. This applies to several other bird species. Hatching asynchrony and variation in egg size seem to result from selection pressures other than those connected with size differences between nestlings. *Received 19 June 1987, accepted 30 December 1987.*

A PRONOUNCED size hierarchy is found within broods of many bird species (e.g. Bancroft 1984, Shaw 1985, Wiklund 1985). The first nestling hatched is considerably heavier than the last one when the last hatches. Several studies have shown that asynchronous hatching places the last-hatched nestlings at a disadvantage. Last nestlings generally suffer a higher rate of mortality than their older and larger siblings (Davis 1975, Howe 1976, Bryant 1978a, Lundberg and Väisänen 1979, Horsfall 1984, Shaw 1985), and, in some cases, their growth rate is depressed (Davis 1975, Bryant 1978a, O'Connor 1978, Zach 1982). It has been proposed that a size hierarchy is an adaptation to unpredictable food conditions during the breeding season (Lack 1947, 1954, 1968; Ricklefs 1965; Howe 1976).

Within-brood size hierarchies can be brought about by the combined effects of intraclutch variation in egg size, asynchronous hatching, and nestling growth rates. Hatching asynchrony is a result of incubation before egg laying is complete. A hatching span of a day or more for a brood is quite common (e.g. Clark and Wilson 1981), and the chick that hatches first will have received a considerable amount of food, and have grown correspondingly, before the last egg hatches.

Hatchling mass is highly correlated with egg size for a large number of bird species (e.g. Parsons 1970, Howe 1976, Ricklefs et al. 1978, Williams and Burger 1979, Furness 1983, Bancroft 1984, Horsfall 1984, Rofstad and Sandvik 1985). The pattern of variation in intraclutch egg size differs between taxonomic groups, however (e.g. Slagsvold et al. 1984), and does not lend itself to a straightforward explanation.

To evaluate the relative importance of egg-size variation and hatching asynchrony in the establishment of a size hierarchy in the brood, additional knowledge about nestling growth rates and the relation between egg volume and chick mass at hatching, is needed. We evaluated these factors for the Shag (*Phalacrocorax aristotelis*).

METHODS

The fieldwork was conducted during April–July 1985, on islands in the Røst archipelago (67°28'N, 11°57'E), Lofoten, northern Norway.

We visited nests at 3-day intervals during the egg-laying period. This is the customary laying interval between consecutive eggs of the Shag (Snow 1960, pers. obs.). We recorded clutch size and laying sequence, and numbered all eggs with waterproof ink. Egg breadth and length were measured to the nearest 0.1 mm with a digital caliper. Egg volume was calculated from the formula $V = 0.51LB^2$ (Hoyt 1979), where L is egg length and B is maximum egg breadth.

Hatching intervals and hatching mass.—We defined the time of hatching as the time when the chick became free from its eggshell. Each nest was visited daily, from 1–2 days before the estimated hatching time of the first egg until either all the eggs had hatched, or no further hatching could be expected.

On the final visit before hatching, we recorded the prehatching stage (egg surface broken, hole in egg surface, etc.). We found that the duration of the entire hatching process, from the first sign of hatching (egg slightly broken) until the chick was free, was roughly 24 h. The duration of each prehatching stage was estimated from the relative frequency of that stage (Table 1). Based on the observed prehatching stage, we then determined the time interval within which the chick could be expected to hatch. We used the midpoint of that interval as the estimate of hatching time.

First and second eggs often were observed in the same prehatching stage simultaneously. In these cases the same hatching times were assigned to the eggs, although the actual hatching interval may have been several hours (maximum 13 h for the most common prehatching stage; cf. Table 1). This probably underestimated the hatching interval between the first and second chicks.

Each chick was weighed to the nearest 0.1 g (using a Pesola spring balance) at the first visit after it hatched. We used these initial masses to calculate the relationship between egg volume and hatching mass. A linear-regression equation of initial mass on egg volume was calculated from the subsample of masses made 5 h or less after the estimated time of hatching. We then calculated the hatching mass from egg volume by R1(V), where R1 is the regression equation referred to above, and V is the volume of the egg from which the chick hatched.

Early growth.—In addition to the visit during the hatching period, we visited all nests 1-4 times during the next 7 days. Chicks were weighed on each occasion (to the nearest 0.1 g up to 50 g, to the nearest 0.5 g from 50 to 100 g, and to the nearest 1.0 g when over 100 g). These records of body mass constituted the basis for a polynomial regression R2(A) of body mass on age, from age 0 (hatching day) until an age of 7 days. We eliminated the variation in body mass that was due to differences in egg size by subtraction of the estimated hatching mass, R1(V), before the regression analysis was done. Successive powers of age (A^k) were added to the regression equation until no significant improvement of fit was obtained. At each step we tested the null hypothesis that the kth-order term contributed nothing to the increase of r^2. The resulting equation was interpreted as the expected cumulative growth up to an age of 7 days. We assumed all chicks to have the same growth rate, independent of egg volume. This assumption seemed, from our data, to be reasonable (Table 2).

Initial mass hierarchy.—A marked initial mass hierarchy was established in the broods. The body mass of each chick in the hierarchy on the hatching day of the last chick was calculated from the formula: $W_i = \mathrm{R1}(V_i) + \mathrm{R2}(A_i)$, where W_i is the body mass of chick i, V_i is the volume of the egg from which chick i hatched, and A_i is the age of chick i when the last chick hatched (which equals the hatching interval between chick i and the last chick). R1 and R2 are the regression equations defined above.

TABLE 1. Empirical basis used in the estimation of hatching time from various prehatching stages of Shag eggs, Røst, 1985.

State of egg surface	No. of observations	Estimated duration (h)	Estimated time until hatching (h)
Cracked	106	8	20
Surface broken, no hole	9	1	16
Distinct hole	180	13	9
Cut by chick	27	2	1

The mass difference between two consecutive chicks, chicks i and j, at the time of hatching of the last chick was calculated as $W_i - W_j$. In this calculation, $\mathrm{R1}(V_i) - \mathrm{R1}(V_j)$ was interpreted as the effect of egg volume on the mass difference, and $\mathrm{R2}(A_i) - \mathrm{R2}(A_j)$ as the effect of hatching asynchrony.

The total mass difference in a brood at the time of hatching of the last chick was calculated as $W_1 - W_n$, where n is the brood size.

RESULTS

The clutch size of Shags on Røst ranged from 2 to 4 eggs. The most common clutch size was 3 eggs (87%; 2 eggs: 9%, 4 eggs: 4%; $n = 184$).

In 3-egg clutches the second egg was generally the largest, with a mean volume of 48.8 cm^3 (SD = 3.7, $n = 129$). The first and third eggs laid were almost equal in size, with mean volumes of 47.4 cm^3 (SD = 3.5, $n = 138$) and 47.7 cm^3 (SD = 3.8, $n = 139$), respectively (ANOVA: $F = 5.67$, df = 2, $P < 0.01$). The mean hatching interval between the first and second eggs was 11.7 h (SD = 14.1, $n = 42$), and 48.3 h (SD = 16.3, $n = 45$) between the second and third eggs.

There was a pronounced initial size hierarchy among the siblings. On the hatching day of the third chick, we found a mean difference in body mass of 13.4 g between the first and second chicks, and of 19.9 g between the second and third chicks (Table 3). Mean body mass of third chicks on the day of hatching was 36.8 g. Thus, the day the last chick hatched, the first chick was nearly twice (1.9 times) as heavy as the last.

Effect of egg volume on the initial size hierarchy.—We found a highly significant correlation be-

TABLE 2. Mean body mass (g) of Shag chicks at different ages, adjusted by subtraction of the respective hatching mass. "Small" eggs were less or equal to mean egg volume, "large" eggs were greater than mean egg volume. The mean volumes of the two groups differ by 6.0 cm^3.

	Hatched from "small" eggs			Hatched from "large" eggs			
Age (days)	Mean	SD	*n*	Mean	SD	*n*	Significance[a]
0	1.4	3.1	145	1.5	2.8	130	$P = 0.84$
1	6.5	6.4	28	6.9	4.5	35	$P = 0.90$
2	20.0	7.8	28	20.2	7.6	23	$P = 0.92$
3	28.8	9.4	18	33.6	8.1	21	$P = 0.07$
4	55.8	13.9	20	50.6	13.3	19	$P = 0.16$
5	78.6	13.9	12	79.3	20.1	13	$P = 0.83$
6	94.4	14.2	9	115.6	17.6	9	$P < 0.05$
7	129.7	23.7	39	141.7	27.4	41	$P < 0.01$
17	642.0	74.5	19	660.9	106.5	14	$P = 0.57$
37	1,645.4	144.1	16	1,680.2	151.3	7	$P = 0.59$

[a] Mann-Whitney *U*-test, two tailed.

tween egg volume and body mass for chicks weighed within 5 h after the estimated time of hatching ($r = 0.88, P < 0.001, n = 65$). The linear regression showed that body mass close to hatching time was related to egg volume according to the equation: $y = 0.80x - 2.14$ ($r^2 = 0.78$; Fig. 1). Thus, a difference in egg volume of 1.0 cm^3 would be expected to result in a difference of 0.8 g in hatching mass.

Second eggs were generally larger than first-laid eggs, and this difference reduced (mean value −1.2 g; Table 3) the body-mass difference between the first and second chicks. On the other hand, second eggs were generally larger than third eggs, which increased (mean value 1.0 g; Table 3) the body-mass difference between the second and third chicks.

Effect of hatching asynchrony on the initial size hierarchy.—The initial growth rate of the chicks was high (Fig. 2). Thus, hatching asynchrony led to considerable differences between the body mass of consecutive chicks. The hatching interval between the first and second chicks accounted for an estimated mean difference of 8.3 g in body mass at the hatching time of the third chick (Table 3). The hatching interval between the second and third chicks was much longer and caused an estimated mean difference of 18.5 g.

Relative importance of egg volume and hatching asynchrony.—The estimated and observed mean differences in body mass between the second and third chicks were similar. They differed by only 0.6 g, whereas the mean values for the first and second chicks differed by 6.2 g. In both cases the observed mean was higher than the estimated mean (Table 3). The greater deviation in the latter case probably was due to an underestimation of the hatching interval between the first and second chicks (see Methods).

The total mass difference in the brood, defined as the estimated body-mass difference be-

TABLE 3. Estimated effects of egg-size variation and hatching asynchrony on the initial mass differences between chicks at the time of hatching of the last chick, together with the estimated and observed overall mass differences, for Shag broods of 3 chicks, Røst, 1985.

	Body-mass difference (g)							
	Chicks 1 and 2				Chicks 2 and 3			
	Mean	SD	Range	*n*	Mean	SD	Range	*n*
Estimated								
Egg-volume variation	−1.2	1.7	−6.6 to 3.1	129	1.0	1.9	−3.7 to 5.5	128
Hatching asynchrony	8.3	9.3	−5.6 to 37.2	30	18.5	8.8	2.5–44.7	45
Total	7.2	9.9	−8.7 to 36.4	30	19.3	9.4	0.4–46.9	45
Observed								
Total	13.4	14.4	−2.0 to 81.0	36	19.9	10.8	2.2–49.0	36

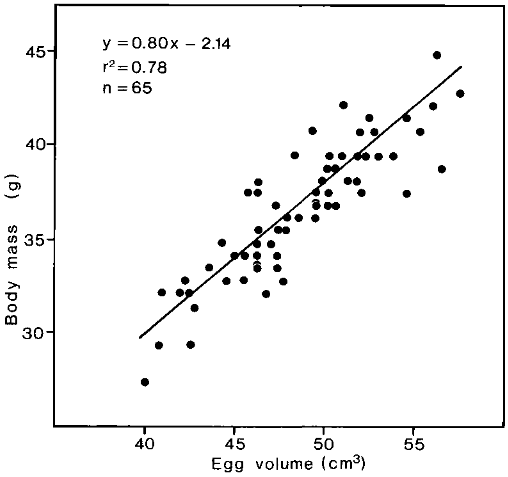

Fig. 1. Relationship between egg volume and body mass within 5 h after the estimated hatching time for Shag chicks on Røst, 1985.

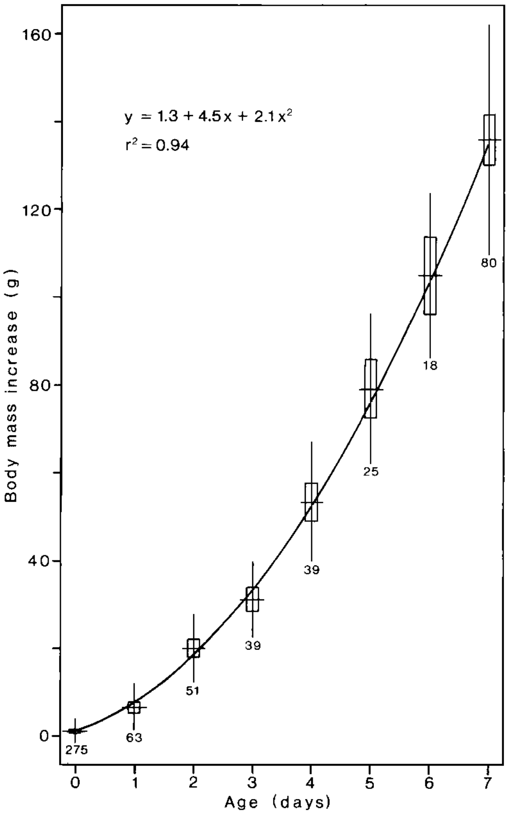

Fig. 2. Relationship between age and increase in body mass (= body mass minus the estimated hatching mass) of Shag chicks on Røst, 1985. Horizontal lines represent mean values, vertical lines one standard deviation on either side of the mean, and open boxes 95% confidence intervals. Sample sizes are shown below each box-plot.

tween first and last chicks at the time of hatching of the last chick, was primarily affected by hatching asynchrony. In 3-chick broods the differences in egg volume accounted for a mean value of −0.3 g of the total mass difference, whereas for hatching asynchrony the mean value was 24.1 g (Table 4). Thus, the effect of the difference in volume between the first and second eggs, on average, neutralized the effect of the difference between the second and third eggs. The total contribution from egg volume was negative for 53% of the clutches, equal or close to zero for 18%, and positive for the remaining 29% (n = 38).

In broods hatched from 2-egg clutches, the difference in egg volume, on average, accounted for −1.0 g of the total mass difference, whereas hatching asynchrony accounted for 23.8 g (Table 4). The respective values for broods hatched from 4-egg clutches were 0.3 g and 73.9 g (Table 4).

DISCUSSION

The initial size hierarchy.—The pattern of egg-size variation in Shag clutches is distinct. In the most frequent clutch size (3 eggs), the second egg averaged 2–3% larger than the first and third eggs. Hatching was asynchronous, with a hatching interval of 2–3 days. Both factors contribute to an initial size hierarchy among the nestlings in a brood.

The initial difference in body mass between the second- and third-hatched chicks in 3-egg clutches was almost entirely the result of hatching asynchrony (accounting for 95% of the difference). Regarding the difference in body mass between the first- and second-hatched chicks, the difference in egg volumes generally counteracted the effect of the hatching asynchrony (reducing the effect of asynchrony by 14%). We think that hatching asynchrony is even more important in the latter case, because the hatching interval between these two chicks probably was underestimated. In broods of two, hatching asynchrony accounted for the entire mass difference (the egg-size difference reduced the mass difference because of a generally larger second egg). In broods of four, the effect of egg size was less important than in broods of three because of a longer hatching span.

TABLE 4. Estimated effect of the variation in egg volume and of hatching asynchrony on the initial body-mass difference (g) between first and last-hatched chicks in Shag clutches of different size, Røst, 1985.

Clutch size	Source of difference	Mean	SD	Range	*n*
2	Egg-volume variation	−1.0	2.6	−5.0 to 4.9	15
	Hatching asynchrony	23.8	0.6	23.2–24.4	3
3	Egg-volume variation	−0.3	2.1	−4.9 to 5.6	128
	Hatching asynchrony	24.1	12.7	2.5–64.7	38
4	Egg-volume variation	0.3	1.4	−1.4 to 2.5	6
	Hatching asynchrony	73.9			1

Similar size differences at hatching, where the largest nestling is approximately twice the size of the smallest, can be calculated from published data for Blue-eyed Shags (*Phalacrocorax atriceps;* Shaw 1985), Crowned Cormorants (*P. coronatus;* Williams and Cooper 1983), Tree Swallows (*Tachycineta bicolor;* Zach 1982), Fieldfares (*Turdus pilaris;* Wiklund 1985), and Boat-tailed Grackles (*Quiscalus major;* Bancroft 1984). Haydock and Ligon (1986) reported that, in the Chihuahuan Raven (*Corvus cryptoleucus*), the largest nestling was typically 4 times the size of the smallest. In Herring Gulls (*Larus argentatus*), however, first-hatched chicks were only slightly larger (1.2 times) than the last-hatched when they hatched (Parsons 1975).

Several authors have pointed out that hatching asynchrony is most important in determining the size hierarchy within a brood (e.g. Bryant 1978b, Zach 1982, Bancroft 1984, Ricklefs 1984, Shaw 1985, Haydock and Ligon 1986), although none of them estimated the relative importance of the two factors involved. Parsons' (1972) study on the Herring Gull, however, indicates that egg size may be the most important factor for this species. The general validity of our conclusion, that hatching asynchrony is by far the most important factor, depends on whether the difference in egg volumes, degree of hatching asynchrony, and nestling growth rates of the Shag are similar to those of other bird species.

The intraclutch egg-size pattern we found in Shags, where the second egg was generally largest, has been reported for colonies elsewhere (Snow 1960, Coulson et al. 1969, Barrett 1983). The pattern may be unique to the species. In the Crowned Cormorant (Williams and Cooper 1983) and the Blue-eyed Shag (Williams and Burger 1979, Shaw 1985), egg size generally decreases over the laying sequence. In 19 altricial nonpasserine species the last egg is generally smaller (on average by 3.9%) than the mean for the entire clutch (Slagsvold et al. 1984). For 17 open-nesting passerines the last egg is on average 3.6% larger than the clutch mean, but for 13 hole-nesting passerines there is no significant deviation in the size of the last egg. In our study the mean deviation of the last egg was −0.6%, when calculated in the manner adopted by Slagsvold et al. (1984). The last egg, however, was on average 2.3% smaller than the second one laid. The first egg was on average 3.0% smaller than the second egg.

In 41 passerine species the normal hatching spread is 1–2 days in 61% of the species, and more than 2 days in 15% (Clark and Wilson 1981). Among nonpasserines the hatching spread varies considerably, but in many groups it is generally larger than in passerines. In several gulls the total hatching span approximates 1.5 days (Paludan 1951, Ytreberg 1956, Parsons 1972). Mikkola (1983) found a similar degree of asynchrony in smaller owls; in the larger species a larger degree of asynchrony occurred. A mean hatching span of 2 days or more has been found among cormorants (e.g. Shaw 1985), eagles (Edwards and Collopy 1983), and herons and egrets (Werschkul 1979, Fujioka 1984, Mock 1985). Thus, the hatching spread of 2–3 days for the Shag is slightly longer than that commonly found among passerines but is similar to that of many nonpasserine species.

Ricklefs (1968) compared the nestling growth rates of 105 species. The Shag nestlings had a higher growth rate than most other seabirds. On the other hand, the growth rate of nestlings of many raptors and passerines is as high, or higher.

We calculated the relative importance of egg volume and hatching asynchrony, for different values of these two parameters, with a growth rate like that of the Shag. For the Shag and species with similar nestling growth rates, a difference of 0–10% in egg volume will account

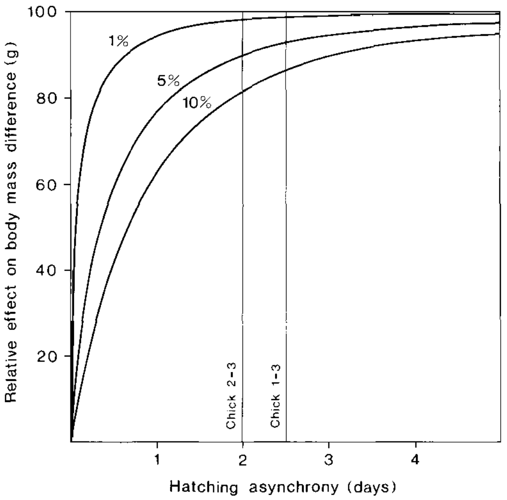

Fig. 3. Relative effect of hatching asynchrony on the initial differences in the body mass of pairs of Shag chicks. The residual effect (proportion above the curves) is due to differences in egg size. The curves represent differences in egg size of 1, 5, and 10%. The vertical lines indicate the mean hatching intervals between chicks.

for less than 25% of the overall difference in nestling body mass when the hatching interval exceeds 1.5 days (Fig. 3). We conclude that hatching asynchrony is the most important factor in determining the initial size differences between consecutive chicks. This finding may apply to many other bird species. One exception may be gulls (see Parsons 1972) because their nestlings grow significantly slower than Shag nestlings (Ricklefs 1968). In addition, the third egg of many gulls is 5-10% smaller than the first two (Paludan 1951, Coulson 1963, Barth 1967, Vermeer 1969, Davis 1975, Mills 1979, Runde and Barrett 1981).

Correspondence between egg volume and nestling growth rate.—A positive correlation exists between egg volume and the survival rate of the chicks in several species (Parsons 1970, 1975; Nisbet 1973, 1978; Schifferli 1973; Davis 1975; Williams 1980). Few studies have tested whether a similar relationship exists between egg volume and nestling growth rate. Schifferli (1973) experimentally neutralized the effects of hatching asynchrony and of parental quality in the Great Tit (*Parus major*) and found that chicks hatched from small eggs grew more slowly than chicks hatched from large eggs. Nisbet (1978) experimentally interchanged eggs of the Common Tern (*Sterna hirundo*) and the Roseate Tern (*S. dougallii*), from nests of birds laying very large eggs to those of birds laying very small eggs, and vice versa. He found differences in the growth rates of nestlings from the two groups, for both species. In the Common Tern the chicks hatched from small eggs but, reared by large-egg parents, exhibited the highest growth rates, whereas the opposite situation was found for the Roseate Tern. Williams (1980) found that Great Skua (*Catharacta skua*) chicks hatched from small eggs grew at a slower rate than those hatched from large eggs (unmanipulated broods). It is difficult to determine the relative importance of the egg characteristics and parental quality on nestling growth rate from these studies. For many species, including the Shag (Amundsen and Stokland unpubl.), interpretations are complicated by the fact that the variation in egg size is larger between than within clutches.

We found no significant difference in the growth rates of chicks hatched from small or large eggs during the first 5 days (Table 2), when body mass increased to more than 3 times the mass at hatching. Significant differences were found at ages of 6 and 7 days (Table 2).

The adaptive significance of a size hierarchy.—The intrabrood size differences in the Shag probably confer no particular advantage with respect to numbers and quality of chicks reared (Amundsen and Stokland 1988). In comparisons of synchronous and asynchronous broods, asynchronous hatching was the superior pattern for only 1 of 12 species. Therefore, we sought an explanation of hatching asynchrony unconnected with the brood-rearing period. In particular, selection pressures to begin incubation before laying is completed (egg predation, thermal stress, defense of nest) deserve critical investigation.

If a large size difference between the nestlings is advantageous for individuals of a certain species, however, a successive decrease in egg size during the laying sequence may be adaptive (Ricklefs et al. 1978, O'Connor 1979, Clark and Wilson 1981, Zach 1982). Hatching asynchrony is a highly important factor in determining the size differences found among chicks. We found that egg size contributed a 2.5-h increase in asynchrony. A lack of even further increases in the degree of hatching asynchrony is curious.

The pattern of an increase in egg size with the laying sequence has been found to be common among passerines (e.g. Howe 1976, Rydén 1978, Ojanen et al. 1981, Slagsvold et al. 1984, Weatherhead 1985, Haftorn 1986). Howe (1976: 1206) argued that "Increased egg size with laying sequence and asynchronous hatching are antagonistic forms of differental investment within the brood. Presence of both adaptations suggests that young are maintained as long as possible along with a pattern of initial investment which insures starvation of some individuals if food is insufficient to raise the entire brood." His view gained some support in subsequent studies (Rydén 1978, Horsfall 1984), but was challenged by Clark and Wilson (1981: 270), who emphasized the problem of reconciling "hatching asynchrony and egg weight as two adaptations working simultaneously in opposite directions." We agree with Clark and Wilson (1981) on this point.

If large, intrabrood nestling size differences are not selectively advantageous, then asynchronous hatching must be a side effect of selection on another trait and should be considered as an evolutionary constraint with regard to these differences. Accordingly, egg size will be a mechanism to reduce the intrabrood size difference and egg size should increase with laying order (Clark and Wilson 1981). The decrease in egg size found in seabirds and others is inconsistent with this hypothesis.

Slagsvold and co-workers (1984) suggested that asynchronous hatching evolved for different reasons among various groups of birds. They argued that in most passerines, where egg size increases with laying order, asynchrony represents an evolutionary response to nest predation. In seabirds, raptors, and other species in which egg size decreases progressively, asynchrony reflects unpredictable food conditions. Alternative explanations exist (Amundsen and Stokland 1988). Hatching asynchrony, and differences in egg size, may be responses to pressures other than those connected with size differences among nestlings. In many species these two factors counteract each other. Size differences within broods may be neutral or, in some species, even disadvantageous.

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