

NEST FAILURES IN THE FULMAR: THE EFFECT OF OBSERVERS

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INTRODUCTION

Numerous seabird studies have dealt with the factors affecting breeding success (e.g., Coulson, 1966; Mills, 1973; Davis, 1976; Brooke, 1978; Ollason and Dunnet, 1978). Complementary to these studies is the investigation of causes and timing of breeding failures. Unfortunately it is impossible in practice to examine natural losses of eggs or chicks in isolation from unnatural ones because the observer's presence is likely to increase the losses, i.e., cause disturbance. However, the stage in the breeding cycle (egg or chick) at which losses are more likely to occur and their timing in relation to date can be determined.

In the Fulmar (*Fulmarus glacialis*) Dunnet et al. (1963) suggest that most failures occur at the egg stage: of all egg losses in the first 9 days after laying, 71% occur within the first 3 days. Mougín (1967) shows two peaks in egg losses, one shortly after laying, the other around hatching. Ollason and Dunnet (1978) demonstrate that late-laid eggs are more likely to fail.

Breeding success in the Fulmar can vary widely from year to year, e.g., on the island of Eynhallow in Orkney, Dunnet et al. (1979) quote a range of 16% to 52% over 28 years, although no known change occurred in conditions on the island. This does not account for variations between years in observer effort, which will now be considered in detail.

The aim of this paper is to determine for the Fulmar the most vulnerable stage of the breeding cycle, to describe the pattern of egg losses in relation to date, and to examine the effects of observers studying breeding biology on the response of breeding adults and their subsequent breeding success. Causes of failure for a generalized seabird will be described theoretically, and the Fulmar fitted into this framework.

METHODS

In 1950, R. Carrick and G.M.D. began color-banding breeding Fulmars caught from their nests on the small uninhabited island of Eynhallow, Orkney. Observations during the breeding season have continued annually to the present time. General methods have already been described (Dunnet and Ollason, 1978). The initial aims of the study were to collect data on breeding and survival. Only recently was it realized that we have useful data on the effects of disturbance.

The data analyzed here were collected over 21 years from 1958 to 1978. Three annual visits were taken to Eynhallow: in May (to count eggs), in July (to determine hatching success), and in August (to determine fledging success).

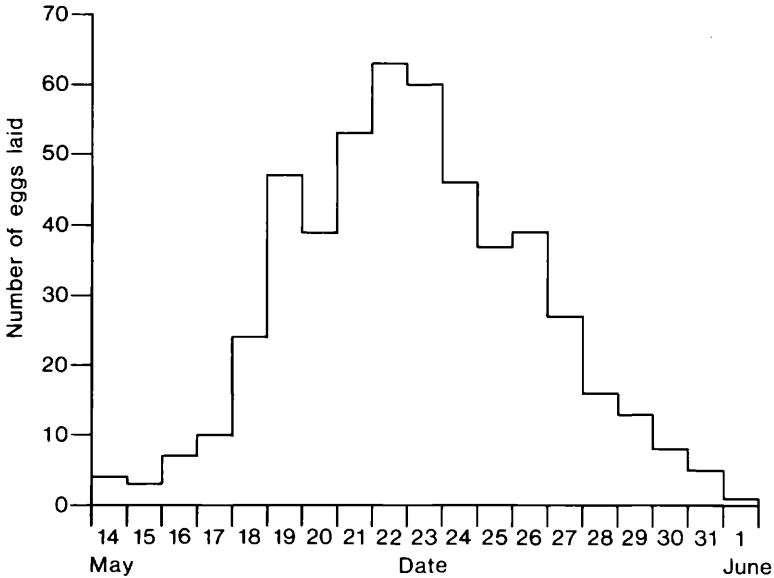


FIGURE 1. Average number of eggs laid in 1960, 1961, 1962, and 1978.

Visit in May

In 1960, 1961, 1962, and 1978 the May visit lasted for about three weeks during laying. Nests were checked as often as possible (usually daily) to obtain laying dates and the number of eggs laid (apart from any eggs laid and lost between consecutive checks of nests). The mean laying dates in these years ranged from 21.6 May in 1961 to 23.5 May in 1962 (Variance Ratio $F = 7.61$, $df = 3.498$, $P < 0.001$). However, it was felt that combining the data from all four years should produce a distribution of laying dates typical of an average year (Fig. 1). In the remaining 17 years (1958, 1959, and 1963 to 1977), Eynhallow was visited during the fourth quarter of the laying distribution for 2 to 6 days beginning between 26 May and 8 June. The number of eggs *observed* in each of these years is therefore less than the total laid (because some egg losses would have occurred before the first annual visit); it consists only of the number of eggs present on the first day of the visit, plus any laid subsequently. A correction therefore needs to be applied to the *observed* totals of these 17 years to allow for egg losses before the first day of the May visit. Using the data from 1960, 1961, 1962, and 1978, the pattern of eggs laid and eggs lost during laying has been determined for an average year: Figure 2 shows (a) the number of eggs to be laid after a particular day, expressed as a pro-

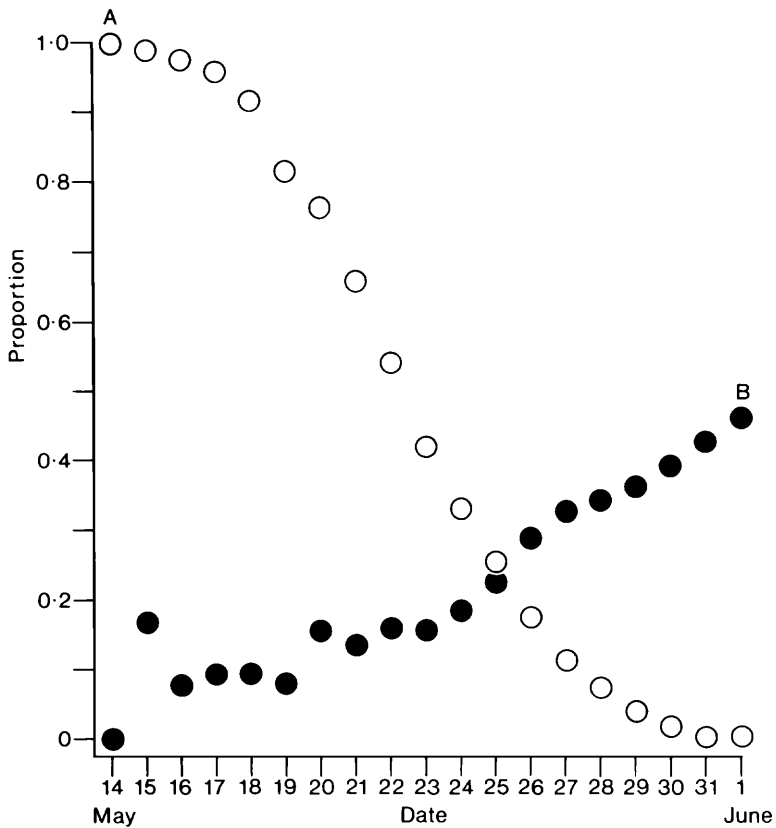


FIGURE 2. Pattern of egg-laying and egg-loss during the laying period of an average year: (A) eggs laid after day x as a proportion of eggs present on day x plus eggs laid after day x ; (B) eggs lost by day x as a proportion of eggs present on day x . Data from 1960, 1961, 1962, and 1978.

portion of those present on that day plus those laid subsequently, and (b) the number of eggs lost by a particular day, expressed as a proportion of those present on that day. The totals were *adjusted* as follows: the *observed* total was multiplied by the proportion (a) referring to the first day of the May visit to give an estimate of the number of eggs laid after the first day of the visit. Subtracting this number from the *observed* total gives an estimate of the number of eggs present on the first day, which is then multiplied by the relevant proportion (b) referring to the first day of the May visit to give the estimated number of eggs lost by that day. Adding the three estimates gives an *adjusted* total for each of the 17 years which can then be compared with each other and with the *observed* totals of 1960, 1961, 1962, and 1978. No significant difference was found between the distributions of the *observed* and *adjusted* totals

(Kolmogorov-Smirnov test $\chi_2^2 = 5.29$, NS) and the overall breeding success (percentage eggs that fledge) calculated from the *observed* totals is highly correlated ($r_s = 0.961$, $df = 17$, $P < 0.001$) with that calculated from the *adjusted* totals. The *observed* number of eggs present on the first day is not significantly different from the estimated number of eggs present on the first day ($\bar{x} = 144.9$ and 148.8 ; $SD = 36.28$ and 39.39 , $n = 16$) and they are highly correlated ($r = 0.988$, $P < 0.001$). Therefore in all subsequent analyses in this paper, the *adjusted* total number of eggs has been used for 1958, 1959, and 1963 to 1977.

Visit in July

In all years of the study, a second visit to Eynhallow of three or four days occurred in July, covering part of the hatching period. By the end of this visit most eggs had hatched. However, some eggs remained, a few of which may have hatched but failed before fledging. Hatching success will therefore tend to be slightly underestimated.

Visit in August

The final annual visit, of one day, occurred during August, by which time almost all adults had left the area. All nests with fledglings were recorded, and therefore a good estimate of overall breeding success could be determined. Since the estimate of hatching success will be less accurate than that of overall breeding success, all analyses involving hatching success have also been carried out on overall breeding success.

In 1978, the response of Fulmars on an egg or a chick to the standardized approach of one particular observer (J.C.O.) was categorized as follows: "on"—bird remained on the egg or chick all the time while the observer was visible; "at"—bird left its egg or chick but did not fly away and usually stayed within a few inches of its nest site; and "off"—bird left its egg or chick and flew away. For each nest observed more than five times, an index of remaining "on" the nest was determined by observing the number of times that the parent(s) remained "on" the nest and expressing this as a proportion of the total observations of parents at that nest, while it had an egg or a chick. Nests with fewer than six observations (55% of the total 215 nests) were eliminated to avoid the biases of small samples. This procedure will also have removed nests with birds very sensitive to disturbance, i.e., nests that failed after five or fewer disturbances. Thus the index of remaining "on" the nest cannot include the most sensitive parents.

The data were coded and stored on magnetic disc in a data base (using the Aberdeen University Data Base Management System). Most analyses were carried out using a Honeywell Level 66 computer.

RESULTS

The Laying Period: Eggs Laid and Eggs Lost

The combined laying distributions for 1960, 1961, 1962, and 1978 are assumed to be typical of an average year ($\bar{x} = 22.7$ May, $SD = 3.40$,

TABLE 1.
Mean percentage failures before hatching for various sets of years.

	Mean	SD	n	d	P
(a) Years with long May visit = 1960 to 1962 and 1978	66.90	3.289	4		
(b) Years with short May visit = 1958 and 1959, 1963 to 1977	65.78	8.624	17	NS	
(c) Years with large group in July = 1971 to 1978	71.79	7.007	8		
(d) Years with small group in July = 1958 to 1970	62.42	6.115	13	3.119	<0.01
(e) Years with large group in July excluding years with long May visit = 1971 to 1977	71.79	7.568	7		
(f) Years with small group in July excluding years with long May visit = 1958 and 1959, 1963 to 1970	61.57	6.804	10	2.854	<0.02
(g) Years with long May visit and small group in July = 1960 to 1962	65.27	0.473	3	NS	

n = 502; Fig. 1). The proportion of eggs laid each day that fail to reach hatching increased significantly with laying date ($r_s = 0.759$, $df = 17$, $P < 0.001$). No similar change occurred with laying date in the proportion of chicks hatching that eventually fledged.

During the laying periods of 1960, 1961, 1962, and 1978, the day on which each egg was lost was known. The proportion of eggs lost each day was not constant (Kolmogorov-Smirnov test $\chi_2^2 = 13.52$, $P < 0.01$) but varied in an inconsistent way with date.

Disturbance

The presence of observers on Eynhallow likely caused disturbance to the breeding Fulmars, possibly resulting in lower hatching success and overall breeding success. In the years 1960, 1961, 1962, and 1978, the first annual visit covered about three weeks during laying, whereas in the remaining years from 1958 onwards, the May visit covered only 2 to 6 days. In all years, 2 to 6 people were present at this time. Since the egg stage especially is vulnerable to predation, the years with a long May visit might be expected to have a higher failure rate. This was the case, but the mean failure rates for the two sets of years were not significantly different at hatching (Table 1, a, b) or overall (Table 2, a, b).

TABLE 2.
Mean percentage overall breeding failures for various sets of years.

	Mean	SD	n	d	P
(a) Years with long May visit = 1960 to 1962 and 1978	73.98	4.568	4		
(b) Years with short May visit = 1958 and 1959, 1963 to 1977	72.54	8.038	17	NS	
(c) Years with large groups in July = 1971 to 1978	77.69	7.366	8		
(d) Years with small groups in July = 1958 to 1970	69.82	5.890	13	2.560	<0.05
(e) Years with large groups in July, excluding years with long May visit = 1971 to 1977	77.27	7.854	7		
(f) Years with small groups in July, excluding years with long May visit = 1958 and 1959, 1963 to 1970	69.23	6.645	10	2.211	<0.05
(g) Years with long May visit and small group in July = 1960 to 1962	71.77	1.429	3	NS	

In the years 1971 to 1978, groups of from 8 to 12 students plus 3 or 4 staff visited Eynhallow for 3 or 4 days during July, at the beginning of the hatching period. In the earlier years of the study, the July visit was similar in date and duration, but the group consisted only of 3 or 4 people. Comparison of these two sets of years shows that the hatching success and the overall breeding success were significantly worse in the years when larger groups visited the island, regardless of whether the years with long May visits are included (Table 1 and 2, c, d), or not (Tables 1 and 2, e, f). Since the larger groups apparently had a significant effect, this effect might be masking the effect of the long May visit (Tables 1 and 2, a, b). Therefore using only years with no large group in July, years with a long May visit were compared with years with a short May visit and found to have lower success (Tables 1 and 2, g, f), but differences were still not significant.

From the data it is possible to determine at what stage failures occurred and approximately at what date (Table 3). Egg failures occurring before the July visit, or in and after the July visit have been compared for (i) the short-May-visit-small-July-group years (1958–1970, excl. 1960–1962) and the short-May-visit-large-July-group years (1971–

TABLE 3.
Timing (in relation to date) of egg and chick failures.

(a) Failures at egg stage	(i) Short		(ii) Long	
	Small 1958-1970 (excl. 1960-1962)	Large 1971-1977	Small 1960-1962	Large 1978
May visit				
July group size				
Years				
Before July visit	828	724	172	68
In and after July visit	121	236	42	82
	$\chi_1^2 = 43.18$ $P < 0.001$		$\chi_1^2 = 46.66$ $P < 0.001$	
(b) Failures at chick stage	(i) Short		(ii) Long	
	Small 1958-1970 (excl. 1960-1962)	Large 1971-1977	Small 1960-1962	Large 1978
May visit				
July group size				
Years				
In July visit	46	23	5	6
After July visit	62	55	16	13
	$\chi_1^2 = 2.80$ NS		$\chi_1^2 = 0.04$ NS	

1977) (Table 3a [i]) and (ii) the long-May-visit-small-July-group years (1960-1962) and the long-May-visit-large-July-group year (1978) (Table 3a [ii]). Both tables show significant differences between the sets of years, there being a much larger proportion of failures in and after July in the years with a large group present in July. Using the same sets of years, comparisons of failures at the chick stage in July or after July did not show significant differences associated with the large group present in July (Table 3b, [i] and [ii]).

In this long-term study, adults need to be recaptured at regular intervals in order to ensure that color and metal bands remain legible. Most captures were made in July, and usually birds were caught off chicks. Perhaps the larger group of people present in July allowed more birds to be caught and thereby decreased breeding success by increasing disturbance. However, captures, expressed as percentage captures of the number of breeding adults for each year, was not significantly correlated with overall breeding success ($r_s = -0.058$, $df = 19$) or with hatching success ($r_s = -0.111$, $df = 19$). However significant negative correlations were found between hatching success and man-days in July for each year ($r_s = -0.630$, $df = 19$, $P < 0.01$; Fig. 3) and between overall breeding success and man-days in July ($r_s = -0.538$, $df = 19$, $P < 0.02$;

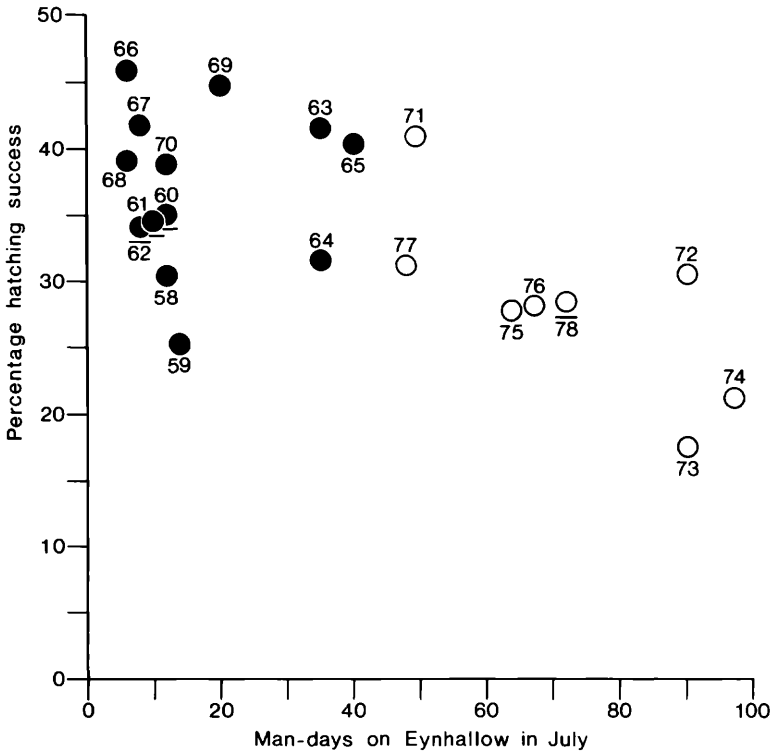


FIGURE 3. Percentage hatching success plotted against man-days spent on Eynhallow during July for 1958 to 1978. Closed circles: years with small July group. Open circles: years with large July group. Underlined symbols: years with long May visit. Captures (as percentage of breeding adults) were most numerous in 1960, 1959, 1962, and 1958, respectively.

Fig. 4), but neither hatching success nor overall success correlated significantly with man-days in May ($r_s = 0.146$, $df = 19$ and $r_s = 0.117$, $df = 19$, respectively). If the years are arranged into those with a large group present in July (1971–1978) and those with a small group present in July (1958–1971), overall breeding success correlates with man-days in July when the group was large ($r_s = -0.838$, $df = 6$, $P < 0.01$) but not when the group was small ($r_s = -0.149$, $df = 11$).

Response of Breeding Adults to Approach of an Observer

The response of a Fulmar on an egg or a chick to the approach of an observer varied considerably. Some birds allowed an observer to see its color and metal bands and to remove an egg or chick for weighing without becoming disturbed or leaving the nest site. At the other extreme, birds left their nest site as soon as the observer appeared, and did not return while the observer was able to see the site.

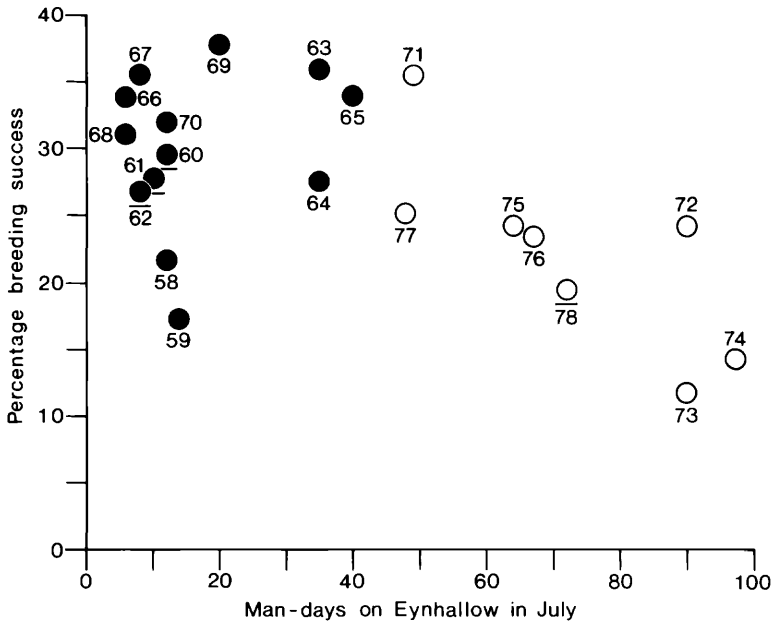


FIGURE 4. Percentage overall breeding success plotted against man-days spent on Eynhallow in July for 1958 to 1978. Closed circles: years with small July group. Open circles: years with large July groups. Underlined symbols: years with long May visit. Captures (as percentage of breeding adults) were most numerous in 1960, 1959, 1962, and 1958, respectively.

Nests that failed during the egg stage had a significantly lower mean proportion of birds remaining "on" (see methods) than nests in which the egg hatched or the chick fledged (Table 4). The variation in proportion "on" was significantly greater for nests that failed at the egg stage (Table 4).

Some evidence indicates that the proportion "on" increases as the breeding experience of the bird increases; e.g., for nests in which the length of breeding experience of the male was known, those in which the male's experience was 1 to 3 years had a significantly lower mean proportion of parents "on" than those in which the male's experience was over 3 years (Table 5a). A similar, but nonsignificant trend is apparent in relation to the female's experience (Table 5b). If breeding success is held constant by partial correlation, the proportion of parents "on" still correlates significantly with length of experience of the male ($r = 0.242$, $df = 76$, $P < 0.033$).

DISCUSSION

Possible Causes of Failure for a Generalized Seabird

Figure 5 is a schematic representation of a bird breeding season, from egg production to fledging, showing various factors that may increase

TABLE 4.

Mean proportion of occasions when parent remains "on" the nest at the approach of an observer, for nests successful to (i) the egg stage, (ii) the chick stage, or (iii) fledging.

Stage which nest reaches	Mean proportion "on"	SD	n
(i) egg only	0.6375	0.311	40
(ii) chick only	0.7813	0.177	18
(iii) fledgling	0.7612	0.213	36

Comparisons:	<i>F</i> ratio	<i>P</i>	<i>t</i> or <i>d</i>	<i>P</i>
(i) with (ii)	3.09	<0.015	2.23	<0.030
(ii) with (iii)	1.45	NS	0.35	NS
(i) with (iii)	2.13	<0.025	2.04	<0.046

the probability of breeding failure. The factors can be classified as those due to either or both birds and those due to external causes. Their relative importance will vary depending on the species and the parental contributions of the male and female.

The past history of both parents (age, breeding experience, and pair-bond) is known to affect breeding success (e.g., in Kittiwake, Coulson, 1966; Red-billed Gull, Mills, 1973; Arctic Skua, Davis, 1976; Manx Shearwater, Brooke, 1978; Fulmar, Ollason and Dunnet, 1978). These factors are presumably effective in terms of the physiology and behavior of the parents during the breeding season. Thus physiological condition (Fig. 5a) of both birds is probably important during egg production: poor quality eggs are less likely to result in fledged chicks; e.g., a small egg produces a small chick (fowl, Wiley, 1950; Brown-headed Cowbird, Nolan and Thompson, 1978; Laughing Gull, Ricklefs et al., 1978), with a lower survival rate (Herring Gull, Parsons, 1970); or the egg may be

TABLE 5.

Mean proportion of occasions that parent remains "on" the nest at the approach of an observer, for parents with 1 to 3 years breeding experience, or over 3 years breeding experience.

Length of breeding experience, years	Mean proportion "on"	SD	n	<i>t</i>	<i>P</i>
(a) Male					
1 to 3	0.6368	0.262	13		
over 3	0.7769	0.209	56	2.08	<0.042
(b) Female					
1 to 3	0.6570	0.264	19		
over 3	0.7335	0.213	47	1.23	NS

infertile; or it may have constituents in the wrong proportions. Possibly undue stress at this time might result in resorption of the egg, but this is unlikely to be detected. If physiological condition is not good at the beginning of breeding, there may be effects later in the season; e.g., nutritional state of the female may affect overall breeding success (Red Grouse, Moss et al., 1975).

If an egg is laid (Fig. 5b), both birds need to be efficient incubators (Fig. 5c; Baerends, 1959; Drent, 1973) and communicate with each other to maintain a shared incubation schedule. Poor incubation behavior may result in eggs being left uncovered: although eggs may have some chilling resistance (Manx Shearwater, Mathews, 1954) and effects of weather are not always predictable (Adélie Penguin, Ainley and LeResche, 1973), the probability of killing eggs will be increased by exposure to excessive heat (Herring Gull, Hunt, 1972), cold (Wilson's Storm Petrel, Beck and Brown, 1972) or wind (Common Tern, Gochfeld, 1978). Uncovered eggs are also vulnerable to predation (Lesser Black-backed Gull, Davis and Dunn, 1976). Similarly any disruptive external factors that cause the incubating bird to leave the nest will expose the eggs to weather and predators (gulls, Harris, 1964; Herring Gull, Hunt, 1972; Double-crested Cormorant, Kury and Gochfeld, 1975; Western Gull, Robert and Ralph, 1975; Double-crested Cormorant, El-lison and Cleary, 1978).

If the egg hatches (Fig. 5d) the parents need sufficient foraging skill to obtain food for themselves and their young (Fig. 5e; Adélie Penguin, Ainley and Schlatter, 1972; Brown Pelican, Orians, 1969 and Blus and Keahey, 1978) and they must be able to feed them efficiently. The chicks also need protection from predators and weather, and disturbance of the parents may reduce or remove this protection (Adélie Penguin, Reid, 1968; Glaucous-winged Gull, Gillet et al., 1975). However, in some species adults brooding chicks have been shown to be more tolerant of disturbance than those with eggs (Double-crested Cormorant, Kury and Gochfeld, 1975), or chicks have become less frightened after repeated disturbance (Western Gull, Robert and Ralph, 1975). The vulnerability of the egg and chick stages therefore varies with the species.

Thus the probability of breeding failure is increased if the parents are in poor condition or if their behavior is inadequate. External disturbance, whether intentional or not, exaggerates the losses by altering the behavior of the parents. Some species may be less susceptible, since their success is improved when they nest under cover (gulls, Brown, 1967; Lesser Black-backed Gull, Davis and Dunn, 1976; Common Tern, Nisbet, 1975). In others it is shown that adults nesting on the periphery of the colony fled more easily at the approach of an observer than those nesting in the center (Adélie Penguin, Tenaza, 1971). Also disturbance in one year can have an effect on breeding in the following year (Adélie Penguin, Oelke, 1975 and Reid 1968; Fulmar, Ollason and Dunnet, 1978).

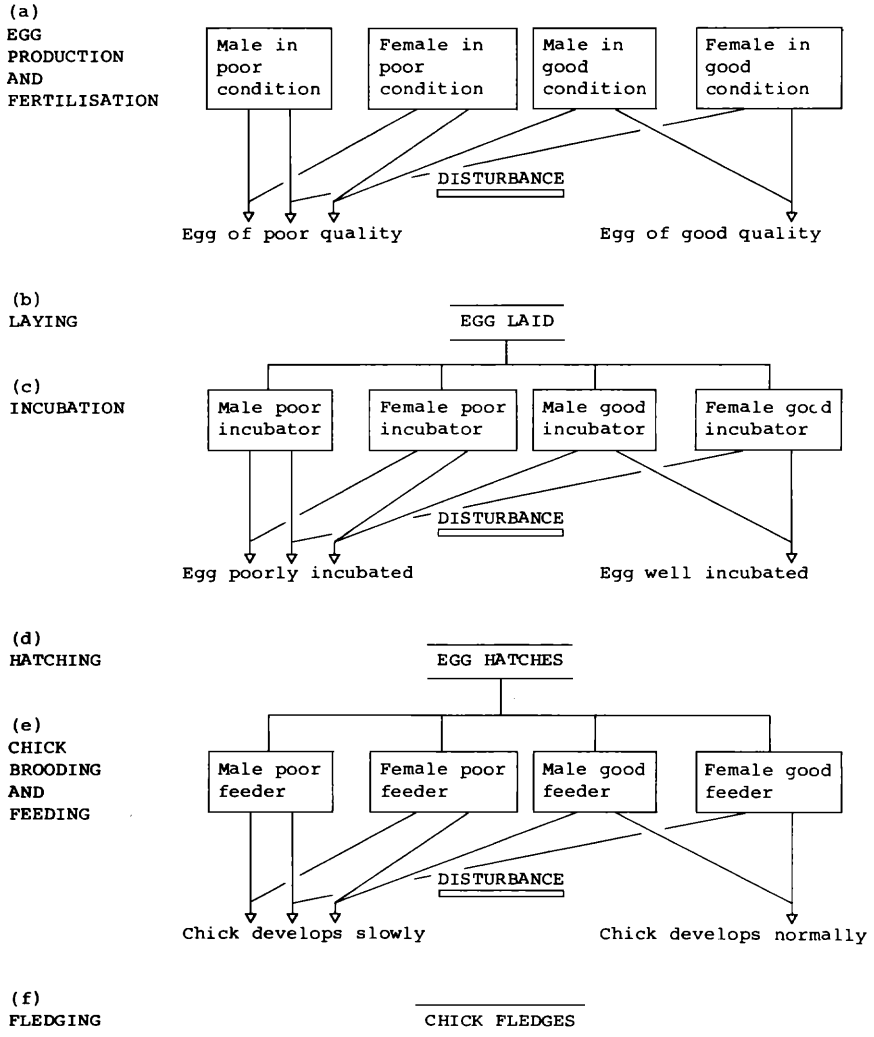


FIGURE 5. Schematic diagram of a generalized seabird breeding season from egg production to fledging. Disturbance refers to any factor external to the parents which alters the behavior of the parents. In general, factors which cause the flow to be down the left side of the diagram will increase the probability of breeding failure.

Causes of Failure in the Fulmar

In the Fulmar, both parents go on a prelaying exodus (Dunnet et al., 1963), which is typical of Procellariiformes (Warham, 1964): on the average the female is away for 20 days; the male is away for 9 days and

returns before the female (Macdonald, 1977). Presumably they go to distant feeding grounds to build up reserves for the breeding season. The nutritional state and physiological condition of both birds would therefore seem to be critical (Fig. 5a). The single egg weighs about 13% of the female and relaying has never been known to occur. Some unpublished evidence suggests that, within the history of a female, larger eggs are more likely to be successful than smaller ones; i.e., larger eggs are of a better quality and presumably use more of the female's reserves. Possibly disturbance during egg production might cause resorption, but this would be difficult to demonstrate, and was unlikely in this study since observers were not normally present at this time and the female is away from the colony.

After the egg is laid, the male normally relieves the female at the nest within a few hours, and then incubates for about 10 days. Thereafter the incubation stints are approximately equal (Dunnet et al., 1963). Therefore, for incubation to be successful the male and female must be in the right place at the right time and communicate successfully with each other (Fig. 5c). The egg is white (i.e., not camouflaged) and no nest material is present, so that if the egg is left uncovered it is vulnerable to predators as well as to extremes of weather. Late-laid eggs seem more at risk than early-laid ones, since fewer of the late-laid eggs reached hatching. This is consistent with the fact that more experienced Fulmars tend to lay earlier and are more successful (Ollason and Dunnet, 1978). The data presented here show some lowering of hatching success (and overall success) in the four years in which observers were present during the whole of laying (Tables 1 and 2; a and b, g and f) although the differences were not significant, probably because the number of observers was small. A significant increase in breeding failure was found in years in which a group of at least 12 people was present for 3 or 4 days during hatching (Tables 1 and 2; c and d, e and f), i.e., at a time corresponding to the second peak of egg losses of Mougins (1967). Thus disturbance (measured in terms of man-days) during incubation (Fig. 5c) does have a significant effect upon hatching success (and overall success).

After the egg hatches, both parents feed and brood the chick. It is not known what food is obtained, nor at what distance the parents forage. Disturbance at this time (Fig. 5e) leaves the chick exposed, although Fulmar chicks can protect themselves to some extent by ejecting noxious oil (Armstrong, 1951). In this study, most captures of adult birds occurred when the chick was present—capture of breeding Fulmars can affect their subsequent breeding success (Ollason and Dunnet, 1978). However, no relationship was found here between overall breeding success of the population as a whole each year and captures in that year. This is probably because capture only affects the success of the nest at which an individual was captured, and captures normally only occurred at about 10% of nests in any one year. But it is interesting to note that

in two years (1958 and 1959, Figs. 3, 4) in which success was low and man-days were low, disturbance due to captures was relatively high. Thus disturbance at the chick stage can have some effect, but at least in this study, the chick is not as vulnerable as the egg.

Response to the Approach of an Observer

How does an observer cause disturbance? Significant differences between birds are shown (Table 4) in the response to a particular observer at nests that subsequently failed (64% remained on site) and those that were subsequently successful (76% remained on site). The differences are similar to those described for the Adélie Penguin by Tenaza (1971), and the behavior of birds at unsuccessful nests is more erratic. Thus putting a bird off its nest an additional once or twice out of 10 occasions could make the difference between a successful and an unsuccessful nest.

The evidence indicates that the behavior of birds to the approach of an observer tended towards staying on the nest as breeding experience increased (Table 5), and this may be one of the factors that results in improved success of more experienced birds (Ollason and Dunnet, 1978), rather than being a consequence of it.

Effects of disturbance probably vary with species (e.g., Glaucous-winged Gull, Gillet et al., 1975; Double-crested Cormorant, Kury and Gochfeld, 1975), as well as with habitat (gulls, Brown, 1967; Lesser Black-backed Gull, Davis and Dunn, 1976; Common Tern, Nisbet, 1976) and frequency of disturbance (Western Gull, Robert and Ralph, 1975). Perhaps factors such as these should be considered when designing field projects.

SUMMARY

Data were collected over 21 years as part of a long-term study of breeding Fulmars on the uninhabited island of Eynhallow in Orkney. The pattern of egg losses is described. Eggs laid early in the season were more likely to hatch than those laid late.

The relationship between number of observers each year and subsequent breeding success that year was examined. In four years in which 2 to 6 observers were present for 2 to 3 weeks during laying (May), hatching success and overall success were lowered, but not significantly so. No relationship existed between man-days present in May and breeding success. In eight years in which at least 12 observers were present for 3 to 4 days during hatching (July), hatching success and breeding success were significantly lowered. A significant negative correlation was found between man-days present in July and breeding success.

Capture of breeding adults had no significant effect upon subsequent breeding success of the population as a whole, probably because captures only occurred at about 10% of nests. The responses of sitting birds to the approach of an observer varied: at nests which were subsequently

successful, 76% of birds remained on site: the figure for unsuccessful nests was 64% and their behavior was more erratic.

The causes of failure for a generalized seabird are described, and the Fulmar is fitted into this framework.

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