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A statistical procedure for estimating Grey seal pup production from a single census

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CONTENTS

ABSTRACT

The variable start and duration of the Grey seal breeding season makes the estimation of total pup production from a single census very difficult. Classifying the count into morphological age classes enables the form and timing of the birth rate curve and estimates of pup mortality rates to be elucidated. A simulation technique is described which enables the duration of each morphological stage to be determined from a series of such classified counts taken over one season. A further statistical technique uses these estimates to calculate the mean timing and duration of the breeding season from a single classified count taken from similar populations in subsequent years. This information allows total pup production to be calculated for any appropriate breeding colony. Some guidance is given as to the optimal timing of that single census which would yield the best estimate of production, although the precise date is not critical to the success of the technique. Results from single census estimates obtained in this way are compared with known production data from more detailed surveys for a number of different colonies.

INTRODUCTION

The most useful estimates of population size in the Grey seal, *Halichoerus grypus* (Fabricius 1791), are derived from pup production data (Boyd & Campbell, 1971; Bonner, 1976). Pup production is most accurately measured if censuses are made throughout the whole breeding season (Boyd, Lockie & Hewer, 1962; Coulson & Hickling, 1964; Summers, Burton & Anderson, 1975), but for reasons of economy and logistics it is sometimes advantageous if production estimates can be made from a single pup count. Such a procedure is possible if pups are classified into age categories with distinct morphological characteristics, and if the duration of each stage is known. Boyd *et al.* (1962) used five development stages defined by certain physical features and E. A. Smith (unpublished) estimated that these were each of 5 days duration and proposed the following further definitions which apply to normally nourished animals—deserted pups suffering from starvation present an appearance atypical of their age (see Plate 2c).

Stage I – Body contour thin, neck well defined, skin in loose folds round body. Coat often stained yellow by prenatal excreta. Umbilical cord conspicuous, pink or brown, not dried (variable character). Claws soft, whitish. Voice a weak bleat. Docile.

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Stage II – Outline smoother with neck still recognizable, but no loose folds on body. Cord atrophied, or a conspicuous scar. Claws dark and hard. Voice loud, snarl when handled.

Stage III – Outline rounded to barrel-shaped. Neck indistinguishable and navel inconspicuous. Vigorous attack and escape reactions to handling.

Stage IV – As III but with patches of white natal fur moulted to reveal under-yearling pelage. These pups are either weaned or approaching weaning.

Stage V – Fully moulted to under-yearling pelage. All weaned and often segregated (with some IV's) from breeding area.

To make reliable estimates of total pup production from a classification scheme requires that the average duration of each stage be known, and although daily growth rates of young Grey seals have been determined by several authors (Coulson & Hickling, 1964; Boyd & Campbell, 1971; Bonner & Hickling, 1971) these studies do not provide this information because in no case were the pups classified. Davies (1949) found that the moult at Ramsey Island, Pembrokeshire, started when pups were 6–18 days old and was completed when 11–27 days old. This would suggest a mean duration for stage IV of about 6–8 days. Estimates for the duration of all five stages combined are given by Davies (1949) who states that Ramsey pups stayed on land for only 2 or 3 weeks compared with 3 to 6 weeks for pups in Scotland, and by Coulson & Hickling (1964) who reported an average stay on land of 32 days and a maximum of over 40 days for the Farne Islands. This average was calculated from the integral of the graph of pup numbers over the season after 'making allowance for mortality'. The number of pup-days thus obtained was divided by the total of surviving pups to obtain the average number of days that pups remained on land. Coloured dye-marks had been applied at or soon after the birth dates of all pups, thus enabling them to be assigned to the appropriate part of the production curve.

A series of classified counts taken during a joint N.E.R.C./Nature Conservancy Council expedition to North Rona in 1972 (Summers *et al.*, 1975) has been used to test a techique for estimating average durations of each of the five stages of pup development. Since it was not possible to apportion mortality between development stages prior to the moult (because, by definition, the diagnostic characters of each class describe only healthy animals), the method of Coulson & Hickling (1964) could be used only to calculate the duration of stage V. A new method of estimating the duration of all five stages has therefore been derived using a computer simulation model and assuming a constant pre-moult neonatal mortality.

A knowledge of the length of each stage allows a single classified count to be used to construct the magnitude, form and timing of the birth rate curve and hence obtain an estimate of total pup production. Boyd & Campbell (1971) computed total pup production at North Rona for a number of years and assumed that the birth curve is distributed with invariant mean date and variance. These assumptions are undesirable since the mean date of pupping is liable to some fluctuation at any particular assembly (Bonner & Hickling, 1974; Hickling & Hawkey, 1975), Furthermore for assemblies from which there are no reference data an exact estimate of pup production based on the mean date and variance of some other known breeding season will lead to gross inaccuracies (e.g. mean date of pupping at newly colonized breeding sites in Orkney is up to a week later than nearby but long-established localities).

The present paper describes the application to this problem of a statistical technique (Bhattacharya, 1967) which overcomes the difficulty by explicitly estimating the means and variance of the birth rate curve using classified count data. The pup production curve is assumed to be normally distributed but, in all cases studied, even large departures from normality have not unduly disturbed the estimates of total pups born.

METHODS AND RESULTS

1. The computer simulation model

The twelve independent counts of seal numbers provided by the North Rona 1972 expedition

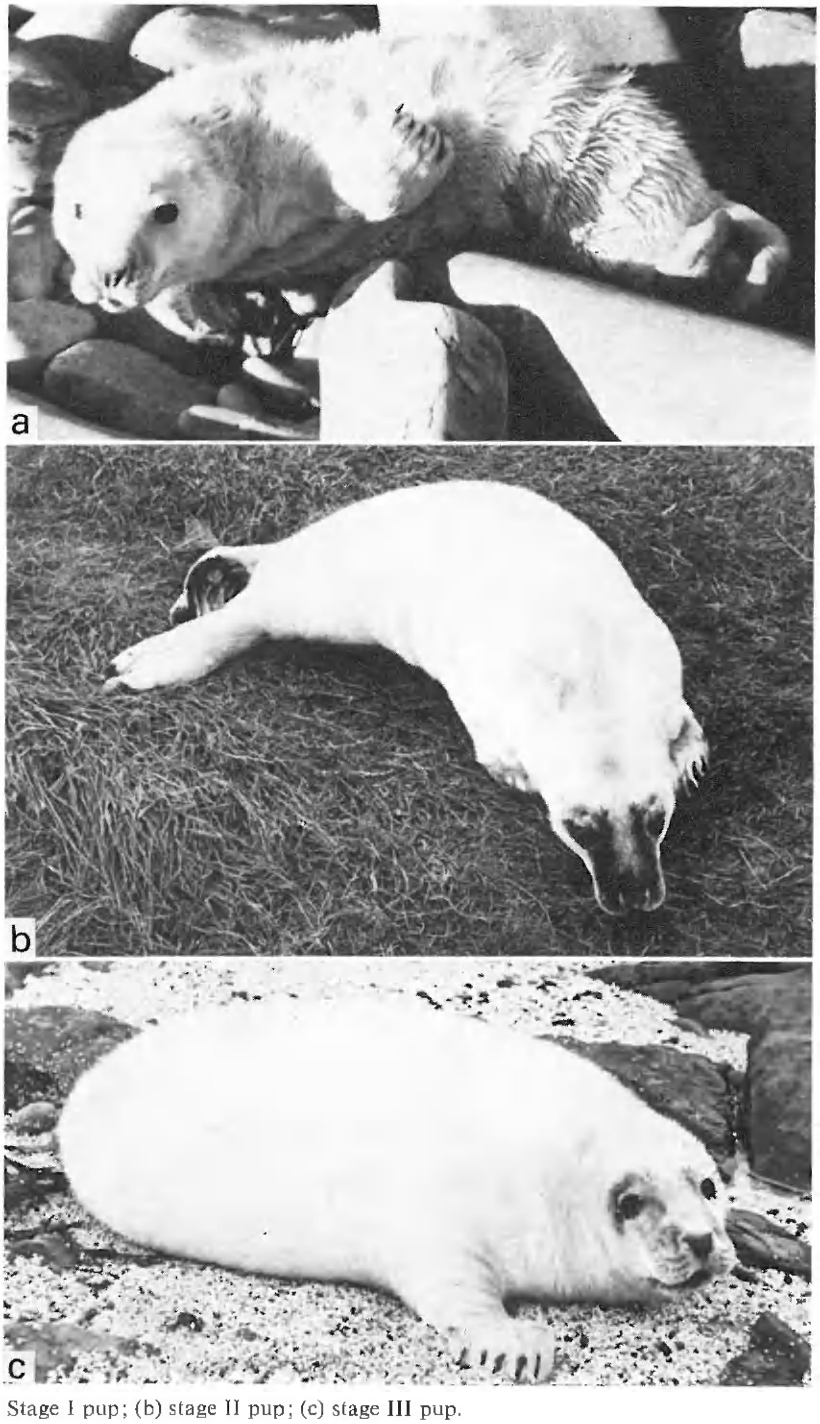

Plate 1. (a) Stage I pup; (b) stage II pup; (c) stage **III** pup.

(*Facing p. 36*)

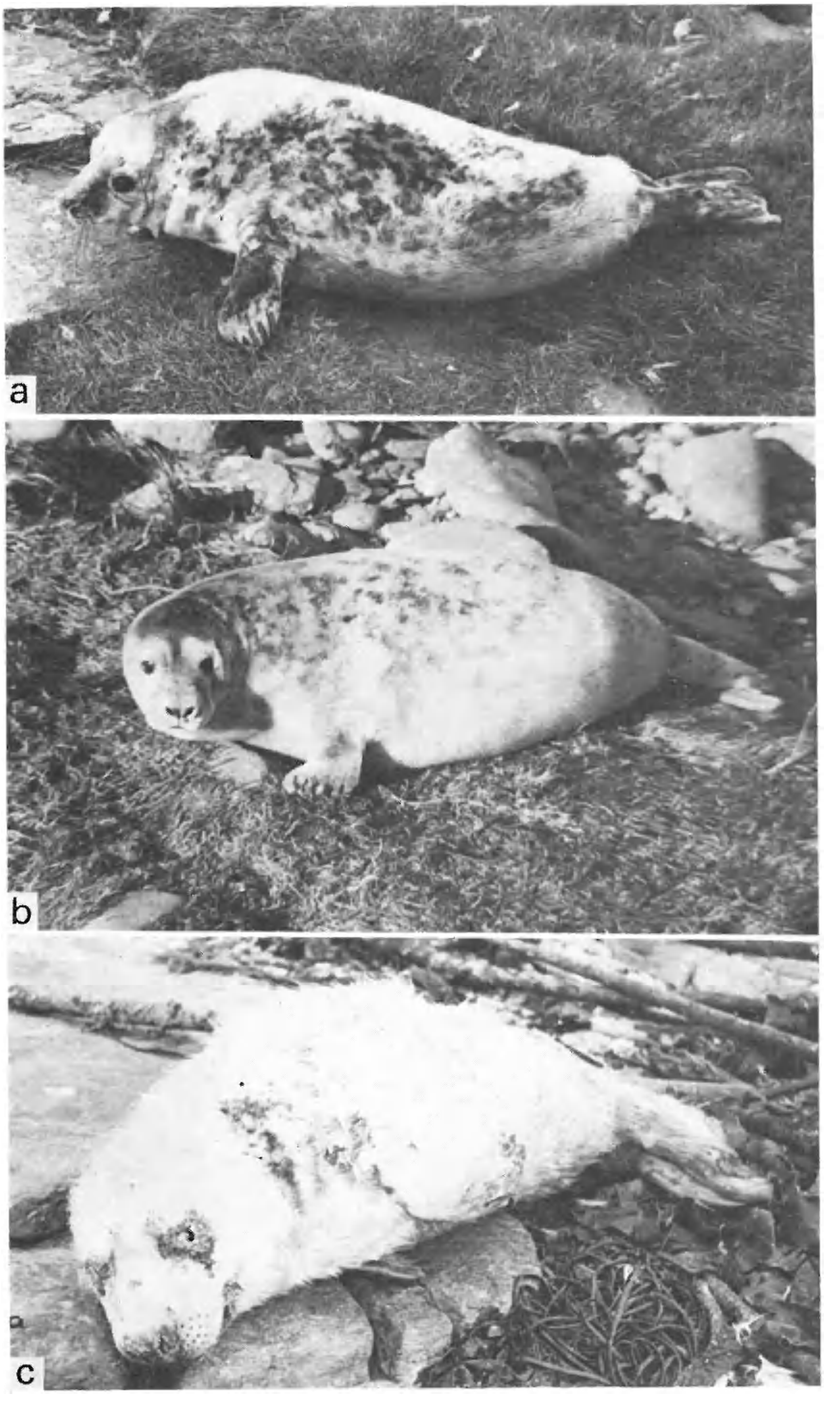

Plate 2. (a) Stage IV pup; (b) stage V pup; (c) starveling pup in moult.

included the following data: (i) the numbers of pups in each of the five development stages (I–V); (ii) the average birth rates between counts; (iii) the average mortality rates between counts; (iv) the average emigration rates between counts.

Estimates of daily birth and emigration rates obtained from these data, together with estimates of relative mortality rates, were used as inputs for a simulation model of pup development. A flow diagram of this model is given in Fig. 1. The estimated birth rate is added into 'day class 1' and the estimated relative mortality is applied to that figure. These data are then transferred to 'day class 2' and the whole procedure repeated for each day of the simulated season. The day classes (N) provided in the model are sufficient to ensure that the known maximum land stay is possible. The estimated emigration curve is used to remove fully moulted pups from 'day class N' at the appropriate rate. The simulation proceeds for the whole of the breeding season, the simulated totals for consecutive day classes being summed into groups which correspond to all possible pup stage durations. A chi-squared test was used to compare the equivalent observed and simulated counts, and as the criterion for selecting those values of pup stage durations which most closely agreed with the data. The computer simulation model was written in the language C.S.M.P. (I.B.M., 1967).

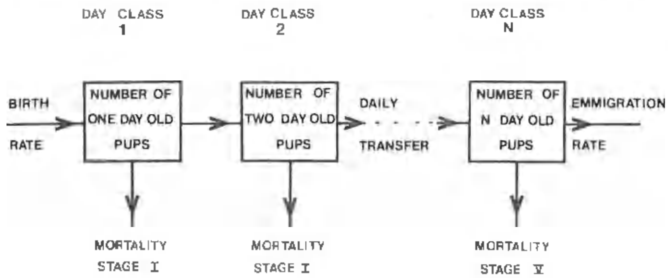

Fig. 1. Flow diagram for the simulation model of seal pup development. Simulation proceeds in daily increments from the initial conditions until the end of the breeding season.

Results of simulation

Fig. 2 shows the observed and simulated counts of the numbers of pups in each category, plotted cumulatively for those particular pup stage durations which yielded the minimum chi-squared values. The total count data (I + II + III + IV + V) fitted this solution very closely ($\chi^2 = 9{\cdot}7$), indicating no significant departure from the model at the 5% level. By successive elimination of the data from each individual group the cumulative stage durations found to be associated with the minimum chi-squared values were selected and are given in Table 1.

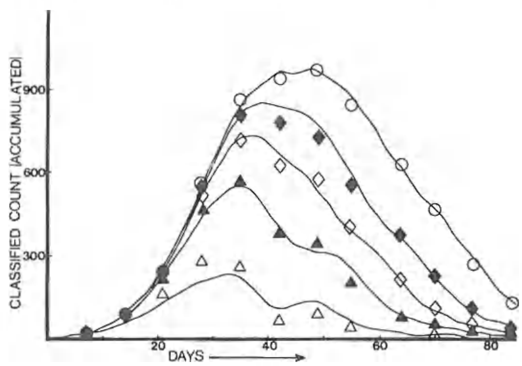

Fig. 2 Output from the simulation model of seal pup development. The simulated classified count is compared with the data obtained from North Rona (1972). Symbols represent: observed stage I (△), observed stage I + II (▲), observed stage I + II + III (◇), observed stage I + II + III + IV (◆), observed total count (○) simulated results (—).

The chi-squared values associated with individual stages showed minimum values for the same durations as those implied by the cumulative results. Many of these values indicated significant departures of the model from the data but this was to be expected due to natural variability in stage durations and errors of classification made in the field. The most objective classification is that which distinguishes between pre- and post-moult pups (i.e. I + II + III *vs.* IV + V). For this grouping the model did not significantly differ from the actual counts ($\chi^2 = 15{\cdot}8$). The duration of stage V pups was obtained from the simulation model by integrating the pup numbers for this group over time, making allowances for measured mortality during this period and dividing by the number of surviving pups. This indicated that the time spent on land after completion of the moult was 9 days. Adding this to the total of 23 days derived for classes I–IV from the simulation model, a figure of 32 days is obtained for the mean period that pups remain on North Rona.

Table 1

The durations, in days, of morphological stages of pup development which provide the best fit between observed and simulated counts for North Rona (1972). Chi-squared values provided the criterion for the closeness of agreement for both individual stages and cumulative counts

Cumulative stages	Cumulative durations	Individual stages	Implied stage duration	Individual stage duration
I + II + III + IV	23	IV	6	6
I + II + III	17	III	6	6
I + II	11	II	7	7
I	4	I	4	4

2. Estimation technique

Method

From a single classified count and estimates of stage durations and pup mortality, points on the birth rate curve can be calculated. Assuming that the birth rate is approximately constant during the period of each stage, the relevant count is divided by its respective stage duration to yield the mean birth rate of surviving pups. These figures are increased on a daily basis according to the known mortality rates which apply over the period. This technique is extended across the 32 birth days represented by the individuals present on the day of the count. Maintaining the same number of degrees of freedom associated with the five classes, the pups are re-classified into five groups of 6-day periods. The means of these groups ($b(t)$) represent five equidistant points on the birth rate curve. A normal distribution is fitted to these points using the technique of Bhattacharya (1967). More conventional techniques were unsuitable because no information is available regarding the 'tails' of the distribution. For each consecutive pair of birth rate estimates $\Delta\log b(t) = \log b(t+6) - \log b(t)$ was plotted against t on linear graph paper and a straight line drawn through the four points. Then (according to Bhattacharya) the mean $\hat{\mu}$ and variance $\hat{\sigma}^2$ are given by

$$\hat{\mu} = \lambda + 6/2 \quad (1)$$

$$\hat{\sigma}^2 = (6\, d \cot \hat{\theta}/e) - (36/12) \quad (2)$$

where d and e represent the relative scales for $\Delta\log b(t)$ and time(t) respectively; $\hat{\theta}$ the angle which the line makes with the time axis(t); and λ the value of t when $\Delta\log b(t) = \phi$. From these estimates of the mean and standard deviation of the birth curve the proportion (P) of the total pup population (T) represented by the classified count can be calculated using Normal Probability tables. The actual number counted (N) enhanced by the mortality figures (M) can therefore be equated to this proportion, total pup production being estimated from the equation:

$$T = \frac{N + M}{P}$$

An advantage of this procedure is that it may be programmed for automatic computation; the algorithm has been written in the computer language BASIC PLUS for use on a PDP 11/40 minicomputer.

Results of estimation

Results from one classified count taken at North Rona in 1972 are shown in Appendix I. The format is that of the combined input and output of the program which is written in conversational mode. A question mark (?) represents a request for data by the computer program: all inputs have been underlined. The observed mortality for the first four pup stages combined was 2·2% per day but only 0·4% for the fifth group. The mean date is expressed in days from 1 September as a convenient base line. The classified count is entered in the rational order, I, II, III, IV and V. The computer calculates mortalities on a daily basis and regroups the gross data into 6-day categories.

Table 2

Actual and estimated counts of total pup production for eight occasions from breeding sites at North Rona, the Monachs and the Farne Islands. All dates are counted in days from 1 September

Year	Locality	Day of count	Estimated			Actual
			Birth-date mean	S.D.	Total births	Total births
1970	Brownsman	83	74	10·0	709	654
1972	North Rona	43	40	11·6	1767	1736
1973	Brownsman	87	71	8·6	440	442
1974	Brownsman	80	69	9·1	484	524
1974	Staple	80	62	12·3	814	758
1975	Ceann Ear	59	49	11·3	654	591
1975	Stockay	57	41	19·3	1269	1306
1975	Monach*	45	47	11·9	2512	2250

*Includes Stockay, Ceann Ear, Ceann Iar and Shillay

The values of $\Delta\log b$ are plotted by the teletype to give an instant impression of the scatter of the points. The directive RUN $LINREG causes the least squares straight line to be fitted to this data. The value of time (X) when $\Delta\log b$ (Y) is zero is calculated from the ratio of the intercept and the gradient of the line. This becomes input data for the program NWGRYP which then calculates the mean ($\hat{\mu}$) and standard deviation ($\hat{\sigma}$) for the birth rate curve. The limits of the new 6-day age groupings are expressed as standard normal deviates, i.e. as deviations from the mean in standard deviation units ($(x - \hat{\mu})/\hat{\sigma}$) and hence the area under the birth rate curve (A9) represented by the single classified count may be computed (where A9 = P2 − P1) using a suitable sub-routine for calculating Normal Probabilities. Finally, the classified count grossed to include mortality is divided by A9 to give the total estimated births for the season. Table 2 gives a summary of this data from North Rona together with similar results of seven other independent classified counts from several other locations. The total births estimated using these single counts may be compared with the actual numbers counted (obtained by a series of counts spread over the breeding season in each case). The average deviation is about ±6% which is remarkably good considering the errors inherent in both field and statistical techniques.

The technique may be applied to any classified count, but the precision of the final result depends upon the timing of the count relative to the mean birth date. To demonstrate this, a simulation was performed with a birth curve normally distributed with mean equal to zero plus 35 days and standard deviation 13 days (where day zero is 1 September). Classified counts from this simulation run were sampled throughout the simulated breeding season and the estimation technique applied to each of them. Table 3 presents these results compared with the known population values. Estimates of total births were inaccurate for all samples taken before the mean birth date. However, from day zero plus 45 to day zero plus 60, i.e. from 10 to 25 days after peak pupping, estimates agreed to within 8%. Subsequently, estimates had unacceptably large errors. These results are to be expected since during the period of best estimates the classified count contained about 60% of total pups born over the whole season.

If two or more counts are available for any one population, these should be combined to provide a better estimate of total births. Table 3 includes the results of combining two or four samples. The method of combination is a simple extension of the technique described for one sample and the computer program has been adapted to cope with this possibility.

Table 3

Results of applying the single classified count technique to a simulated population of seals with birth dates of known mean and standard deviation. The population parameters may be compared with estimates based on simulated counts at various times throughout the breeding season. The increased precision obtained by using data from two or four counts is also demonstrated

		Estimated		
Total count/s	Day of count/s	Birth-date Mean	S.D.	Total births
87	15	40·6	14·2	2743
321	20	17·1	7·9	565
510	30	29·9	10·9	1181
1028	45	35·5	12·9	1743
1070	50	36·0	13·2	1757
892	60	34·7	14·3	1871
343	75	27·2	15·6	3198
1349	20,45	31·5	11·3	1665
1538	30,45	35·3	12·9	1738
1413	50,75	36·3	13·2	1725
3500	30,45,50,60	36·1	12.9	1772
Population	—	35·0	13·0	1736

CONCLUSIONS

The results of the simulation model indicate the average duration for each morphological stage measured to the nearest day. The variation from the mean is reported to be high for some individual pups as mentioned in the introduction. However, the departure of the North Rona classified count data from the model is not significant for the most morphologically distinguishable categories. This indicates that variations from the mean are not important when considering the population as a whole. The technique is particularly useful when large numbers of pups are assembled and it is in these situations that a quick means of assessing age structure is most valuable. The average total duration of stay of the pups on land reported here, agrees with the 32 days measured by Coulson & Hickling (1964) from Farne Islands data and the values for individual classes are a refinement of those estimated by Boyd *et al.* (1962). It is important to note that the pup stage durations obtained do not necessarily apply to other breeding assemblies but the technique may be similarly applied with relevant modification where a series of classified counts is available from at least one previous season.

The method for estimating total pup production from a single classified count is not fundamentally new but brings together the most appropriate group of statistical methods to yield the required result. The use of a computer enables mortality data to be applied more rigorously than is possible in manual computation. The regrouping of seals into categories of constant duration simplifies the fitting of a normal distribution to the data and helps to smooth out artificial discontinuities between successive pup classes. The techniques of Bhattacharya (1967) overcomes the problem of fitting a normal distribution to incomplete frequency data, and estimates of means and standard deviations of the birth rate curve obtained by this method enable more reliable pup production totals to be obtained. The accuracy of these estimates has been tested in the eight independent counts listed in Table 2, yielding agreements on average of ±6%. For the 1975 counts the computations were available before the total pup count had been made, thus giving credence to the objectivity of the technique. The results shown in Table 3 indicate that the best timing for classified count to estimate pup production is after peak production. This coincides with the period when the maximum number of pups is to be found on land. In practice there is a period of about 30 days (in this case, day 40 to day 70) within which it is advisable to take a classified count, if it is desired to estimate total pups to within ±10%.

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```
RUN GRYP1
MORTALITY % PER DAY FOR EACH STAGE
?2.2, 2.2, 2.2, 2.2, .4
DATE OF FIRST SAMPLE IN DAYS FROM SEPTEMBER 1ST
?43
NO OF PUPS IN EACH STAGE I,II,III,IV,V
?255, 307, 155, 102, 43
DAY NUMBERS WITH DELTA LOG B
  16     22     28     34     40
  1.08  0.36  0.38  0.20
TOTALS (B)
 48.7 143.7 205.8 301.8 368.8
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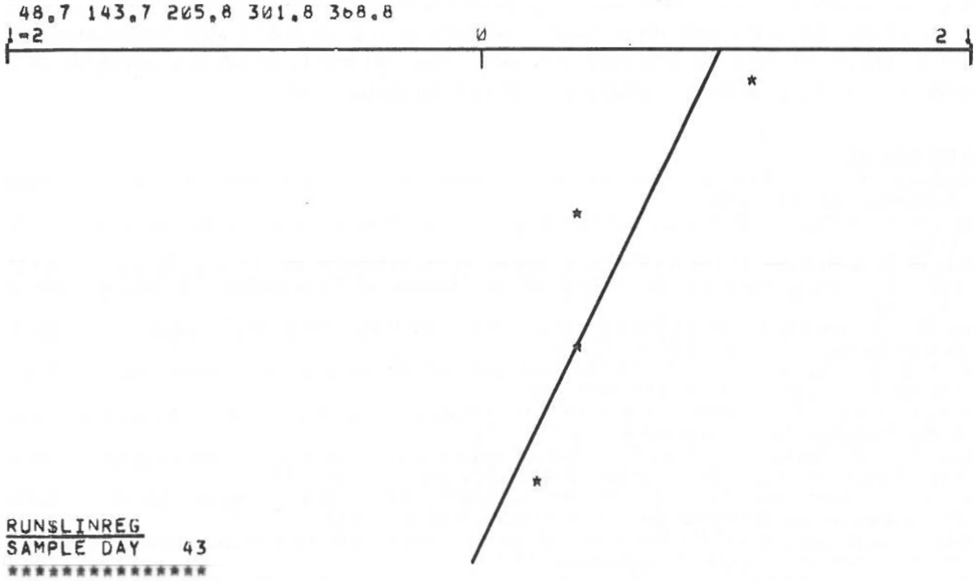


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RUNSLINREG
SAMPLE DAY   43
****************
REGRESSION EQUATION :

Y= 1.59833                   +                  -.436848E-1   X
  +/- .469474                                   +/- .181374E-1

PRINT 1.59833/.043685
      36.5876

RUN NWGRYP
INTERCEPT ON X AXIS
? 36.5876
GRADIENT(SIGN REVERSED)
? .043685
NO OF UNITS TO INCH X AXIS,Y AXIS
? 1,1
MEAN= 39.5876 STDV= 11.5968
STANDARD NORMAL DEVIATES
 -2.294 -1.776 -1.259 -0.741 -0.223  0.294
   13      19      25      31      37      43          DAYS
       49     144     206     302     369              NUMBER
ESTIMATED TOTAL OF ANIMALS IN EACH STAGE
P1               P2               A9
 .108996E-1       .615776          .604877

ESTIMATED BIRTHS OVER 30 DAYS 1069
ESTIMATED BIRTHS OVER SEASON  1767
```

APPENDIX 1.

Printout of inputs and outputs for programs used to generate data points, fit a regression line and derive a normal distribution (for fuller explanation see text).