FACTORS DETERMINING THE NUMBER AND SIZE OF EGGS LAID BY THE HERRING GULL

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Egg-laying in birds has been classified into two general groups according to whether eggs lost during the laying period can be replaced. Indeterminate layers can compensate for a loss of eggs by continuing to lay until their nest contains a definite number of eggs, whereas determinate layers lay a set number of eggs irrespective of how many or few eggs are in the nest. Despite these well-defined categories of laying, the Herring Gull (*Larus argentatus*) has been claimed by Davis (1942) and Tinbergen (1953) to be a determinate layer, while experiments by Paludan (1951) indicated it was an indeterminate layer. Previously, Salomonsen (1939) had induced Herring Gulls to lay a series of eggs, in one case 16 eggs in 39 days, while more recently Harris (1964) recorded laying of up to eight eggs in succession. However, true protracted laying requires that the interval between successive eggs should be the same as that between eggs in a normal clutch. Although Weidmann (1956) achieved this pattern with continuous laying in the Black-headed Gull (*L. ridibundus*), Paludan's (1951) results were less complete.

In view of this conflicting evidence, I studied the ability of the Herring Gull to lay more than the normal clutch of three eggs on the Isle of May, Scotland. This investigation was planned not merely to determine whether the species is an indeterminate layer, but also the factors affecting the number and size of eggs laid by gulls. Further information was obtained from an egg removal program designed to delay the breeding season, which showed that both clutch size and egg size decreased as the season advanced (Parsons 1975a). My earlier studies had shown an inverse relationship between egg size and post-hatching chick mortality (Parsons 1970), which contributes to the higher mortality suffered by chicks from the small third eggs laid by Herring Gulls (Parsons 1975b). I therefore wished to investigate reasons why the third eggs laid in this species are smaller than the first two. This study was to include an analysis of the variability in yolk content, as well as egg size, since yolk is the food reserve for the developing embryo. Yolk lipids were also examined,

as they form the largest part of the organic solid matter in the yolk, and are indispensible to the life and growth of the chick embryo (Romanoff and Romanoff 1949).

STUDY AREA

The Isle of May (lat 56°10'N, 2°35'N) lies 10 km off the Fife coast in the mouth of the Firth of Forth, Scotland, and is approximately 1.6 km long by 0.5 km wide. The investigations took place in 1968–69, when an estimated 13,000 pairs of Herring Gulls nested on the island, most commonly in dense sub-colonies around the rocky perimeter.

METHODS

Nests under study were labelled as soon as the first egg was laid and this, and later eggs, were individually marked. During egg removal or additional experiments, no nests were used for more than one experiment. The normal interval between laying of consecutive eggs was obtained from visiting 85 nests every 12 hours during the laying period. In a further 160 nests, all completed clutches were removed so that the interval required for relaying could be determined. None of the 24 color-banded adults moved from their territories following the loss of their eggs, but relaid on their original nest sites. There was therefore no confusion between relaying and new pairs laying their first clutches.

The ability of Herring Gulls to lay a series of eggs was investigated by carrying out various egg removal and addition experiments in 454 nests visited every 12 hours during the laying period. The lengths and breadths of all eggs were measured to 0.1 mm, and all removed eggs were weighed to 0.01g, hard-boiled and separated into shell, yolk and albumen which were likewise weighed. Egg volume was calculated from the formula: length $\times$ breadth^2 $\times$ 0.476 (Harris 1964). The yolks and albumens of 112 first-laid and 71 repeat clutches of three eggs were also weighed. The division between yolk and albumen breaks down during the early stages of incubation, rendering the separation of these constituents by hard boiling an impossible task. It was therefore necessary to remove each egg of a clutch within 12 hours of being laid, prior to the onset of incubation. Each egg removed was replaced by another egg so that normal laying was not affected.

Hexane-soluble lipids were extracted from the yolks of a sample of 15 clutches using the soxhlet technique with a petroleum-ether mixture.

The first, second and third eggs laid in a clutch will be termed the "a-," "b-," and "c-eggs" and subsequent eggs laid during continuous layings will be called the "d-egg" (fourth), "e-egg" (fifth) and so on. The yolks and albumens of eggs will also be referred to as, for example, the "a-yolk" and "a-albumen," or "b-yolk" and "b-albumen." A clutch of two eggs is termed "C/2," a clutch of three, "C/3" and means are given where possible ± one standard error.

TABLE 1. Number of days between the removal of the first clutch and the laying of the a-egg of the repeat clutch, according to the time in the season and the state of incubation at the time of removal.

	Mean interval in days	
Date of laying first clutch	State of incubation at removal of first clutch	
	Directly after laying c-egg	After 15 days incubation
	P – NS	
Before 25 May	12.6 ± 0.2 (37)[a]	13.0 ± 0.1 (77)
	$P < 0.05$[b]	$P < 0.001$
After 24 May	13.5 ± 0.4 (25)	14.7 ± 0.4 (21)
	$P < 0.02$	

[a] Number of clutches shown in brackets and the mean interval given ± one standard error.
[b] Significance of difference between each mean.

RESULTS

NORMAL LAYING

Interval between eggs and between repeat layings. Although the clutch size of the Herring Gull decreases through the season, it is most commonly made up of three eggs. The average intervals between laying a- and b-eggs, and b- and c-eggs were 48.6 ± 1.0 and 49.1 ± 1.0 hours respectively, and similar to the figure given by Drent (1967).

If a Herring Gull loses its eggs after incubation has started, it can usually produce a substitute clutch after a fairly well-defined interval. The mean interval from the removal of the first clutch to the laying of the a-egg of the repeat clutch was 13.2 ± 0.1 days. The data were also analysed to investigate which factor caused the greatest delay in relaying; firstly the amount of time spent incubating before the loss of the eggs, and secondly the time of the season that relaying took place (table 1). Birds that laid their first clutch late in the season (after 25 May) took significantly longer to relay than those laying earlier in the season ($P < 0.05$), and this difference was increased in those whose first clutches were removed after 15 days incubation ($P < 0.001$). The number of days spent incubating prior to removal did not have a significant effect early in the season, but for later-laid clutches relaying took longer for those that had incubated for 15 days ($P < 0.02$). The lack of variation between the shortest (12.6 days) and longest (14.7 days) relaying interval is of considerable interest. It indicates that the physiological mechanisms involved in preparing for a repeat laying, following the loss of a first clutch, have a fairly regular time periodicity irrespective of the length of the incubation period before this loss.

TABLE 2. The percentage of relaying in relation to the lateness of the season and the time interval between the laying of the first clutch and its removal.

Approximate date of removal	17 May		27 May	7 June	
Days incubating before removal	0–4	5–8	9–14	15–20	21–24
No. clutches removed	84	37	67	47	21
No. clutches relaid	59	18	29	18	7
% relaid	70	49	43	38	33

Ability to relay. Not all gulls relaid, and this ability waned as the season progressed, so that by late June very few relaid clutches were found. The proportion relaying after egg removal is shown in table 2. It was not possible to separate the variation due to the interval of incubation prior to removal and to the lateness of season. The results show that the percentage of birds relaying decreases progressively as the season advances, or as the days between laying and removal of eggs approaches the full incubation period of 27–30 days.

Relaying requires a repetition of the behavioral activities which precede the completion of a clutch. Usually this clutch is laid in the original or renovated nest. It is possible that if this nest as well as the first clutch were removed, an additional strain might be placed on the adults. I tested this by dividing a subcolony into two sections, both with eggs at the same stage of incubation, and removing all the eggs on the same day (6 June). In one area all of the 238 nests as well as eggs were removed and only 84 repeat clutches were subsequently found. This 35% relaying was significantly less than the 50% which was recorded from the 195 nests from which only the eggs were taken ($P < 0.01$).

DETERMINATE OR INDETERMINATE LAYING

Laying of a fourth egg. Occasionally full nests were found with four-egg clutches, though the frequency was on average only 1 in 450. The color and laying interval of these eggs indicated that in each case the four eggs were produced by the same female. Moreover, during normal laying in an undisturbed area of 903 nests, a fourth egg was laid in 9 out of 16 nests when the a-egg disappeared soon after laying. To investigate the ability of Herring Gulls to lay this d-egg, the a-egg was removed within 12 hours of being laid in 79 nests. Sub-

sequent eggs were left in the nest and in 47 cases a d-egg was laid. This result closely resembles the occurrence in the undisturbed control area (59 and 57% respectively). The mean interval between the laying of c- and d-eggs was 53.2 ± 1.3 hours which was significantly longer than the normal laying interval ($P < 0.002$), but it was still a continuation of the same clutch. A significantly smaller proportion of birds were capable of laying a d-egg later in the season (72 and 48% before and after 19 May respectively, $P < 0.05$). In 110 nests, both the a- and b-eggs were taken, but only after the b-egg had been laid. In this case 89 laid only one further egg (the c-egg), 20 produced a d-egg and only one an e-egg.

These experiments indicated that the Herring Gull is capable of supplementing the loss of an a-egg, by laying a further three eggs to produce a normal-sized clutch. However, if the a-egg remained in the nest during the laying period, then no additional d-egg was laid, even when both the b- and c-eggs were removed. Similarly, in the majority of cases, the d-egg was withheld when the eggs were removed after the laying of the b-egg. Paludan (1951) stated that this happens if the egg removal occurs later than 24 hours after the laying of the b-egg.

Under natural conditions, the a-egg is usually the most vulnerable and is lost more frequently than the other two. From 800 C/3s studied, the disappearance of eggs within the first week of laying was 34, 15 and 8 for a-, b- and c-eggs respectively. Predation by other Herring Gulls is the most common form of egg loss at this stage, before the full incubation behavior is functioning, and the least protection is given when the a-egg is the sole occupant of the nest. As a result it suffers significantly higher loss than the b-egg ($P < 0.01$). Also, if heavy rain follows the laying of an a-egg, the adult may cover this egg with new nest material, in an attempt to make a dry nest. I saw this in six out of the 800 nests, and in each case the a-egg was completely buried and subsequently not incubated. However, in situations such as these, the Herring Gull can compensate for the loss of this a-egg by laying a d-egg.

Protracted laying. To evaluate whether more than a fourth egg can be laid by Herring Gulls, 102 nests were visited every 12 hours and all eggs laid were successively taken, each egg therefore within 0–12 hours of being laid. Nests were restricted to those in which laying commenced before 14 May, so that any bias due to the seasonal decrease in clutch and egg

TABLE 3. The total number of eggs laid by each pair during the continuous egg removal experiment.

	No. eggs laid									
	1–3	4	5	6	7	8	9	10	11	12
No. nests	13	8	13	20	19	17	6	4	1	1

size could be reduced to a minimum. Only 13 gulls failed to lay more than the normal three eggs (table 3). In 68 nests (66%) six or more eggs were laid, the equivalent of at least a second clutch. In general, the pattern of laying fell into five categories, based on the position of the longest interval between the laying of consecutive eggs as follows:

i) between the c- and d-eggs, giving the appearance of a C/3 followed by subsequent eggs—29 nests.

ii) between the d- and e-eggs, similar to the laying of an initial C/4—39 nests.

iii) between the e- and f-eggs, so that the longest interval seemed to separate 5 eggs from later laid eggs, even though this interval was quite small—11 nests.

iv) those nests in which a C/4 (5 nests), or a C/3 (5 nests) or even fewer (8 nests) were all that were laid.

v) a miscellaneous group which fitted none of these categories—5 nests.

When the pattern of laying was grouped in this manner, the mean interval between the laying of the a-egg and each of the following eggs was calculated, to give the average laying pattern for each category. This could then be compared with normal repeat laying shown by 63 nests in the same area, from which all eggs were removed after laying of the c-egg and a repeat C/3 subsequently laid (table 4). In all the three major patterns (i, ii, iii) the longest interval between eggs was significantly shorter than that between repeat layings ($P < 0.001$). Nevertheless, the groups that initially laid C/3 (i) and C/4 (ii) resembled an abbreviated form of relaying, rather than protracted laying. Only in the third group (iii) was a more continuous production of eggs recorded, in which the interval between the laying of each egg was similar to that of normal laying. Of the 102 pairs studied, 57 (56%) produced at least four eggs in succession, so that the laying of a d-egg occurred in the same frequency as in the previous experiment.

These results show that the Herring Gull is not a determinate layer, since it is capable under certain conditions of laying more than

TABLE 4. The mean pattern of laying for three categories following continual removal of eggs compared with normal repeat laying. In each category, the mean interval between the laying of apparent groups of eggs is shown ± one standard error (days). 0—denotes egg laying.

Category	No. nests	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Normal repeat laying	63	0		0		0←						12.7 ± 0.2							→0	0		0		
Continuous removal																								
(i) C/3 ...	29	0		0		0←			8.4 ± 0.5						→0		0		0					
(ii) C/4 ...	39	0		0	0				0←		7.2 ± 0.4					→0			0	0			0		
(iii) C/5 ...	11	0		0	0			0		0←	4.6 ± 0.4				→0			0		0					0

a set number of three eggs. However, only a small proportion of those studied were capable of indeterminate laying, and the experiment illustrated how individual gulls react differently to the same situation. It is possible that some of the variability in laying pattern was due to the interval between laying of the a-egg and its removal, since some eggs would have been taken almost immediately, and others nearly 12 hours after being laid. Nevertheless, there appears to be considerable natural variation in the ability of gulls to lay eggs, and some females are able to lay more and possibly larger eggs than others.

With this in mind, the mean weights of the first three eggs laid in the different laying categories were compared. Gulls which laid an initial C/3 (i) produced eggs that were on average lighter than those from birds which laid a C/4 (ii) and the same was true in the previous experiment to produce a d-egg (table 5). Moreover, the eggs of the protracted layers (iii) were significantly heavier than those laid as an initial C/3 ($P < 0.01$). In addition, when nests were grouped according to the total number of eggs laid by each female during the continuous removal experiment, those

laying the largest number of eggs laid, on average, the heaviest a-eggs (table 6). Although the normal clutch size in the control areas was three eggs, some gulls lay C/2; and the first two eggs of 50 C/3 were significantly larger in calculated egg volume than the two eggs of 30 C/2 (Parsons 1975a). Therefore, Herring Gulls which, either in the control or experimental areas laid smaller clutches, also tended to lay lighter eggs. A further difference was noted between females laying in the various categories. Those that initially laid a C/3 (i), not only laid lighter eggs but also laid fewer subsequent eggs than those that laid a C/5 (iii) ($P < 0.05$, table 7).

Experiments to reduce clutch size. In order to determine whether the stimulus of eggs in the nest could affect the normal laying pattern, eggs were added to nests before and during laying. An extra egg was placed in 54 nests as soon as the a-egg was laid. This had no effect on the total number of eggs laid, for in 48 nests three eggs were laid, while in the remaining 6 nests only two eggs were laid. The average clutch size was therefore 2.89 eggs, which was the same as in the control areas. Nor did the addition of more than one

TABLE 5. The size of the first three eggs laid by the various categories in the continuous egg removal experiment and in the experiment to produce a d-egg ± one standard error. The size of eggs not removed from nests was measured by egg volume calculated from length and breadth rather than egg weight.

	N	Egg wt. (g)			% difference between a- and c-eggs
		a-egg	b-egg	c-egg	
Continuous removal					
(i) C/3 .. interval	29	86.7 ± 1.1	84.4 ± 1.2	82.1 ± 1.2	5.3 ± 0.9
(ii) C/4 .. interval	39	89.1 ± 0.8	87.3 ± 1.0	84.7 ± 1.0	5.0 ± 0.8
(iii) C/5 .. interval	11	90.9 ± 1.7	90.6 ± 1.4	89.0 ± 2.3	2.0 ± 1.1
		Egg volume (ml)			
d-egg experiment					
C/3, no d-egg laid	31	79.0 ± 0.9	76.1 ± 1.0	73.3 ± 0.9	7.2 ± 1.0
C/4, d-egg laid	38	79.0 ± 1.0	77.6 ± 1.0	75.0 ± 1.0	5.2 ± 0.8
Control laying	50	78.8 ± 1.0	78.1 ± 1.0	70.6 ± 1.0	10.4 ± 0.9

TABLE 6. Mean egg and yolk weights of the last eggs laid in a series during the continuous removal experiment and in control clutches of C/3 and C/2. Eggs are grouped according to the total number laid by an individual gull, and the mean weights of the a-eggs are also shown.

No. eggs laid by each gull	No. nests	Mean a-egg wt. (g)	Mean wt. of last-laid egg (g)	Mean yolk wt. of last-laid egg (g)
Control laying				
2	30	86.8 ± 1.60	84.7 ± 1.25	21.3 ± 0.39
3	112	90.6 ± 0.73	83.9 ± 0.65	21.9 ± 0.17
Continuous removal				
4	8	85.5 ± 1.45	84.4 ± 2.77	20.7 ± 0.78
5	13	85.6 ± 1.50	79.7 ± 1.31	19.5 ± 0.56
6	19	87.8 ± 0.98	82.7 ± 1.06	20.4 ± 0.32
7	18	90.0 ± 1.02	83.0 ± 1.60	19.8 ± 0.41
8	17	90.5 ± 1.15	81.6 ± 1.16	19.8 ± 0.35
9	6	86.3 ± 2.47	78.4 ± 1.04	19.5 ± 0.65
10–12	6	91.0 ± 2.30	81.8 ± 1.80	20.0 ± 0.28

egg make any difference (87 nests). However, when eggs were added to 22 nests before the beginning of laying, the clutch size was reduced and in at least three cases completely suppressed. In the latter, these additional eggs were incubated for several weeks though they were eventually found to be addled. On six occasions, the eggs were rejected by the adults, but in the remaining 16 nests a mean of 1.81 eggs were laid. This was significantly smaller than the expected clutch size ($P <$ 0.001).

Paludan (1951) recorded a similar result, and stated that the introduced eggs are accepted about 9 days before laying of the a-egg, which corresponds to the time when the follicles enter their final growth phase. Prior to this time, eggs introduced to the nest are eaten or removed. This indicates that developing follicles can be suppressed by the brooding on introduced eggs. It is therefore possible that the variations in egg size within a normal clutch are also a result of physiological and hormonal changes that occur with the onset of incubation.

EGG SIZE AND LAYING SEQUENCE

The smaller c-egg. Although there are large variations in the weights of newly-laid Herring Gull eggs (65–110g), the variation within a clutch is very little, since gulls laying large a-eggs tend to lay large b- and c-eggs. This is illustrated by the correlation between the weights of a- and b-eggs ($r = 0.87$, N $= 112$, $P < 0.001$) and a- and c-eggs ($r = 0.75$, N $= 112$, $P < 0.001$) within a clutch. Nevertheless, the c-egg is significantly and, on average, 11% smaller than the a-egg (Parsons 1972), whereas the b-egg is rarely more than 2% smaller than the a-egg. This pronounced dis-

parity between the sizes of a- and c-eggs has been recorded elsewhere in the Herring Gull (Harris 1964, Barth 1967), and also in other gull species, such as the Lesser Black-backed Gull (*L. fuscus*)—9.4% (Paludan 1951), Laughing Gull (*L. atricilla*)—7.0% (Preston and Preston 1953) and Black-legged Kittiwake (*Rissa tridactyla*)—7.3% (Coulson 1963). In the past, small last-laid eggs have been attributed to a deficiency of material, especially in research into the domestic fowl (Romanoff and Romanoff 1949). However, Paludan (1951) pointed out that the eggs of Herring Gulls that produced protracted layings did not show the decrease in volume anticipated by the situation in the c-egg.

When the a-egg was removed soon after it was laid, the subsequent difference between a- and c-eggs was significantly less marked. For example, in the experiment to produce a d-egg, the c-egg was only 5.2% smaller than the a-egg compared with 10.4% in control layings taking place at the same time in the season ($P < 0.001$, table 5). A similar result was recorded during the continuous egg removal experiment, with the least difference between a- and c-eggs occurring in the group that produced protracted layings—(iii) (2.0%,

TABLE 7. The mean number of eggs laid per nest for each of the laying categories in the continuous removal experiment, ± one standard error.

Pattern	No. nests	Mean no. eggs laid per nest
(i) C/3 followed by ___ 2.9 eggs*	29	5.9 ± 0.3
(ii) C/4 followed by ___ 3.2 eggs	39	7.2 ± 0.2
(iii) C/5 followed by ___ 4.1 eggs*	11	9.1 ± 0.4

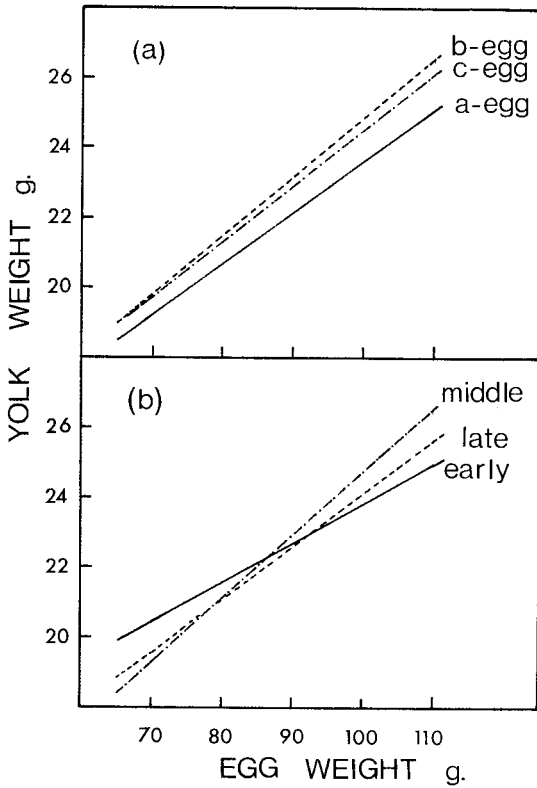* Significance of difference between (i) and (iii)—$P <$ 0.05.

FIGURE 1. (a) Regressions of yolk weight against egg weight according to the laying sequence for 112 first-laid clutches.

$$y \text{ (a-yolk)} = 9.01 + 0.146x \quad r = 0.63$$
$$y \text{ (b-yolk)} = 7.98 + 0.168x \quad r = 0.62$$
$$y \text{ (c-yolk)} = 8.51 + 0.160x \quad r = 0.61$$

(b) Regressions of yolk weight against egg weight for eggs laid early (up to 8 May, N = 150), middle (9–17 May, N = 126) and late (after 17 May, N = 60) in the season. ·

$$y \text{ (early)} = 12.51 + 0.114x \quad r = 0.48$$
$$y \text{ (middle)} = 6.19 + 0.183x \quad r = 0.71$$
$$y \text{ (late)} = 8.95 + 0.150x \quad r = 0.74$$

table 5). Indeed, even the ninth egg laid in this group was only 7.4% smaller than the a-egg. The c-eggs laid during these experiments were therefore on average significantly larger than those laid by the controls ($P < 0.02$). When eggs were left in the nest after removal of only the a-egg, it was the d-egg which showed a reduction in size, so that it was significantly smaller than the c-egg (68.7 ± 1.0 and 75.0 ± 1.0 ml respectively, $P < 0.001$), but similar in size to c-eggs laid in the control clutches i.e. 70.6 ml, table 5. However, when all eggs were removed as they were laid, the d-egg did not show this size decrease, but was the same size as the c-egg (75.4 ± 1.0 and 75.5 ± 1.00 ml respectively) and significantly larger than the d-eggs previously mentioned i.e. 75.4 ml compared with 68.7 ml respectively, $P < 0.001$.

The addition of an extra egg after the laying of the a-egg did not result in a further reduction in the size of the c-egg, which was on average 9.6 ± 0.9% smaller than the a-egg in this case.

These comparisons lead to the conclusion that when the a-egg is left in the nest, a smaller c-egg is laid, whereas the removal of the a-egg as it is laid results in a c-egg of similar size as the first two. It is therefore suggested that the presence of the a-egg stimulates brooding behavior, and that this onset of incubation affects the size of the c-egg. Although Harris (1964) stated that effective incubation probably does not start until the c-egg is laid, a study on the Isle of May showed that effective incubation of the a-egg occurs even before the b-egg is laid (Parsons 1972). As a result, there is complete degeneration of the fourth follicle as well as the laying of a c-egg of reduced size.

Component parts of eggs. Harris (1964) suggested that c-eggs were merely scaled down a- or b-eggs. Similarly, Paludan (1951) argued that the depressive action of incubation on the c-follicle was based on the assumption that small eggs correspond to small yolks. To investigate which part of the c-egg was being affected during the onset of incubation, eggs were divided into the two components of yolk and albumen.

Although yolk and egg weight were correlated ($r = 0.69$, N = 318, $P < 0.001$), larger eggs contained relatively less yolk and more albumen than smaller eggs, and absolutely greater quantities of all constituents. Between the extremes of egg size, the albumen varied from 40–75g but the yolk from 16–26g. This would indicate that the a- and b-eggs, being of similar size within a clutch, should have on average the same amounts of yolk and albumen, while the smaller c-egg should have less yolk by weight, but more as a percentage of egg weight. However, the regressions of yolk against egg weight for 112 first-laid clutches shows a trend for the a-egg to contain relatively less yolk than the other two (fig. 1). Therefore, although a- and b-eggs had similar mean weights, their mean yolk weights differed significantly by 0.7g or 3.2% ($P < 0.01$, table 8). This is further illustrated by the regression of b-yolk against a-yolk weight within the same 112 clutches (fig. 2). The c-egg was, as expected, significantly smaller than the first two ($P < 0.001$, table 8), and its

TABLE 8.   Mean egg, yolk and albumen weights of 112 first-laid clutches of three eggs.

	Laying sequence		
	a-egg	b-egg	c-egg
Mean egg wt. (g)	90.60 ± 0.73	90.01 ± 0.68	83.89 ± 0.65
Mean yolk wt. (g)	22.37 ± 0.18	23.11 ± 0.18	21.87 ± 0.18
% yolk	24.5	25.7	26.1
Mean albumen wt. (g)	60.19 ± 0.60	59.30 ± 0.68	55.31 ± 0.90

yolk was on average 1.2g or 5.1% lighter than the b-yolk ($P < 0.001$). However, the difference between the a- and c-yolk weights, while significant (0.5g or 2.2%, $P < 0.05$), was far less than would be expected from the difference in egg weights (table 8, fig. 2). Instead, it was the albumen content rather than the yolk which contributed to this difference, as the mean a-albumen weight was 4.9g or 8% greater than the c-albumen ($P < 0.001$, table 8).

If broodiness during the laying period affected the c-follicle, the resulting yolk would be expected to be smaller than the a-yolk. Conversely, when broodiness is inhibited by removing the a-egg, the c-yolk should show an increase in weight corresponding to the ensuing increase in the size of the c-egg. The c-eggs from 45 clutches laid in the control area were compared with the same number of c-eggs laid at the same time of the season during the continuous removal experiment, and these expected differences were not apparent (table 9). In the latter, the egg weight and albumen plus shell weights were significantly heavier ($P < 0.05$ and $P < 0.01$ respectively) than the controls, whereas the yolk weights re-
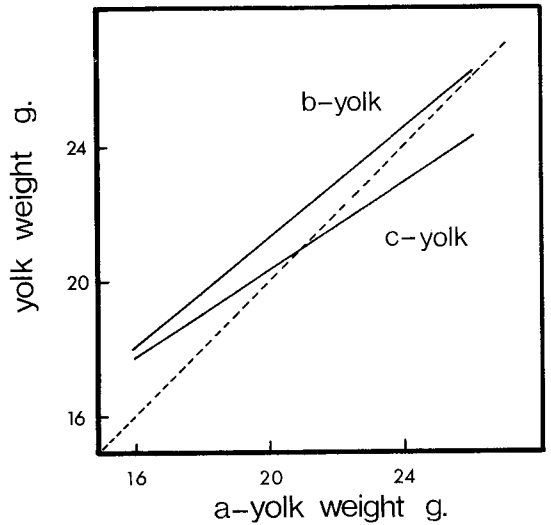
TABLE 9.   Comparison of the weight of yolk and albumen plus shell of c-eggs laid under control conditions and during the continuous egg removal experiment ± one standard error.

	N	Mean c-egg wt. (g)	Mean albumen plus shell wt. (g)	Mean yolk wt. (g)
Control	45	82.6 ± 1.0	60.7 ± 0.8	21.8 ± 0.3
Expt.	45	85.7 ± 1.0	63.9 ± 0.9	21.9 ± 0.2
Probability of difference between control and experiment		$P < 0.05$	$P < 0.01$	N.S.

FIGURE 2.   Regressions of b- and c-yolk weights against a-yolk weight within a clutch (N = 112). The dotted line represents yolks of equal weight.

y (b-yolk) = 4.81 + 0.82x   r = 0.79
y (c-yolk) = 7.29 + 0.65x   r = 0.65

mained the same. This indicates that the depressive effect of incubation during the laying period is restricted to the albumen, although it obviously causes complete degeneration of the d-follicle under normal conditions.

I have previously noted that egg size decreased through the season (Parsons 1975a). This decrease was least in the a-egg and most in the c-egg except in repeat clutches, in which the seasonal effect was less marked and mainly due to a reduced size of the a-egg. These seasonal variations were also reflected in the yolk weights, in which the difference between early- and late-laid eggs was greatest in the c-yolks ($P < 0.05$, table 10). In addition, the difference between a- and c-yolks increased through the season (0.4 to 2.9%), although the yolk weights of relaid a- and c-eggs were the same (table 10). Regressions of yolk weight against egg weight showed that eggs of the same size had a similar composition early and late in the season, whereas in the middle of the laying period there was relatively more yolk in larger eggs (fig. 1).

Variations in the soluble lipid content of eggs were examined in 15 clutches of three eggs (table 11). The soluble lipids represented approximately 60% of the dry yolk weight, and were positively correlated with egg weight (lipid = 0.09 egg wt − 1.03, r = 0.81, N = 45, $P < 0.001$). This strong correlation indicates that egg size is an appropriate guide to the energy available to the chick embryo. The

TABLE 10. Mean yolk weights of first-laid and repeat clutches of three eggs according to the date of laying, and the percentage difference in weights of a-and c-eggs and b- and c-eggs.

First-laid clutches	N	Mean yolk wt. (g)			% difference	
		a-egg	b-egg	c-egg	a : c eggs	b : c eggs
Laid before 9 May	50	22.40 ± 0.23	23.23 ± 0.25	22.32 ± 0.22	0.4%	3.9%
Laid 9–17 May	42	22.16 ± 0.32	23.06 ± 0.34	21.71 ± 0.31	2.0%	5.9%
Laid after 17 May	20	22.03 ± 0.35	22.85 ± 0.38	21.39 ± 0.36	2.9%	6.4%
Repeat clutches	71	20.94 ± 0.17	22.11 ± 0.20	20.94 ± 0.19	0%	5.3%

mean yolk and lipid weights were least in the c-egg, although the results from this small sample were not significant (table 11).

Follicle development prior to laying. Paludan (1951) examined an ovary just before the first ovulation, and measured the diameters of the four largest follicles. Using these figures, an approximate reconstruction of the events prior to the laying of the c-egg can be made (fig. 3). Ovulation in most birds occurs just after the laying of the previous egg, and so successive ovulations take place at an interval of the same magnitude as that between eggs (Sturkie 1954). The ovum (yolk) of the c-egg is therefore released into the body cavity two days before the actual egg is laid, and two days after laying of the a-egg. At the time that the a-egg is laid, the c-follicle has almost attained maximum size, and so unless broodiness elicits an immediate and depressive response, it will have no effect on the ultimate size of this follicle.

It is during the two days after ovulation that fertilization, followed by secretions of albumen, shell membranes and shell take place in the oviduct (Sykes 1959). Without chemical analysis of the albumen, it is not possible to conclude whether protein deposition or water uptake or both contribute to the differences between the albumen weights of these c-eggs. Nor is it easy to understand how the onset of incubation can cause these differences. It is, however, known that in the domestic fowl the oviduct is more sensitive than the ovary to factors adversely affecting egg formation (Romanoff and Romanoff 1949). Also, it is the rapidly-growing follicles that maintain the oviduct in a highly functional state, by the secretion of estrogen. Broodiness is effected by the secretion of an anterior pituitary hormone, prolactin, which also decreases the production of gonad-stimulating hormones. Without the latter, the d-follicle and others degenerate and the ovarian secretion of estrogen is depressed. This chain of events might account for the slightly less productive oviducal materials laid down for the c-egg in the control conditions.

Finally, I observed that the last egg laid by most individuals was very similar in size and yolk content irrespective of the total number of eggs that preceded it. Those that laid only five eggs produced an e-egg no larger than the 10th egg of a more prolific layer (table 6). The relatively constant size of this last-laid egg is demonstrated by the small variation about the mean egg weight compared with a- and b-eggs. For example, 2 standard deviations of the last-laid eggs were 10g, compared with 16g and 15g for a- and b-eggs respectively. An equivalent situation occurred in the control nests, in which the b-egg of a C/2 was not significantly larger than the C-egg of a C/3 (table 6).

DISCUSSION

The Herring Gull is not a determinate layer as suggested by Davis (1942) and Tinbergen (1953), but contains more developing follicles than the three ovulated during normal laying. This allows the female to replace the loss of the a-egg, providing that such loss occurs soon after laying. This appears to be an adaptation to the vulnerability of the a-egg before full incubation behavior is effected. However, the Herring Gull is not a true indeterminate layer,

TABLE 11. Mean wet and dry yolk weight and hexane-soluble lipid weight of 15 clutches of three eggs.

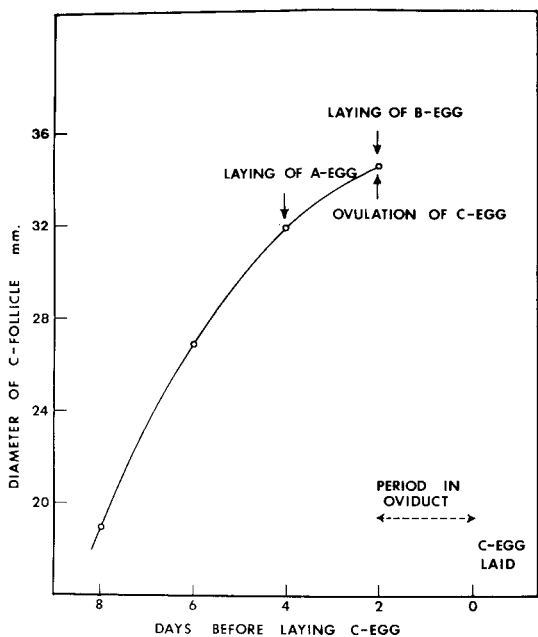|	Laying sequence		
	a-egg	b-egg	c-egg
Mean wt. g			
Egg wt.	90.6 ± 2.6	91.2 ± 2.4	84.0 ± 2.4
Wet yolk	22.7 ± 0.8	23.0 ± 0.9	21.8 ± 0.8
Dry yolk	11.5 ± 0.4	11.6 ± 0.5	11.1 ± 0.4
Lipid	6.92 ± 0.26	7.02 ± 0.29	6.75 ± 0.28
Lipid × 100/egg wt.	7.6%	7.7%	8.0%

FIGURE 3. Estimated change in the diameter of the c-follicle prior to laying of the c-egg, illustrating the timing of the events during the laying sequence (based on measurements of follicle size from Paludan 1951).

for although 56–59% of birds were able to lay a d-egg, continuous production of eggs was evident from only a small proportion of those studied. Furthermore, no additional eggs beyond the usual three are laid if the a-egg remains in the nest, even if both b- and c-eggs are removed.

The stimulus provided by the presence of the a-egg in the nest initiates the onset of incubation, and this results in a significant reduction in the amount of albumen laid down in the last egg laid in a clutch. The 11% size difference between a- and c-eggs is therefore mainly due to a smaller albumen rather than yolk content. Removal of the a-egg on laying does not encourage these changes to take place, and a c-egg more similar in size to the other two is laid.

The c-egg is therefore more comparable to the a-egg in terms of energy reserves of the yolk than would be expected from its size. The c-yolk was on average 2.2% lighter than the a-yolk and contained approximately 2.5% less soluble lipids. The difference between the mean a- and c-chick hatching weights was 11–12% (Parsons 1975b), which is larger than might be expected from the differences in yolk content, although the data were obtained from a sample of only 21 broods.

The c-chick is known to suffer a higher mor-

tality than its siblings and, as egg size and post-hatching chick mortality are inversely related in the Herring Gull, the smaller size of the c-egg was regarded as a contributory factor (Parsons 1970, 1975b). However, during an egg transfer experiment, it was shown that c-chicks hatching first survived markedly better than those hatching last, but the survival (58.5%) was still less than that of a-chicks hatching first (64.7%). Similarly, a-chicks hatching last survived better than c-chicks hatching last (49.3 and 41.3% respectively, Parsons 1975b). I suggest, therefore, that although the poorer survival of the c-chick under normal conditions is attributable mainly to asynchrony at hatching, the small but significant difference between a- and c-yolks shown during the study may account for the remaining differential mortality.

It is possible that the smallness of the c-egg is adaptive. Intraspecific predation of eggs is a major cause of egg loss in the Herring Gull (Paynter 1949, Brown 1967) so an early onset to incubation could reduce the losses suffered by unattended a- and b-eggs. By laying a c-egg with reduced albumen rather than yolk, the incubation period of the smaller egg becomes less than that of the larger a- and b-eggs, since incubation period is related to egg size (Parsons 1972). Initially, the development of the c-egg lags behind the b-egg by 32 hours, but this is reduced to 18–24 hours at hatching (Parsons 1972). Any post-hatching mortality attributable to asynchronous hatching would therefore be lessened by a reduction in the hatching interval between b- and c-chicks.

It is difficult to determine whether the significantly larger size of the b-yolk has any effect on the post-hatching survival of the b-chick. The b-chick survives as well as the a-chick even though it hatches up to 12 hours later (Parsons 1975b). No studies were carried out to compare the mortality of a- and b-chicks hatching at the same time, which could indicate whether the larger b-yolk confers an advantage on the b-chick. In the 21 broods weighed as each chick hatched, I found no difference in the weights of a- and b-chicks (Parsons 1975b), but this aspect requires further study.

Reasons for the laying of a significantly larger b-yolk are difficult to determine. A possible cause is an increase in physiological efficiency as development passes from the a-follicle to the b-follicle. However, on this assumption, the yolks of c-eggs and of protracted layings should be the same size as the b-yolk. Instead, the c-yolks have been shown

to be 5% smaller. Even the 11 gulls which laid in a protracted manner (pattern iii) produced a- (22.1g), c- (22.2g) and d-yolks (22.1g) that were on average smaller than the b-yolk (23.4g). This may be an indication of the stresses involved in laying a clutch of three eggs totalling about 260g, approximately 25% the weight of a female gull. Only a small proportion were induced to lay continuously, each bird producing at least 9 eggs totalling more than 780g over a 22-day period. Although more than four follicles are maturing prior to egg laying in the Herring Gull (Paludan 1951), most birds during the continuous removal experiment postponed further layings after producing 3 or 4 eggs, even though the non-laying period was less than the normal interval between first and repeat clutches. It is therefore possible that follicles must reach a certain size before ovulation occurs. After laying 3 or in many cases 4 eggs, a female may require a resting period during which food reserves needed for further egg production can be obtained. It is not known how much stored food reserves can be utilised for egg formation in the Herring Gull, but Murton et al. (1974) discussed the role of calcium as a possible limiting factor in egg laying of the Wood Pigeon (*Columba palumbus*) and other nutrients may be involved.

A further indication that follicle size may limit the number of eggs laid by an individual was gained from this study. The number and size of eggs laid by Herring Gulls varied considerably, due to differences in the physical abilities and also to the age of the females (Davis 1975). However, despite this, the last eggs laid by any female gull during these experiments were similar in weight, as were the yolk weights. Therefore, although broodiness would normally limit the clutch to three eggs, there also appears to be a minimum egg size which prevents laying of a full clutch of three by some individuals. This may be an adaptation to avoid the laying of progressively smaller eggs with little chance of producing fledged young.

Birds which laid only two-egg clutches were not examined to find out whether other follicles were present which could have been laid, although the evidence from protracted layings would suggest that this was so. As the season progresses, the size of eggs decreases and the greatest decrease in yolk weights is in the c-yolk. Possibly as a result of this, more C/2 are laid with a resulting decrease in mean clutch size. Indeed, there is evidence that the egg size of late and repeat layers does not de-crease below a minimum level, and this level is similar to size of the smallest eggs laid earlier in the season. In consequence, the clutch size reaches its lowest level of, on average, 1.7 eggs per nest and, as the season advances, this is followed by the cessation of laying (Parsons 1975a).

The question then arises as to why egg and clutch size are reduced as the season advances. The availability of food is unlikely to have an effect, since the eventual cessation of laying occurs at a time when there is sufficient food for adults to feed young as well as themselves. In addition, the numbers of Herring Gulls have been increasing at a rate of 10–20% per year in the British Isles and elsewhere (Harris 1970), which indicates a favorable food supply. The age of the female accounts for some of this seasonal variability. Davis (1975) demonstrated an increase in clutch-volume with age until females were 8 years old, after which there was a decline, and Drost et al. (1961) showed that young Herring Gulls breed later in the season than older birds. It would be interesting to know whether females of the same age lay larger and more eggs earlier in the season as has been shown in the Shag (*Phalacrocorax aristotelis*) and Black-legged Kittiwake (Coulson et al. 1969).

Also in the Shag, the interval between nesting and laying is closely correlated with size of eggs, which indicates that young and late laying birds may have insufficient time for the maximum development and functioning of the reproductive system (Coulson et al. 1969). The same may occur in the Herring Gull, for late-laid eggs contained the least amount of yolk, especially in the c-egg. It is possible that late layers begin ovulation prematurely, and that the disadvantages of producing smaller and fewer eggs are thereby offset against the advantages of synchronised laying, since chicks hatching during the peak of the season were the most successful (Parsons 1975a).

A seasonal decrease in clutch size has been demonstrated in other species, and is regarded by Perrins (1970) as an adaptation to the poorer chance of raising young later in the season. Pre-fledging success of Herring Gulls on the Isle of May has been shown to be related more to the synchronisation of nesting than to an adverse effect of the lateness of the season. However, recent evidence supports Perrins' argument, for post-fledging mortality in one out of three year classes studied increased progressively with lateness of hatch-

ing (Parsons et al., in press). In this year also, broods of three fledged chicks survived less well to age of breeding than broods of two.

The availability of food required for egg formation is unlikely to be a major factor regulating the onset of the laying period in the Herring Gull. Early-nesting birds lay the largest eggs and yolks, and also the most eggs per clutch. This, and evidence from the number of eggs Herring Gulls are capable of laying, indicates that females could lay even earlier than they do. However, since early breeders suffer greater egg and chick loss than those laying in the middle of the season, very early laying is selected against.

SUMMARY

The Herring Gull (*Larus argentatus*) can compensate for the early loss of its first laid egg by laying an additional egg, so that the normal clutch size of three eggs is incubated. It is therefore not a determinate layer, and some individuals are capable of the protracted laying of a series of eggs. The presence of the first-laid egg stimulates the onset of incubation and the cessation of laying beyond the normal clutch size. Broodiness appears to result in a significant reduction in the amount of albumen rather than yolk laid down in the third and last-laid egg. This egg is therefore significantly smaller than the first two under normal laying conditions, but is not so small when the onset of incubation is delayed by the early loss of the first egg. It is suggested that the smallness of the third egg reduces its incubation period and the degree of asynchrony at hatching. Although there is considerable variability in the number and size of eggs laid by Herring Gulls, the last eggs and yolks laid during protracted laying were similar in size. While the normal clutch size is three eggs it appears that a minimal egg size limits the clutch to two or fewer eggs in some individuals. This may be an adaptation to prevent the laying of small eggs with little chance of producing fledged young.

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