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Observations on the breeding biology of the Razorbill

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INTRODUCTION

THE BREEDING BIOLOGY of the Razorbill *Alca torda* has been little studied. Even the incubation and fledging periods were only inaccurately known until the work of Keighley and Lockley (1947 and 1948). However, Paludan (1947) gave a good general account of the biology, dealing especially with behaviour, and short papers have since appeared on individual aspects of breeding. Some of the latter will be mentioned later in the present paper which is based on work carried out on Skokholm, Pembrokeshire, during the summer of 1964.

PRE-NESTING PERIOD

In 1964 Razorbills were already on the cliffs by 29th February. No significant correlation could be found between the numbers inshore and the prevailing weather on any particular day, though they tended to remain at sea when it was extremely rough. Lockley (1953) observed the same tendency among Puffins *Fratercula arctica* and this also applies to Guillemots *Uria aalge*.

The Razorbills visited the cliffs more frequently towards mid-April and most had settled there by the end of that month. When my observations started on 29th February they were already closely associated in pairs, each male maintaining around his mate an area from which all others were driven. Conder (1950) called this area the 'mated female distance'. It is not clear whether pair formation occurred at sea or during the first visits to the cliffs. There was no evidence of promiscuity during the pre-nesting period.

Nest sites were probably taken up during or soon after the first visits to the cliffs. This point was clearly checked in the Guillemot, in which single bridled birds in three colonies occupied the same positions on the ledges from the time of arrival right through the breeding season. Pairs of Razorbills stood by future nesting sites throughout the pre-breeding period, and three colour-ringed individuals nested in mid-May in sites which they had occupied from at least mid-April.

Copulation was first seen on 27th March, but did not become frequent until after 21st April and was last observed on 15th May.

EGGS AND INCUBATION

The first egg was found on 21st April, an early date, first layings on Skokholm normally occurring between 8th and 14th May. Witherby *et al.* (1941) gave the first laying dates as 9th or 10th May, exceptionally late March. The laying span for eggs in the main study area covered a period of 38 days from 5th May to 10th June, although over 80% of laying occurred in a period of 17 days in mid-May (10th to 26th May).

Moyse (1962) and Diamond (1963), both working on Skokholm, discussed the dimensions of Razorbill eggs. In the present study 186 eggs were measured; the results are shown in table 1. A histogram of the ratio of the length to the diameter gives no indication that the shape of the egg is independent of its size as suggested by Moyse. The 1964 results agree very closely with those of Diamond in this respect.

The average weight of 47 fresh-laid eggs was 92 grams, with extremes of 80 and 107 grams. There appeared to be no seasonal variation in the weights of eggs, both light and heavy eggs occurring throughout the period. Paludan (1947) obtained an average weight of 95.6 grams for fresh-laid eggs of the slightly larger race *Alca torda torda*. His figure represents 12.7% of the average body weight of an adult, compared to 14.5% for *A. t. islandica* in the present study. Brun

Table 1. Measurements of 186 eggs of Razorbills *Alca torda* on Skokholm, Pembrokeshire, in 1964

Minimum length	66.5 (×45.2) mm.
Maximum length	80.5 (×49.2) mm.
Mean length	72.3 mm.
Minimum diameter	42.2 (×80.0) mm.
Maximum diameter	51.2 (×76.3) mm.
Mean diameter	47.0 mm.
Minimum volume	62.5 cc.
Maximum volume	105 cc.
Mean volume	79.7 cc.
Minimum length/diameter	1.45
Maximum length/diameter	1.97

(1958) gave the average weight of 31 eggs as 78.1 grams, but did not state the age of the eggs. During incubation the egg lost weight slowly but steadily until the last week when weight was lost more rapidly. The weight lost varied between 8 and 17 grams from the date of laying to the first sign of chipping.

A wide range of nest sites is used. Most sites on Skokholm are under boulders or on sheltered ledges, but only rarely is a typical Guillemot site used. Some nest in the entrance of old Rabbit or Puffin holes and two cases were known of nests in the entrances of occupied Puffin holes. Crevices and cavities in the cliffs are other common sites. It is probable that ledges are used only when all the available holes are already occupied.

Sandstone chippings were frequently found piled around eggs, both in holes and on ledges. On ledges the chippings clearly prevented the egg from rolling. The absence of chippings around eggs in other similar sites suggests that such 'nests' are only made when the materials occur in the near vicinity of the egg. A nest on Skomer, Pembrokeshire, was composed of plant fragments and Paludan (1947) published a photograph of one made of torn-up plant material.

INCUBATION PERIOD

The incubation periods obtained by different authors are given in table 2. In the present study two quite abnormal incubation periods were found and are excluded from the averages in the table. One egg took 44 days to hatch and another the remarkably long time of 52 days. No reason could be found for these long periods. In both cases incubation behaviour seemed to be as regular as at all the other nests. It is conceivable that a replacement laying might have occurred in the second case, but this was definitely not so in the first.

In the main study area a total of 86 eggs was laid by 80 pairs of Razorbills. This figure includes a double clutch and at least five replacement eggs. Fifty-nine eggs, or 69%, hatched during the course of 31 days, with 50% of the hatchings occurring in the eight days between 19th and 26th June. Of the 27 eggs lost, twelve failed through desertion and nine were broken by the parents, often by rolling them

Table 2. Incubation periods of Razorbills *Alca torda* on Skokholm, Pembrokeshire, in 1964, compared with previous studies

	Paludan (1947)	Keighley and Lockley (1948)	Present study (1964)
Average (days)	35.5	34.3	36.2
Extremes (days)	35-36	33-36	34-39
Number measured	7	18	29

Table 3. Five replacement layings by Razorbills *Alca torda* on Skokholm, Pembrokeshire, in 1964, compared with two recorded by Paludan (1947)

	Paludan		Present study				
Number of days between laying and loss	1	13	1	1	3	7	11
Number of days between loss and replacement	17	14	14	18	16	14	13

down a slope from their holes on to the rocks below; the remaining six disappeared from their holes and might conceivably have been taken by a predator though there was no direct evidence for this. There was also no evidence for infertility.

Five cases of replacement layings were recorded in 1964. Eggs were identified as replacement layings when they appeared in marked nests occupied by colour-ringed adults which had lost their first egg. The only previous author to mention replacement layings was Paludan (1947) although this habit is well known for the Guillemot. Table 3 summarises my data for relayings along with those of Paludan.

Replacement laying in the Razorbill can occur if the first egg is lost within 13 days after laying. The replacements took from 13 to 18 days to be laid, this period being apparently independent of the interval between laying and loss of the first egg and probably depending more on the physiological condition of one or both parents. Of 13 eggs lost, only five were replaced and the others not, even when the first egg had been lost within seven days of being laid. Two of the replacement eggs were lost within six days of being laid, but no third egg followed. Unless relaying occurred, the adults continued to occupy the site from a few days to two weeks and then left the area completely. Only a relatively small number of individuals relay after losing their first egg, unlike Guillemots, which frequently lay replacements. This is presumably related to the great risk of a Guillemot losing its egg from its precarious nesting place. The normally safer eggs of the Razorbill do not face the same dangers and the ability to lay replacements has apparently been much reduced. It appears to have been lost altogether in the Puffin, which has the safest site of the three.

Witherby *et al.* (1941) stated that two-egg clutches occur rarely, and there are few records for Skokholm (e.g. Diamond 1963). What was considered to be a double clutch was found in my study area in a cavity only large enough for one pair of Razorbills. The second egg was laid 17 days after the first, which is equivalent to the period required for the laying of a replacement egg. Both eggs were very similar in colour and pattern, but the second egg was smaller and lighter in weight than the first. The clutch was deserted a few days after the laying of the second egg, although only the first egg had been incubated in that time, the second being cold at all visits to the nest.

Table 4. Fledging periods of Razorbills *Alca torda* on Skokholm, Pembrokeshire, in different years

	Keighly and Lockley (1948)	Brun (1958)	Present study (1964)
Average (days)	15.7	18	18.5
Extremes (days)	12-18.8	16-21.5	14-24
Number measured	18	19	34

In an earlier paper, Keighley and Lockley (1947) listed 16 other fledging periods from the year before with extremes of 10 and 18 days, but some had been estimated by comparison of chicks of unknown age against those of known age and so these have been omitted here; the six that were known accurately averaged 15.7 days like those in the later study

FLEDGING AND BREEDING SUCCESS

The fledging periods recorded by different authorities on Skokholm are compared in table 4; in addition, Paludan (1947) obtained about 16 days as the fledging period in Denmark. The course of 'flying out' occupied 31 days, mainly in the first 15 days of July, only four chicks remaining after 15th July.

Forty-six chicks out of the 59 which hatched developed to the fledging stage, giving a fledging success of 78%. Table 5 compares the hatching, fledging and breeding success of the Razorbill on Skokholm in different years.

In 1964 nine chicks were found dead in the nests at stages varying from one to 13 days. Two of these had their heads pecked (by the parent?) and one had been crushed, presumably by the parent. The other six died after gaining weight at the normal rate and the cause of death in these cases was not determined. Four chicks disappeared from their holes without trace and were possibly taken by predators.

The total breeding success was 53%, 46 chicks being reared by 80 pairs. As can be seen from the tables, the greatest losses were incurred at the egg stage in all three years though the chick mortality was much higher in 1964 than in 1948 or 1958.

Table 5. Hatching, fledging and breeding success of Razorbills *Alca torda* on Skokholm, Pembrokeshire, in different years

	Keighley and Lockley (1948)	Brun (1958)	Present study (1964)
Number of eggs laid	50	31	86
Number of eggs hatched	18	20	59
Hatching success	36%	65%	69%
Number of chicks fledged	18	19	46
Fledging success	100%	95%	78%
Total breeding success	36%	61%	53%

Table 6. Comparison of breeding success of early and late nesting Razorbills *Alca torda* on Skokholm, Pembrokeshire, in 1964

	5th-18th May	19th May-6th June
Number of eggs laid	48	38
Number of eggs lost	13	14
Number of chicks lost	4	9
Breeding success	65%	40%

If the breeding season is arbitrarily divided into two sections, one containing the early layers and the other the later layers, it is found that the later group lost relatively more eggs and young than did the earlier group. This is shown in table 6. The criterion for the division is the middle of the peak of egg-laying which fell between 14th and 22nd May, over 50% of the eggs being laid in those eight days. The difference in breeding success in the two groups is considerable. It is probable that the early breeders are older and more experienced than the later breeders which are likely to be younger birds, ones breeding for the first time or ones nesting in sub-optimal sites. The age structure of the colony was not known so the above hypothesis could not be checked.

This difference in efficiency between early and late breeders does not appear to be reflected in either the growth rates of the chicks or in the fledging periods of the chicks. Both of these features seem to be equally variable throughout the breeding season.

GROWTH OF THE CHICK

Chicks showed great individual differences in their growth rates. The average weight at hatching was 62 grams. The weight increase on the second day was small, between two and five grams. At this age the chicks still had a fairly large yolk sac and this was not completely absorbed until about the third day. Generally the weight of the chicks increased by about ten grams daily until around the twelfth day, after which slightly lower weight increases were recorded. Weight losses were recorded only during the last four to five days in the nest and these were small. At fledging—18 to 19 days—the average weight was 189 grams, or about 30% of the adult weight. Brun (1958) found the weight of the chick at fledging to be 28% of the adult weight. He also found wing length to be a much more reliable guide than weight to ageing chicks.

TWINNING EXPERIMENTS

This work was carried out in order to determine whether one chick is the most that can be raised by a Razorbill pair. Twelve pairs of Razorbills, in a colony away from the main study area, were given two

chicks to rear. In these experiments two one-day old chicks were paired except in the cases mentioned below. Their growth rates were compared with those of normal single-chick broods. The parents readily accepted the introduced chick and appeared to be able to brood both chicks without difficulty. On introduction, however, both chicks pecked furiously at each other and in several cases the heads of both became denuded of feathers and blood was drawn.

Eight twins lost one of the pair after one to six days. Six of these chicks disappeared from the nest without trace, another was found at the bottom of the cliff where it had presumably been pushed by its partner, and the eighth had been battered to death. In the ninth twinning the original chick died after five days from starvation; it had lost 10 grams and at 43 grams was the lowest weight recorded from any chick in the study. In the remaining three twinnings both chicks left the nest alive; as these showed certain individual differences they will be considered separately as A, B and C.

In twinning A a second chick aged three to five days was added when the original chick was one to two days old and both fledged on the same night 19 days from the start of the experiment. The fledging period was therefore slightly longer than average. The weights of these twins at fledging were 161 grams and 167 grams respectively and therefore a good deal lower than the average of 189 grams. The original chick was also stunted in growth although it was close to the introduced chick in weight. Hence the survival of these chicks after fledging may well have been impaired.

In twinning B the introduced chick (added on the day of hatching) gained weight more rapidly than the original and fledged in 13 days when it weighed 150 grams. Its partner was fed on the fourteenth day as shown by an increase in weight; thus one parent at least had stayed behind with this chick, which left on the fourteenth night weighing 159 grams. In this case, then, the fledging period was four to five days shorter than the average and the fledging weights were well below average; this premature fledging could well have impaired their subsequent survival.

Twinning C was started with both chicks approximately five days old. The introduced chick gained weight more rapidly than its twin and left on the thirteenth day when it was about 18 days old. The original chick remained behind, lost weight rapidly and disappeared after the seventeenth day when it weighed only 97 grams. It had, however, developed its wing feathers and resembled a normal fledgling except for its very low weight. During the stay of this chick at the nest beyond the departure of its twin, one parent was in attendance at the nest at each visit, but evidently the chick was not being fed.

Thus in two, or perhaps three, of the twelve twinnings both of the

chicks left the nest alive, but probably with a reduced chance of subsequent survival compared with single chicks. Each of the other pairs successfully reared one chick, but these remaining chicks were not weighed so it is not certain whether they had as good a chance of subsequent survival as normal chicks. Hence the experiment suggests that it is at the least extremely difficult for a pair of Razorbills to raise more than one chick.

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SUMMARY

Observations were made on the breeding biology of Razorbills *Alca torda* on Skokholm, Pembrokeshire, during the summer of 1964. Nest-site selection probably occurred during the birds' first visits to the cliffs in early spring. Weights and dimensions of eggs are summarised and discussed. The average incubation period was 36 days and the hatching success 69%. Replacement laying occurred in five out of 13 cases where the first egg was lost. The fledging period was 18.5 days and the fledging success 78%. The total breeding success was 53%, the earlier nesters having a higher success than the later ones. The growth of the chicks is briefly discussed. Out of twelve pairs experimentally provided with a second chick, only two, or possibly three, reared both chicks to fledging and these young were below the normal weight.

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