VARIATION IN THE EGGS OF THE SHAG (*PHALACROCORAX ARISTOTELIS*)

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The size and shape of eggs are important parameters in avian ecology, yet few studies have been made on their biological significance. Under natural conditions the size of eggs both within a clutch and between clutches laid by different individuals show considerable variation in shape and size and therefore in the quantity and presumably in the quality of their contents. Richdale (1955, 1957) has shown that the Yellow-eyed Penguin (*Megadyptes antipodes*) shows marked changes in egg size related to the age of the females; similar effects have been found in the Kittiwake (*Rissa tridactyla*) (Coulson, 1963), the Gannet (*Sula bassana*) (Nelson, 1966), and the Short-tailed Shearwater (*Puffinus tenuirostris*) (Serventy, 1967). In each case the older birds laid larger eggs and had a greater breeding success, but the role of the larger eggs in this increased success is not known.

Other studies (e.g. Kendeigh et al. (1956) on the House Wren (*Troglodytes aedon*); Paludan (1952) on *Larus argentatus* and *L. fuscus*; Gemperle and Preston (1955) on *Sterna hirundo*; Coulson (1963) on *Rissa tridactyla* have shown appreciable differences in the size and shape of eggs in a clutch according to their position in the clutch sequence.

This paper presents a detailed analysis of the factors correlated with variation in egg size and shape in the Shag (*Phalacrocorax aristotelis*) and it has been possible, by using birds of known age, to determine the effects of age and the date of laying on the size of eggs in both this species and the Kittiwake. This type of investigation is an essential prelude to a study of the effects of egg size and quality on the viability of the embryo and of the newly hatched chick.

It is difficult to determine the age composition of bird populations because no method exists of measuring the age of individual birds. Growth of the young is rapid and once this short period of development is completed there are no further size changes to use as ageing criteria. Some species retain immature plumages for several years, but even here the change to adult plumage probably reflects the bird's physiological state rather than its actual age. None of the ageing methods used in other vertebrates, such as change in eye lens weight, size, annual layers in the teeth, scales, or otoliths, are applicable so far as is known to birds.

It is now known for several birds, particularly long-lived species such as seabirds, that many aspects of their breeding biology and breeding success are closely correlated with age. As a result of the difficulties encountered in ageing individual birds, a method that can be used to estimate the age composition of a population or a group has considerable potential in ecological studies. For instance the shape and breadth of Kittiwake eggs are correlated with age, and these measurements have been used to show that birds forming a new colony were young individuals (Coulson, 1963). A similar method is applicable to the Shag, and it is suggested that this method may have wide application in avian studies.

Methods

The Shags used in this study were part of a ringed and aged population breeding on the Farne Islands, Northumberland, England. Almost all the young Shags reared on the Farne Islands have been ringed since 1950 and many of these have returned to breed. Adult birds have also been ringed, and the survivors of those marked in the early 1950s although of uncertain maximum age, belong to the oldest group used in the analysis. Adults that were first ringed when 2 or 3 years old can be correctly aged by the amount of immature plumage retained on the breast and wings. Once birds become established breeders on the Farnes they are color-ringed for easy identification. Breeding birds are readily sexed by the shape of the bill, overall size, and, more conveniently, by the call (a croak in the male, a hiss in the female).

Almost 1,000 eggs of birds of known age were measured in 1963 and 1964. Subsequent analysis showed no significant difference between the results obtained in each of the 2 years, so that the values for these years have been grouped. Smaller samples of eggs measured in 1965, 1966, and 1967 have been used only for part of the analysis.

The eggs were marked soon after they were laid, and the maximum length and breadth of each egg in the clutch was recorded (using vernier callipers to the nearest 0.1 mm). Shags frequently lose eggs from their nests and many eggs from incomplete clutches were measured. These were excluded from the study of size change in the clutch sequence, but they were used to study the influence of age on the size of eggs.

The egg volumes have been calculated from the length and breadth, but the correction factor has been adjusted to allow for the imperfect ellipsoid form of the Shag egg: egg volume $= 0.51 \times b^2 \times l$, where b is the maximum breadth and l the maximum length of each egg. The shape index $= b/l \times 100$.

The typical clutch size in the Shag is three eggs, but clutches of two and four eggs are sufficiently numerous to allow a study of all three clutch sizes. Unpublished data show that clutch size does not change with age in the Shag. Most females start to breed when 3 years old, a few breed when 2 years of age, and some delay breeding until they are 4 or even 5 years old.

Owing to the effects of natural mortality, fewer birds are available in the older age classes and it is necessary to group age classes to give samples of adequate size. Throughout this paper the 4 and 5 year olds are grouped, as are those 6, 7, and 8, and all birds over 8 (oldest 16 years) form a single category.

Variation in Egg Size and Shape According to Clutch Size and Laying Sequence

A total of 127 complete clutches of three eggs, 38 clutches of four eggs, and 26 clutches of two eggs, were measured where the laying sequence of each egg in the clutch is known. Table 1 gives the mean length, breadth,

TABLE 1

RELATION OF MEASUREMENTS AND SHAPE INDICES TO LAYING SEQUENCE AND AGE OF FEMALE

Age of female (years)	Laying sequence	Length (mm)	Breadth (mm)	Volume (cc)	Shape index	No. of clutches
A. 2-egg clutches						
2 or 3	1	60.64	*37.61*[1]	*43.75*	62.0	7
	2	61.06	37.39	43.53	61.2	
4 or 5	1	61.54	37.86	44.99	61.5	8
	2	62.39	*37.95*	*45.83*	60.8	
6, 7, or 8	1	59.67	38.43	44.94	64.4	11
	2	60.88	*38.65*	*46.38*	63.5	
B. 3-egg clutches						
2	1	60.04	37.37	42.76	62.2	8
	2	60.26	*37.78*	*43.87*	62.7	
	3	60.83	37.49	43.60	61.6	
3	1	62.19	38.08	45.99	61.2	15
	2	62.16	*38.65*	*47.36*	62.2	
	3	62.20	38.27	46.47	61.5	
4 or 5	1	61.35	37.95	45.06	61.9	35
	2	61.89	*38.51*	*46.81*	62.2	
	3	61.43	38.37	46.12	62.5	
6, 7, or 8	1	61.49	38.63	46.80	62.8	37
	2	62.95	*39.01*	*48.86*	62.0	
	3	62.44	38.71	47.72	62.0	
Over 8	1	61.66	38.65	46.98	62.7	32
	2	62.18	39.09	48.46	62.9	
	3	62.77	*39.12*	*48.99*	62.3	
C. 4-egg clutches						
2 or 3	1	61.12	36.22	40.89	59.3	5
	2	60.02	36.90	41.68	61.5	
	3	59.94	*36.94*	*41.71*	61.6	
	4	60.42	36.52	41.10	60.4	
4 or 5	1	59.67	37.61	43.05	63.0	14
	2	59.84	*38.36*	*44.91*	64.1	
	3	60.53	38.09	44.79	62.9	
	4	59.06	37.87	43.20	64.1	
6, 7, or 8	1	61.01	38.23	45.48	62.7	10
	2	62.10	38.37	46.63	61.8	
	3	62.16	*38.42*	*46.79*	61.8	
	4	61.72	36.88	42.81	59.8	
Over 8	1	60.29	38.52	45.62	63.9	9
	2	61.86	39.06	*48.13*	63.1	
	3	61.43	*39.16*	48.04	63.7	
	4	61.24	38.57	46.46	63.0	

[1] Figures in italics show the maximum breadth and volume in each clutch.

volume, and shape index of these eggs in relation to the age of the females laying them. In clutches of two eggs the second egg tends to be broader and has a greater volume, although the differences are small.

In three-egg clutches the first egg is the smallest of the three, the second egg is usually the largest, and the third intermediate. Clutches of three eggs laid by birds over 8 years old are an exception to this because the third egg of the clutch is, on average, the largest. The proportion of these old birds in which the last egg of the clutch is the largest is significantly higher ($P < 0.05$) than in the younger birds, but surprisingly no trend towards this is evident in the 6- to 8-year-old birds; further information is required.

In clutches of four eggs the second and third eggs are typically the largest and are similar in shape and size. Usually the first egg is smaller than the final egg, but the second and third eggs in a four-egg clutch are both smaller than the second egg in a clutch of three.

These measurements confirm that the two-egg clutches are not the result of the first egg of the typical clutch being lost, because they do not correspond to the second and third eggs of a clutch of three in which the final egg is distinctly smaller. (The loss of the second egg can be excluded by considering the time interval between the laying of the eggs.) It is also clear that three-egg clutches tend to have larger eggs than those in four-egg clutches laid by females of comparable age (Table 1).

All clutch sizes show little indication of changes in the shape index within each clutch; differences in egg breadth are usually accompanied by comparable changes in the length.

Attention should be drawn to the discrepancy in the breadth and volume of the eggs laid in three-egg clutches by 2- and 3-year-old females; the figures given in Table 1 are appreciably larger than those shown in Table 3. The young birds that have had all three eggs of the clutch measured are typical of birds that have retained their nests and eggs, whereas the large sample in Table 3 includes many birds that failed to keep a complete clutch and some that failed to complete a clutch before the eggs and nest were lost. Seemingly those young birds that lay larger eggs also tend to be more successful breeders.

Seasonal Variation in Egg Size

Kittiwake eggs laid at different times of the breeding season show a progressive change in mean breadth, shape index, and volume, all three decreasing as the breeding season progresses (Coulson, 1963). A comparable analysis of the measurements for the Shag shows a similar seasonal decrease in the breadth and volume of the egg and a suggestion of a similar trend in the shape index, although the length of the eggs fluctuates irregularly (Table 2). In 1963 the later breeding birds laid eggs 4.7 cc smaller than those laid at the beginning of the breeding season, a 10 per cent change in the mean egg volume. A similar situation occurred in 1964 when the decrease in volume was 5.1 cc or 11 per cent through the laying period.

TABLE 2
VARIATION IN SIZE AND SHAPE OF SHAG EGGS IN RELATION TO THE TIME AND YEAR OF LAYING

	1–14 April	15–28 April	29 April–12 May	13–26 May	After 26 May	No. of clutches
A. Seasonal effects, 1963–67 combined						
No. of clutches	33	114	115	72	47	
Mean breadth in mm	38.8	38.7	38.3	37.6	37.1	
Mean length in mm	61.4	61.8	62.1	61.2	60.9	
Mean volume in cc	47.1	47.2	46.6	44.1	42.8	
Shape index	63.2	62.6	61.7	61.5	61.1	
B. Variation in egg volume by year and season						
1963	47.1	47.5	46.6	44.0	42.4	134
1964	None laid	47.4	47.3	43.0	42.3	136
1965	47.1	46.2	45.7	45.5	42.5	53
1966	None laid	None laid	45.0	46.2	47.1	27
1967	47.1	47.8	43.6	44.3	—	31

INFLUENCE OF AGE AND TIME OF LAYING ON EGG SIZE AND SHAPE

The size and shape of all Shag eggs laid by females of known age are given in Table 3. The breadth and volume show a marked increase with age, and a similar trend is evident in the length and the shape index. The young birds also tend to show more variability in egg breadth. The change in volume with age is more pronounced than any of the other egg characteristics. The percentage difference in volume of eggs laid by 2-year-old females and those over 8 years of age is 12 per cent; the changes in length and breadth are 2.8 per cent and 5.0 per cent respectively.

The time of breeding in the Shag is age specific, with the oldest birds tending to breed first and the young ones several weeks later. Thus the change in egg breadth and volume throughout the season closely fits that with age; and the late breeding young birds produce the smallest eggs. It may be that young individuals lay smaller eggs as a direct effect of their age; alternatively season, or some factor closely associated with season,

TABLE 3
MEAN MEASUREMENTS AND SHAPE INDICES OF EGGS LAID BY FEMALE SHAGS OF KNOWN AGE

Age of female	Length (mm)	Breadth (mm)	Volume (cc)	Shape index	Sample size	SD of length	SD of breadth
2	60.5	37.1	42.5	61.3	109	2.8	1.2
3	61.7	37.6	44.5	60.9	102	2.0	1.4
4 or 5	61.3	38.3	45.9	62.5	290	2.3	1.3
6, 7, or 8	61.8	38.5	46.7	62.3	257	2.4	1.1
Over 8	62.2	39.0	48.3	62.7	190	2.3	1.1
Total	61.57	38.28	46.01	62.17	948		

TABLE 4
INFLUENCE OF TIME OF LAYING ON EGG SIZE AND SHAPE IN FEMALES OF KNOWN AGE

Age of female	Time period	No. of clutches	Mean length (mm)	Mean breadth (mm)	Volume (cc)	Shape Index
Over 8	April	40	61.98	39.02	47.2	63.0
	Later	15	61.76	38.60	46.0	62.5
6, 7, or 8	April	33	62.46	38.81	47.1	62.1
	Later	22	61.43	38.49	45.5	62.7
4 or 5	April	37	62.02	38.65	46.3	62.3
	Later	50	61.45	38.03	44.5	61.9
3	April	11	62.67	38.39	46.2	61.3
	Later	18	61.72	37.14	42.5	60.2
2	April	1[1]	(61.0)	(39.0)	(46.4)	(63.9)
	1–22 May	10	60.58	37.38	42.3	61.7
	After 22 May	13	59.25	36.88	40.3	62.2

[1] The eggs in this clutch were the largest of the 24 clutches laid by 2-year-old females.

could influence the egg size, and the young birds may lay small eggs not because of their age, but because they breed late. These two effects, age and season, can be separated by comparing the eggs laid at different times of the season by females of the same age. This analysis is presented in Table 4 where each age class is divided into early and late layers. In every class the earlier layers laid broader and larger eggs; the average difference is just over 2 cc or 4.5 per cent. Despite this difference, a direct

TABLE 5
EGG VOLUME OF KITTIWAKE ACCORDING TO BREEDING EXPERIENCE AND DATE OF LAYING

		May			
		1–14	15–21	22–28	After 28
Breeding experience					
First	No.	10	16	13	12
	Volume (cc)	41.8	40.8	40.8	40.2
Second	No.	27 (1–21)		47	
	Volume	42.2 (1–21)		41.4	
Third	No.	18 (1–21)		7	
	Volume	44.6 (1–21)		42.2	
Fourth and Fifth	No.	11 (1–21)		11	
	Volume	45.3 (1–21)		43.4	

TABLE 6
WEIGHT OF FEMALE KITTIWAKES IN RELATION TO DATE OF EGG LAYING[1]

	Number	Mean (g)
1–7 May	24	338
8–14 May	35	344
15–21 May	47	344
22–28 May	23	341
29 May–4 June	15	345
After 4 June	15	349
Prebreeders	38	345

[1] All birds (except prebreeders) were weighed after egg laying (usually 2–3 weeks later). No significant difference exists in the mean weight shown in each weekly period.

effect of age on egg volume and breadth is still evident as these values increase with age within April as well as in the later period. Clearly two factors influence egg size, the age of the female and the time of laying.

As a result of this conclusion for the Shag, the data used in the investigations of egg size in the Kittiwake (Coulson, 1963) have been reanalyzed to determine the situation in this species. The results presented in Table 5 show that, in addition to the older females laying the larger eggs, the later breeding birds in any age group lay smaller eggs than do the early breeders. One possible explanation for the late-laying females producing smaller eggs is that these birds are smaller or in a poorer physical condition. The weights of these Kittiwakes taken when they were caught for ringing and analyzed in relation to the date of egg laying in that year (Table 6) show differences in the weights of females breeding at different times of the breeding season. Thus the variations in egg size apparently result from differences in the physiology of the individual, particularly that associated with egg production (see Coulson, 1968 for other differences in the quality of breeding Kittiwakes).

Newly laid Shag eggs are often streaked rather heavily with blood; apparently about 18 per cent of the females rupture blood vessels during egg extrusion. An analysis of 597 freshly laid eggs in 1964 showed no significant correlation between the presence of blood and egg size or age of the parent. The stresses resulting from the final extrusion of the eggs are therefore unlikely to be important factors in determining egg size.

SEASONAL DECLINE IN CLUTCH VOLUME

The seasonal decline in egg volume of the Shag is, at 10–11 per cent, much greater than the 4.5 per cent decline in the Kittiwake (Coulson, 1963). On the other hand the seasonal decline in clutch size of the Shag is very much less marked than in the Kittiwake (Coulson and Potts, MS; Coulson and White, 1961). The explanation for the relatively small

TABLE 7
INTERVAL BETWEEN START OF NEST BUILDING AND LAYING IN THE SHAG, FARNE ISLANDS, 1965

Start of laying	Sample size	Mean number of days (± SD)
9–16 April	20	33.0 ± 21.4
17–24 April	30	30.2 ± 24.1
25 April–2 May	26	28.6 ± 17.4
3–10 May	22	22.5 ± 10.0
11–18 May	11	30.7 ± 28.2
19–26 May	10	23.0 ± 14.0
27 May–7 June	7	11.1 ± 12.2

decline in egg volume of the Kittiwake is probably that the decline in clutch size frees more material to compensate egg volume. If the clutch size of the Kittiwake were constant, then the eggs laid at the end of the season would be almost half size and such a reduction in size would clearly prejudice the survival of the embryo or chick.

A comparison of the seasonal decline in the volume of material used in eggs for three species of seabirds with quite different feeding methods is given in Figure 1. A seasonal decline is apparent in the surface feeding Kittiwake, in the Shag, a littoral nekton predator, and in the Great Skua (*Catharacta skua*), an aerial predator. There is no evidence of a seasonal decline in food availability or food supply during the laying period of either Shag or Kittiwake, and certainly no such change in the food supply of the Great Skua (Bayes et al., 1964). It should also be pointed out that the seasonal decline in clutch size and egg volume in the Shag and Kittiwake is regular from season to season, though the size of the stock of prey species, predominantly *Ammodytes*, is large but irregular (Macer, 1966). Further, the oldest Shags are feeding young at the time that the later breeding birds are egg laying. If food were short at this time, one might expect to find evidence of it in the mortality rate of chicks in the nest, but there is no evidence of chick starvation other than a small amount among very young chicks from inadequate parental attention. Therefore a hypothetical seasonal decline in food supply would not account for the observed seasonal decline in clutch volume.

While it is difficult to correlate the decline in clutch volume or egg size through the season with environmental factors, such changes are easily correlated with factors intrinsic to the population. It seems particularly relevant to point out that the interval between nesting and laying is very closely correlated with size of the eggs (Table 7, Figure 2). It seems probable therefore that one reason why eggs laid by young and late-laying Shags are relatively small is that these birds have insufficent time for the

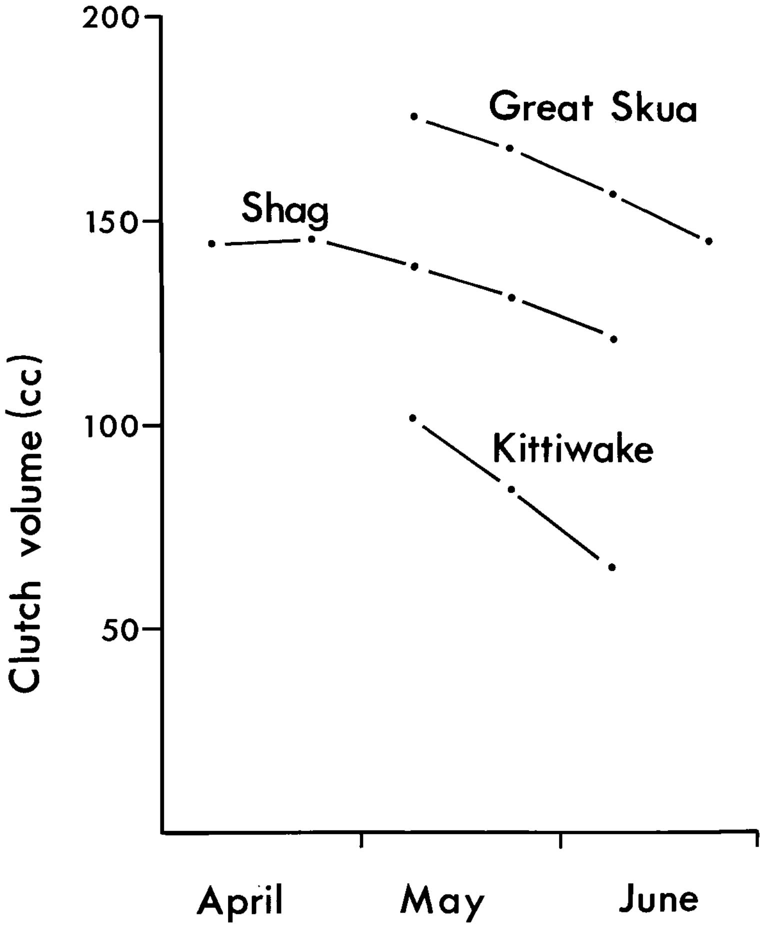

Figure 1. Mean volume of egg material in complete clutches laid by the Kittiwake, Shag, and Great Skua in a single colony at different times of the breeding season. Clutch volume is calculated by multiplying the mean clutch size in each time period by the mean egg volume for that period. Data for the Kittiwake and Shag collected on the Farne Islands, those for the Great Skua on the Faroes (Bayes et al., 1964).

maximum development and functioning of the reproductive system. This explanation would also account for the overall lower clutch size in Kittiwakes breeding in the arctic and forced to nest late by adverse climate and a late thaw in certain years (Belopol'skii, 1961).

VARIANCE OF THE BREADTH

In the Kittiwake it was shown that the variance of the breadth within each clutch of three eggs increases with the age of the parents, apparently

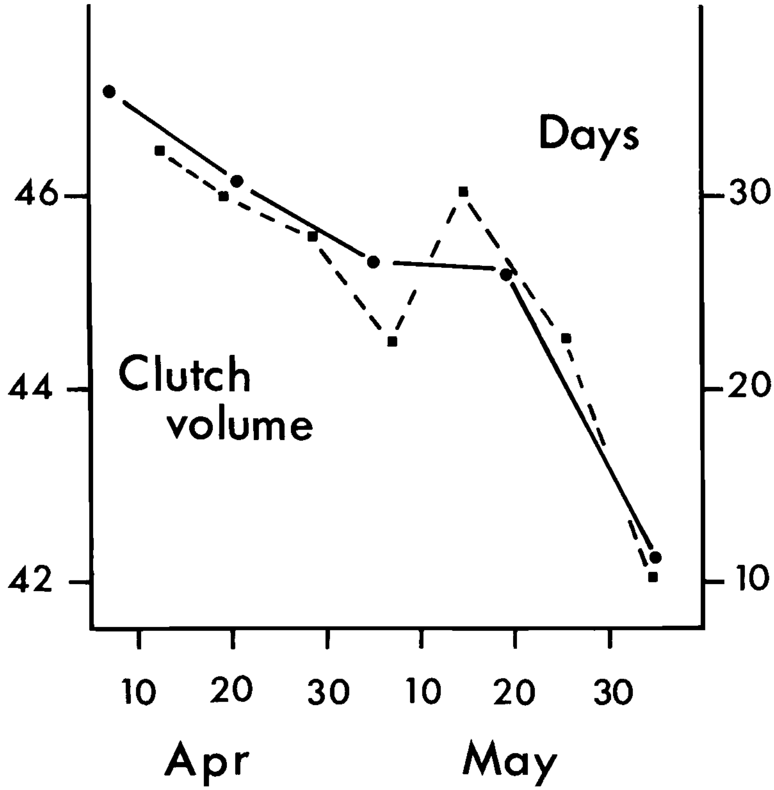

Figure 2. Relationship between seasonal trend in clutch volume in the Shag (dots and solid lines) and the length of time in days between start of nest building and laying of the first egg (squares and dotted lines). Data collected on the Farne Islands in 1964.

caused by the third egg becoming increasingly different from the other two (Coulson, 1963). A similar investigation of three-egg clutches in the Shag (Table 8), showed the reverse trend, the variance being largest in

TABLE 8

THE WITHIN SAMPLE VARIANCE OF THE BREADTH OF SHAG CLUTCHES OF THREE EGGS IN RELATION TO THE AGE OF THE FEMALE LAYING THEM

Age of female	Sample size	Mean within-clutch variance
2	10	0.345
3	17	0.307
4 or 5	35	0.220
6, 7 or 8	37	0.214
over 8	32	0.196

clutches laid by 2-year-old females and progressively decreasing to the oldest (over 8) group. Although the variability within an age class is large, the variance of the breadth in each clutch could be used to estimate the age composition of populations.

No significant correlation existed between the difference in the breadth in clutches of two eggs and the age of the female laying them.

APPLICATION OF EGG BREADTH TO DEMONSTRATING AGE COMPOSITIONS OF TWO GROUPS

In 1965 egg measurements were collected for two groups of breeding Shags on the Farne Islands, those breeding in the center and those nesting on the periphery of a colony. Measurements were taken only over a restricted period of time to reduce the influence of time of laying on egg size. The mean breadth of eggs from the birds nesting in the center was 38.49 mm (SE $\pm$ 0.16) for those on the periphery 37.72 (SE $\pm$ 0.13). The difference in the mean breadth of these two groups is highly significant ($P < .01$), implying that the birds nesting on the periphery are mainly young birds, those in the center predominantly old ones.

As many of the birds breeding on the Farne Islands are ringed as nestlings and are of known age, this conclusion has been confirmed, but it took many years of ringing and study to obtain the aged population, whereas the sample of eggs can be measured in a single day.

The use of egg measurements in this manner or in that described by Coulson (1963) offers a rapid means of estimating the age composition of groups or making comparisons between two groups of birds. Although this method does not have the same accuracy as using aged individuals, it provides a means of estimating the age distribution of birds in colonies from comparison with an aged population.

DISCUSSION

In many species of birds, including the Shag, breeding success is closely related to age. This study has shown that the Shag and the other species that have been investigated lay progressively larger eggs as they increase in age, but no attempt has been made to investigate the influence of egg size on the viability of the young, or even on the yolk:albumen ratio. The breeding success of the Red Grouse (*Lagopus scoticus*) has been shown to be low when the egg size is low (Jenkins et al., 1967). In both the Kittiwake and the Shag much the greater part of nestling mortality occurs in the first few days after hatching, and apparently part of this early mortality is related to the size and quality of the egg, particularly the yolk, rather than to inability of the parents to care for the young. This aspect of the study is being investigated. In the domestic fowl about 40 per cent of the total yolk is still available to the chick at the time of hatching (Romanoff and Romanoff, 1949; Romanoff, 1960). In the Adelie Penguin (*Pygoscelis adeliae*) about 50 per cent of the yolk is available on hatching and this has been shown to be a useful reserve if the "off duty" bird is prevented from bringing food to the chick until some time after hatching (Reid and Bailey, 1966).

Clearly the individuals in a population of seabirds do not reach the same state of reproductive drive. In any year individuals can be found that reach only an intermediate stage in the breeding cycle, e.g. birds that take up a nest site but do not pair, pairs that do not build nests, and those that lay but do not incubate. It is also evident that this reproductive drive is intimately bound up with the timing of the breeding cycle of individuals. Typically the early breeders in any season lay larger eggs or larger clutches, and have a high success. At the other end of the scale are the birds that return to the colony generally at the end of the laying season, but do not pair up, or, as in many 1-year-old Shags, pair but do not nest or lay. The solution of many problems, such as the change in egg size, appears to depend on an understanding of the mechanisms that determine the timing of laying, particularly the widely observed tendency for younger birds to start their reproductive cycle later in the season. Possibly the age specificity of timing is dependent on age-specific rates of gonad development or hormone synthesis, but what advantage their slower rate of development or their later nesting or laying has in younger birds is being investigated. Much more study is needed of the behavioral aspect.

Acknowledgments

We wish to thank the Farne Islands Committee of the National Trust for permission to carry out studies on the Shags breeding on the Farne Islands, Northumberland. We are also grateful to Grace Hickling for much assistance in identifying details of Shags ringed on the Farne Islands by the Northumberland & Durham Natural History Society over the past 15 years.

This study was made with the assistance of a grant from the Nature Conservancy which is gratefully acknowledged.

Summary

A study of factors causing variation in the length, breadth, volume, and shape index of eggs laid by Shags (*Phalacrocorax aristotelis*) was made on a population where most of the birds were of known age and sex. Well defined patterns of size and shape occur in clutches of three and four eggs where the first egg is the smallest in the clutch and the last egg next in size.

Within any clutch size the breadth and the volume of eggs laid by females increase progressively as they become older. The difference between the mean volume of eggs laid by 2-year-old females and those over 8 years old is 13 per cent. This change in egg breadth or volume can be used to determine the age composition of birds in different groups or populations.

As older birds breed earlier than young ones, the volume of eggs laid throughout the breeding season decreases progressively. This decrease is only partially caused by the age of the females, and within an age class the early breeding birds lay larger eggs. A similar effect has been found in the Kittiwake (*Rissa tridactyla*).

The Shag, Kittiwake, and the Great Skua (*Catharacta skua*) all show a marked decrease in the amount of material females use in egg production as the breeding season advances, and this trend is probably common to many species of seabirds. That this trend results from food shortage is unlikely, and it is suggested that it results from the different degrees of reproductive development reached in seabirds, earlier breeding birds showing a higher reproductive drive. Further detailed studies are needed to determine the significance of egg size in relation to reproductive success in birds.

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