MONITORING BREEDING BIOLOGY PARAMETERS FOR MURRES *Uria* spp.: LEVELS OF ACCURACY AND SOURCES OF BIAS

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Monitoring of seabird populations by accurate determination of the number of breeding pairs on selected sample areas of their breeding colonies has become an important tool for detecting changes in population size and this in turn may provide a clue to the health of marine ecosystems (Cramp et al. 1974, Nettleship 1976, 1977, Birkhead and Nettleship 1980). The most important seabird family in the Northern Hemisphere is the Alcidae and within this group the most convenient species for monitoring are the Murres (*Uria* spp.) which are numerous and widespread, and nest on open sites where they can readily be observed (Birkhead and Nettleship 1980).

Early studies on timing of breeding and reproductive success in the genus were generally conducted by flushing breeders from their sites and counting numbers of eggs and chicks exposed (Johnson 1941, Uspenski 1956, Tuck 1961). However, this method causes heavy losses and therefore grossly underestimates breeding success.

The technique of determining reproductive success for murres by observing them from a distance, so that they are not disturbed, was introduced by Birkhead (1976) for Common Murres (*Uria aalge*) on Skomer Island, Wales. The method has subsequently been adopted by the Canadian Wildlife Service through the initiative of D. N. Nettleship to determine timing of breeding and reproductive success in Thick-billed Murres (*Uria lomvia*) and Common Murres (Birkhead and Nettleship 1980, Type I method). To monitor murre populations the information is required for three purposes:

(1) Information on the timing of breeding is necessary to correct counts and census data relative to some reference point in the breeding cycle.

(2) The total number of eggs observed on a particular plot is used as an estimate of the number laid and hence the number of pairs breeding in a given year. This is used to derive a correction factor (K) used to convert counts of individual murres to estimates of breeding pairs.

(3) Breeding success is used to estimate the annual recruitment of nestlings into the juvenile population.

Although certain limitations and biases in the method have been recognized from the start, only slight attempts have been made to estimate its limits of accuracy. In the course of studies on the Thick-billed Murre colony at Digges Island, N.W.T. (62°34′N, 77°39′W) during June to September 1981, we tested the method for comparability between observers and for accuracy in relation to the three principal aims.

A. J. Gaston et al.

METHODS

Five study plots were used for estimating reproductive success. Two of these were selected for special treatment and the other 3 were dealt with in the "normal" manner. At the special plots (A and B) the duration of daily observations was fixed and the same 2 observers (MP, DN) watched throughout the season. At Plot A both observers watched 1 h per day alternating between morning and afternoon. Each kept separate notes and they did not discuss them so that neither knew what the other had seen. This schedule was maintained until median date of hatching (4 August). At the start of egg-laying they observed the plot together for several days to ensure that the numbers assigned to particular sites were known to both. At Plot B two watches were carried out each day; one of 2 h and the other of 1 h with observers alternating the length of their watches. Notes were kept separately for the 1- and 2-h watches, but the observers discussed their observations and the information gained on one watch was therefore familiar to the observer undertaking the next. At the other 3 plots (D, F, and J) the amount of time spent observing varied depending on the demands of other field work and observations were shared among 5 observers.

Notes were kept at all plots on the amount of time spent each day, the weather conditions, and the number of sites unoccupied (designated a), the number seen to have eggs (e) or chicks (c), or to have nothing (o), and the number occupied but for which the presence or absence of an egg or chick could not be established (?). Observations on the 2 special plots were continued only until the median date of hatching, so that differences in the detection of chicks were not fully evaluated. Experience elsewhere suggested that hatching is more easily detected than laying and we therefore felt that it was most important to evaluate biases caused by differences in the detection of eggs.

In evaluating and discussing the results of these observations, eggs and chicks will be divided into 2 categories: (1) known; those for which the date of laying/hatching was known within 48 h, (2) unknown; those for which this date was known less accurately. Our criterion for establishing a date to within 48 h was that a definite absence (of egg or chick) was followed within the next 2 days by a definite presence. Daily observations at each site will likewise be divided into 2 categories: (1) successful; an egg or chick was seen or the absence of either was definitely established, (2) unsuccessful; the presence or absence of egg or chick could not be definitely established.

RESULTS

At Plot A the observers recorded 34 and 37 eggs of known laying date and 21 and 20 other eggs, respectively, out of a total of 59 seen altogether (Table 1). There was a strong tendency for both people to record the date of laying for the same sites. Laying dates were recorded for 17 eggs by one observer but not the other, 12 were seen by the

TABLE 1.   Comparison of laying data obtained by two observers watching independently for 1 h per day at Plot A.

	Observer 1	Observer 2	Combined data
Eggs of known laying date	34	37	44
Other eggs seen	21	20	15
Total eggs	55	57	59
Median laying date	30 June	1 July	1 July
Hatching success of first eggs, % (N)	44.7 (47)	43.7 (48)	40.4 (52)

other observer within 3 days, four were seen later, and one was never seen at all. Median dates of laying differed by one day between the observers, and the same was true of the median date of first sighting for unknown eggs.

Eggs disappeared before they hatched at 37 sites, and this was recorded in 34 and 36 cases, respectively. Both observers recorded the loss on the same day in 21 cases and in a further 9 cases they were only one day apart. Three other records were within 4 days and in the remaining instances one observer never saw the egg at all.

At Plot B records for the 1-h and 2-h watches were combined to show the results of three hour's watching per day. Dates of laying and hatching were known from the 3-h watch for approximately twice as many sites as from the 1-h watch, with the 2-h watch intermediate (Table 2). The number of egg losses recorded was similar, however. The median date of laying based on the 1-h watch was later than those based on the longer watches, but the median date of hatching was latest for the 3-h watch. The total number of eggs recorded was higher for the longer watches, but the difference was not as great as for the samples of known laying date.

How comparable are the results?—Comparison between the observers at Plot A suggests that differences due to observers is rather small. One

TABLE 2.   Comparison of 1-h, 2-h, and 3-h daily watches at Plot B.

	Length of watch (h)		
	1	2	3
Eggs of known laying date	16	20	29
Chicks of known hatching date	9	16	21
Total eggs seen	61	65	67
Egg losses recorded	21	20	21
Total chicks seen	38	43	43
Median date of laying	3 July	1 July	1 July
Median date of hatching	29 July	29 July	29 July
Hatching success of first eggs (%)	65.6	69.2	68.7

observer had used the same method on the same plot the previous year, while the other was inexperienced at the start of the season. Despite this, differences in all parameters recorded were negligible.

Comparison of 1, 2, and 3 h of observation at Plot B demonstrate that some of the results are sensitive to the amount of time invested, particularly the number of eggs for which dates of laying and hatching were determined accurately. However, for the most important results from the point of view of monitoring (i.e., the total eggs seen, the median date of laying, and the estimated hatching success) the method appears to be more robust and differences between the 2- and 3-h watches were small. The similarity between 2- and 3-h watches in numbers of eggs recorded, number of chicks seen, and median date of laying suggests that, for the plot concerned, increased observations beyond 2 h provide relatively little improvement in the results.

Known laying dates were compared with dates of laying obtained for 3 other study plots where eggs were weighed and measured at intervals during the incubation period and the relationship between the age and density of the eggs used to extrapolate dates of laying (Appendix 1). Median hatching dates obtained by this method were 28, 29, and 30 June, broadly comparable to those recorded by observation.

Both of the methods compared suffer from the deficiency that some eggs recorded as first eggs will actually be replacements, the first eggs laid on those sites having been lost before they were detected. This means that true median laying dates are probably earlier than those observed, the size of the error being dependent on the proportion of first layings detected. This is discussed further in the next section.

How accurate is the method in estimating total number of eggs laid?—The number of eggs observed represents a minimum estimate of eggs laid. The accuracy of the estimate depends on (1) the rate of egg loss (R) and (2) the length of time that eggs are present before they are detected (T). Both of these parameters can be estimated to give an indication of the error involved:

(1) Egg loss can be calculated from the formula:

$$R = \left(\frac{(E_i - E_{i+1})}{E_i} \right) \times 100 \qquad (1)$$

where E_i is the number of eggs present on day i, E_{i+1} the number remaining the following day, and R the rate of loss in $\% \cdot day^{-1}$. At Digges Island in 1981, R was $1.28\% \cdot day^{-1}$ up to the median date of hatching (4 August), with averages over 5-day periods ranging from 0.91 to 1.76% per day.

(2) The length of time which elapsed between laying and being seen can be calculated for eggs of unknown laying date but known hatching date (H) by estimating date of laying from date of hatching using the mean incubation period for eggs of known laying

TABLE 3.   Frequency distribution for the length of intervals between the laying and detection of eggs at Digges Island in 1981, calculated from equation (2).

	Length of interval (days)					
	≤2	3- 5	6- 8	9–11	12–14	≥15
Number of eggs	29	10	6	3	1	4
Percent	54.7	18.9	11.3	5.7	1.9	7.5

and hatching date (32 days, N = 50); and then subtracting this from the date on which unknown eggs were first observed (F).

$$T = F - (H - 32) \text{ days} \tag{2}$$

The distribution of intervals estimated for all study plots in 1981 shows a strong positive skew (Table 3) with a mean of 3.70 days and a median of 2 days. If we assume that this is representative of all unknown eggs (N = 231) and estimate a mean interval of 1 day for known eggs (N = 158) and an interval of 32 days for eggs not seen until after they hatched (N = 18) this gives an estimated mean period between laying and observation (T) for all eggs of 3.90 days.

Using the 2 parameters derived above (R and T) we can estimate the total number of first eggs laid (N_F) from equation (3).

$$N_F = N_O/(1 - R)^T + \frac{N_R}{N_L}[1 - (1 - R)^T] \tag{3}$$

where N_O is the number of first eggs recorded, N_L is the number of first eggs known to have been lost, and N_R is the number of these which were replaced. Substituting observed values for all plots, N_O = 407, N_L = 147, and N_R = 29, giving an estimate for N_F of 423.7. Hence, the actual number of first eggs laid probably exceeds the number observed by about 17, representing an error of 3.9%.

Using the same formula (3) we can vary the parameters T and R to test the sensitivity of the method (Fig. 1). This demonstrates that while the method is very robust where egg loss is small, it becomes quite sensitive to changes in T where egg loss is above 2.0% per day. Over the range of egg loss actually observed for Thick-billed Murre populations (20–50%, Gaston and Nettleship 1981, Birkhead and Nettleship 1981) it appears that effort sufficient to keep T below 4 days should yield satisfactory estimates. Formula (3) can be used to improve estimates of first eggs laid and hence improve K-ratios, but the accuracy of the correction will be dependent on the number of unknown eggs for which the date of hatching was known and a decrease in effort therefore
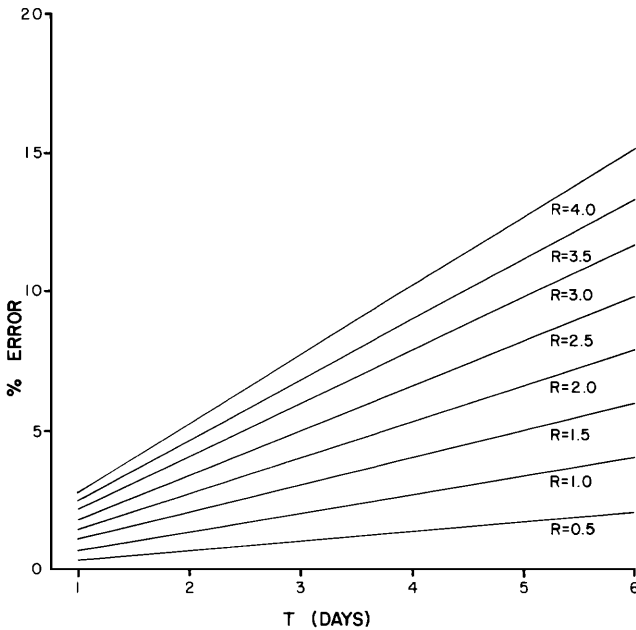
FIGURE 1. Relationship between "T" and percentage error in the number of eggs re-
corded for different values of "R." For further explanations see text.

decreases the accuracy of the correction. From a practical standpoint it
is most useful simply to note that, over the range of effort customary
in Canadian Wildlife Service studies thus far, the Type I method has
probably yielded an estimate of first eggs laid that is no more than 5%
below the true figure.

    How accurate is estimation of breeding success?—The disappearance of
eggs and chicks was by far the most accurately recorded parameter in
our study, being very consistent between observers and among different
periods of observation. Variation in the accuracy of the method for
calculating breeding success therefore occurs mainly through inaccuracy
in the estimation of the number of first eggs laid, as we have already
discussed. Breeding success estimated by this method is therefore con-
sistently higher than true breeding success, the difference in the present
study being estimated as 1.7%. Loss of chicks is generally much lower
than loss of eggs, in this case below 0.5% per day over the 24-day fledging
period, and therefore creates a negligible additional bias.

SUMMARY

    We performed replicate observations on breeding Thick-billed Murres,
using the Type 1 method of Birkhead and Nettleship (1980) to test the

comparability of results obtained by different observers and the accuracy with which timing of breeding, numbers of eggs laid, and breeding success could be determined. All of the critical parameters appeared to be relatively insensitive to observer bias and to differences in the amount of time devoted to observation beyond a certain point.

Some systematic biases in the method can be corrected to improve the accuracy of final results. The accuracy of all the estimates is higher when hatching success is high than when many eggs are lost.

On the basis of these findings the level of effort recommended for this type of monitoring by Gaston and Nettleship (1981) of 3 h per day for a plot supporting 80 breeding pairs of murres appears very adequate and should yield figures for total eggs laid within 5% of the true number.

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APPENDIX 1.   Relationship between density and length of time to hatching for Thick-billed Murre's eggs.

Methods

A sample of 85 eggs was measured (length, breadth) and weighed twice during incubation with an interval between weighings of about 20 days. The timing of hatching was recorded for this sample to within 2 days. For analysis a density index $W/L \cdot B^2$ was calculated for all weighings, and changes in density between first and second weighing were used to predict the density at hatching.

Analysis

Let D = density of eggs "d" days before hatching,
      d = number of days before hatching,
      D_0 = density of eggs at hatching,
      c = rate of change of egg density during incubation.

Two models were considered: (a) linear, (b) exponential.

(a) In the linear model:

$$D = D_0 + cd$$

$$\text{Hence } d = (D - D_0)/c$$

If D_i = density at first weighing, d_i days before hatching,
   D_{ii} = density at second weighing, d_{ii} days before hatching; then for each egg we have the following equations:

$$cd_i = D_i - D_0$$

$$cd_{ii} = D_{ii} - D_0$$

Solving for c and D_0 this gives:

$$c_i = (D_i - D_{ii})/(d_i - d_{ii}) \tag{1}$$

$$D_{0i} = (d_i D_{ii} - d_{ii} D_i)/(d_i - d/ii) \tag{2}$$

Repeating for each egg, c and D_0 for the population can be estimated from:

$$c = (1/n) \, c_i$$

$$D_0 = (1/n) \, D_{0i}$$

(b) In the exponential model we have:

$$D = D_0 e^{cd}$$

$$\text{Hence }\quad d = \frac{1}{c} \ln(D/D_0)$$

and, corresponding in equations (1) and (2) above, we have:

$$c_i = \frac{\ln(D_i/D_{ii})}{d_i - d_{ii}}$$

$$\text{and}\qquad D_{0i} = \exp\frac{d_i \ln(D_{ii}) - d_{ii}\ln(D_i)}{d_i - d_{ii}}$$

c and D then follow as in the linear case.

Application of the exponential model to the data obtained did not improve the accuracy with which date of hatching was predicted and the linear model was therefore adopted.