TECHNICAL REPORT

SOME RECENT ADVANCES IN THE ESTIMATION OF ANIMAL ABUNDANCE

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CONTENTS

PREFACE

The subject matter of these lectures represent a selection of topics from recent advances in the estimation of animal abundance. These topics are somewhat unrelated and have been chosen to encompass as wide an audience as possible. Judging by the many discussions I have had with faculty and senior students, there is a great deal of interest in abundance problems at the University of Washington, and I have enjoyed this stimulating contact.

Parts of lectures I, 2, 4 and 6 and almost all of lecture 5 are based on material submitted to the publishers, Charles Griffin and Co., for the second edition of my book The Estimation of Animal Abundance and Related Parameters. Also part of lecture 4 is based on an article submitted to Wiley, New York, for publication in one of their Statistical Sciences encyclopedias. Lecture 3 is based on some of my current research.

I wish to thank Professor Douglas Chapman, Dean of the College of Fisheries, and Professor Ole Mathisen of the Fisheries Research Institute for their invitation to come to Seattle and for their kind hospitality extended to me and my family while we have been here. Thanks must also go to the Sea Grant organization for financially supporting my visit, and to Mr. Steve Syrjala for proofing the final text.

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SAMPLE SURVEY METHODS: GROUND AND AERIAL COUNTS

Introduction

Sample survey methods, with quadrat and strip sampling, can be used for estimating the population density of animals which are fairly stationary (e.g., soil animals, some species of insects, territorial animals, such as birds, which are readily detected, big game using aerial methods) or even more mobile animals such as small mammals and fish (using echo surveys). Such methods are also very suitable for obtaining population indices or estimates of relative density using animal signs such as dens, nests, tracks, feces, songs, calls and shed antlers. Eberhardt (1976) reminds us that in the latter case there is still a need for careful experimental design: the sampling design should not be ignored just because an estimate is an index and not an absolute density. For example, a new method of stratifying mourning-dove-call count routes reduced the error variance by about 30 percent (Blankenship et al., 1971), while stratification in the aerial survey of a nesting population of bald eagles (Grier, 1977) reduced the variance by about 22 percent. The roadside count index of so many birds heard calling per route has been widely used in the United States for studying population trends--for example, mourning doves (Gates et al., 1975 and Ruos, 1977) and woodcocks (Artmann, 1977)--and surveys based on this technique have slowly adapted the use of random rather than systematically chosen routes.

In using indices, more attention needs to be directed to such questions as sample size and the stability of the index with respect to weather and environmental conditions (Sauder et al., 1971). Reliable indices can be used for estimating survival rates (e.g., Gross et al., 1974:46) or studying population trends (e.g., Grieb, 1970:31). Analysis of variance models are particularly useful for studying indices, because variations in factors such as weather and location can be allowed for in the model. For example, a possible model for studying a given index taken over several years in different areas might be $E[Y_{ij}] = \mu + \alpha_i + \beta_j$, where i refers to year and j to area. Here the interactions are assumed negligible, and generally Y_{ij} will be some transformation of the actual counts, such as the logarithm or square root (e.g., Mathisen et al., 1977).

Eberhardt (1978b) gives a helpful discussion and survey of the variability generally expected from indices. He states that "regardless of any theoretical justification, the coefficient of variation of many kinds of index data seems sufficiently constant in practice to supply an approximate guide for planning purposes." He gives a useful table of population coefficients of variation that might be expected from various species. This table can be used for determining sample sizes to achieve a desired level of precision in the estimation.

Regression techniques can be useful for converting a relative index to an absolute density, or for making comparisons between indices (Bergerud, 1972, ptarmigan; Wagner and Stoddart, 1972, jack-rabbits; Calef, 1973, tadpoles; McCaffery, 1973, road kills of deer; Fischer and Keith, 1974, 596, ruffed grouse; Gross et al., 1974, jack-rabbits; Schwartz, 1974, quail; Brown and Smith, 1976, doves; Dzieciolowski, 1976a, ungulate track counts; and McCaffery, 1976, deer trails). A possible model, for example, is $E[Y_i] = \beta\ E[X_i]$, where X_i and Y_i are approximately unbiased estimates of the relative and absolute population density in the ith sampling area, and β is the correction factor. This equation is commonly referred to as a "functional relationship" and methods are available for estimating β (cf., Moran, 1971 and Seber, 1977:210). However, it is not always easy to obtain a reliable correction factor--for example, to obtain a correction factor to convert counts on haul-out areas and in breeding colonies of marine mammals (Eberhardt et al., 1979). For this reason, pellet groups do not seem to have been very successful as an index method, though they can be useful in comparing habitat usage (Dzieciolowski, 1976b).

Importance of Random Sampling

Provided sampling is random, the population does not need to be randomly distributed--a principle that is not always appreciated. For example, suppose that there are N objects in an area A and we select a sample region of area pA at random. Then, since the region is randomly selected, the probability that it contains any given animal is p. Let $y_j = 1$ if object number $j (j = 1,2,\ldots,N)$ is selected and $y_j = 0$ otherwise. Then $\Pr[y_j=1] = p(=1-q)$,

$$E[y_j] = 1.p + 0.q = p,$$

and, using a similar argument, $\mathrm{var}[y_j] = pq$. If n animals are counted in the sample region, then

$$n = \sum_{j=1}^{N} y_j ,$$

$$E[n] = \sum_j E[y_j] = Np,$$

and

$$\begin{aligned} \mathrm{var}[n] &= \sum_j \sum_k \mathrm{cov}[y_j, y_k] \\ &= \sum_j \mathrm{var}[y_j] + 2 \sum_{j<k}\sum \mathrm{cov}[y_j, y_k] \end{aligned}$$

where

$$\sum_j \mathrm{var}[y_j] = Npq.$$

Thus an unbiased estimate of N is $\hat{N} = n/p$. If the objects tend to be clustered then $\mathrm{cov}[y_j, y_k] > 0$ and $\mathrm{var}[n] > Npq$. On the other hand, if the objects are randomly distributed, then the y_j are mutually independent, $\mathrm{cov}[y_j, y_k] = 0$ and $\mathrm{var}[n] = Npq$. In this case n has a binomial distribution with parameters N and p, and is approximately Poisson with mean $\theta = Np$. However, provided the sampling is random, $\hat{N}$ is unbiased irrespective of the distribution of the objects. It is only when theoretical variances are required that we need to know something about the distribution of the population. Thus, in the random case, $\mathrm{var}[\hat{N}] = \mathrm{var}[n]/p^2 = Nq/p$, while for the clustered population $\mathrm{var}[\hat{N}] > Nq/p$. Variance estimates are best obtained by replication as follows.

Suppose we select at random, without replacement, s plots each of area a from S(=A/a) possible plots. Then $sa = pA$ and $\hat{N} = n/p = \sum_{i=1}^{s} x_i/(sa/A) = \bar{x}\,A/a$, where x_i is the count on the ith sample plot. Thus the estimate of population density D(=N/A) is $\hat{D} = \hat{N}/A = \bar{x}/a$, the mean sample density. From sample survey theory an unbiased estimate of the variance of $\hat{D}$ is

$$v[\hat{D}] = \frac{v}{s}\left(1 - \frac{s}{S}\right) \cdot \frac{1}{a^2} ,$$

where $v = \sum_i (x_i - \bar{x})^2/(s-1)$. This theory can also be applied to stratified random sampling and further details are given in Seber (1973: Chapter 2).

Experimental Design

A major consideration in designing a sampling experiment is the determination of p (the proportion of the population area sampled) and s (the number of plots). Apart from field considerations and the cost of laying out a sample plot, the overriding constraint will be the required accuracy of estimation, as measured for example by the coefficient of variation C (= standard deviation/mean). The safest approach might be to use a small pilot survey; otherwise we need to make some assumption about the distribution of each x_i or n (= Σx_i). If the population is randomly distributed, then n is binomial and $p = 1/(1 + NC^2) \approx 1/(NC^2)$, which can be determined for a prescribed C if a rough estimate of N is available. A rough working rule when $p < 0.2$ is that $C \approx 1/\sqrt{n}$ so that 100 animals must be counted for a coefficient of variation of about 10 percent. Once p is determined, s should be reasonably large, say $s > 30$.

If the population is not randomly distributed, which is usually the case, then it may be more appropriate to assume a negative binomial distribution for each x_i. In this case

$$p = \frac{1}{NC^2} + \frac{1}{SkC^2} ,$$

which can be calculated, for a given C, if rough estimates of N and k (the usual "aggregation" parameter of the negative binomial) are available.

Aerial Survey

Aerial survey is the only practicable means of estimating the number of large animals inhabiting an extensive area on land or in the sea. Although the estimate is usually inaccurate (biased) and often imprecise (i.e., has large variance), it can be used to answer a broad range of ecological and management questions to an acceptable level of approximation. The precision of an estimate can be controlled by careful experimental design and one of the first papers to give adequate attention to the design aspect is that by Siniff and Skoog (1964). Subsequently, the important papers by Jolly (1969a,b), which apply the sample theory of Cochran (1963) to aerial censusing, have encouraged a rigorous application of sound sample survey principles. Jolly (1969a) selected three designs as being particularly suited to aerial survey: (i) simple random sampling with equal-sized units, (ii) simple random sampling with unequal-sized units using the ratio method, and (iii) equal- or unequal-sized units selected with probability proportional to size. Formulae for sampling with or without replacement are also given by Jolly. A helpful, more accessible, discussion of these methods is given by Caughley (1977a), who also considers such questions as systematic versus random sampling, and quadrat versus transect sampling units.

It appears that apart from Siniff and Skoog (1964), the use of sampling methods in aerial censusing began in the mid-1960s in East Africa in the Serengeti National Park, Tanzania (Jolly and Watson, 1979). Previously in East Africa several attempts were made at total counts from the air of certain species, and photography was sometimes used instead of visual counts. Watson evidently first used sample survey techniques in the Serengeti to estimate the zebra population in 1966. He used stratified random sampling with five ecologically defined strata, and within each stratum parallel strips extending the full width of the stratum were chosen at random. Since then, various workers in East Africa have adopted stratified strip (transect) sampling as a standard procedure for monitoring wildlife populations (cf., East African Wildlife Journal from about 1969 and the special 1969 issue of the East African Agricultural and Forestry Journal: some references are Watson et al., 1969a,b; Sinclair, 1972; Bell et al., 1973; Norton-Griffiths, 1973, 1975b; Caughley and Goddard, 1975; and Eberhardt et al., 1979, table 1, marine censuses). Random strip sampling is also being used in Australia (cf., CSIRO publications, for example Frith, 1964, and Bailey, 1971).

The theory of stratified random strip sampling is given by Jolly (1969a) for the two cases, (i) equal probability of selection within a stratum which leads to a ratio-type estimator, and (ii) pps sampling or probability of selection proportional to size, that is proportional to the length of the sample strip. In comparing these two methods, Jolly and Watson (1979) point out that there is little difference in the precision of the two methods when the sampling fractions are small. However, case (ii) leads to an unbiased estimate while the ratio estimate of (i) leads to an estimate with a bias of order s^{-1}, where s is the total number of strips sampled. For this and other reasons, the proportional-to-size method is the one recommended by Jolly and Watson (1979b). Thus if N_j and A_j are the population size and area of the jth stratum ($j = 1,2,\ldots,J$), x_{ij} is the count on the ith strip of area a_{ij} ($i = 1,2,\ldots,s_j$) in the jth stratum, and $d_{ij} = x_{ij}/a_{ij}$, then an unbiased estimate of the total population size, $N = \sum_j N_j$, is given by

$$\tilde{N} = \sum_j \hat{N}_j = \sum_j A_j \bar{d}_j$$

where $\bar{d}_j = \sum_i d_{ij}/s_j$. An unbiased estimate of the variance of $\tilde{N}$ is then given by

$$\tilde{\sigma}_N^2 = \sum_j \hat{\sigma}_N^2 = \sum_j \left\{ \frac{A_j^2}{s_j(s_j-1)} \sum_{i=1}^{s_j} (d_{ij} - \bar{d}_j)^2 \right\}.$$

To determine the population of strips in a stratum, the simplest method is to draw a baseline, usually along the "ecological axis" or direction of least ecological change in the stratum, and then draw parallel lines one strip width apart at right angles to this baseline. Selection with probability proportional to the length of the strip can be accomplished by choosing a point at random in a rectangle on the map enclosing the stratum. Those strips in which the sample points fall then constitute the sample from that stratum. In order to achieve pps sampling, the sampling must be with replacement. If the same strip is chosen say k times then the strip is flown just the once but the count is included k times in the above formula for N_j. In practice the strip is identified from the plane by flying the plane at a given altitude and direction, and counting all animals seen between two markers on a wing strut. This raises the question of calibration and the problem of variations in flight path: the reader is referred to Jolly and Watson (1979b) for a useful discussion of these points. Further practical comments on some of the field problems associated with aerial censusing are given by Larsen, 1972, polar bears; Norton-Griffiths, 1975a; Caughley, 1977a, b; and Eberhardt et al., 1979, marine mammals).

In practice, transects seem to have a clear advantage over quadrats (or irregular shaped blocks determined by natural boundaries) in terms of flying costs, ease of navigation, boundary effects, observer fatigue, and sample error (Norton-Griffiths, 1975a, 26-28; Caughley, 1977a). Quadrat or block counts are more appropriate in rough country, where transect flying is difficult, or where vegetation is very thick and/or patchy, or where animals occur in very large and conspicuous herds. Some examples of quadrat counts are moose (Le Resche and Rausch, 1974; Evans et al., 1966; Peek et al., 1976), coyotes (Nellis and Keith, 1976), caribou (Parker, 1972), and a nesting population of eagles (Grier, 1977). Admittedly, animals are more readily seen using quadrat counts (Laws et al., 1975: 340), but it is of little advantage since a significant proportion of animals still tend to be missed no matter what sampling unit is used. Although there seems to be some reluctance on the part of investigators to admit the fact, there is ample evidence (e.g., Graham and Bell, 1969; Hornocker, 1970, 20-21; Bergerud, 1971, 10; Stott and Olson, 1972; Le Resche and Rausch, 1974; and in particular, Caughley, 1974, 922, and 1977b, 35) that even experienced observers can overlook as much as 20 per cent or more of the animals so that all estimates, whether based on quadrats or transects are underestimates. A number of methods for correcting these underestimates have been proposed. These are described below.

I. Method of correction factors

If accurate ground counts can be made over some of the sample strips, then a correction factor can be calculated (Le Resche and Rausch, 1974; Stott and Olson, 1972; Hopper et al., 1975, 15; Caughley et al., 1976; Eberhardt et al., 1979). For example, if x_i is an accurate count on sample strip i, y_i is the aerial count on the same strip, and P, the probability of an animal being seen from the plane, is constant, then we have the linear regression model $E[y_i|x_i] = Px_i$ and P can be estimated by least squares or by the ratio estimate $\bar{y}/\bar{x}$ (Jolly, 1969b; Jolly and Watson, 1979). This estimate can then be used to correct the total aerial count. Unfortunately, ground counts usually suffer from the same visibility bias, though to a lesser extent (Henny et al., 1972, 4-5).

Correction factors can also be provided by (i) photography (Watson, 1969; Sinclair, 1969, 1972, 1973; Norton-Griffiths, 1973; and Kerbes, 1975); (ii) infrared scanning (Graves et al., 1972, but see Caughley, 1974, 930); (iii) ultraviolet photography (white coats appear black, e.g., Lavigne and Oritsland, 1974a, b, polar bears; Lavigne et al., 1975, harp seals); (iv) simulation experiments (Watson et al., 1969c ; Caughley et al., 1976); (v) conspicuous tags, where P is estimated from the proportion of tagged animals seen from the air (Nellis and Keith, 1976; Rice and Harder, 1977). Further examples of the use of correction factors are given by Goddard (1967, 1969), Watson et al. (1969a,b), and Penncuick and Western (1972). If counts are obtained solely by studying photographs under a low-powered microscope, a correction factor can be obtained by observing some of the photographs under a higher magnification.

Caughley (1977a, 612) states, from personal experience, that "quadrats are a nightmare when it comes to estimating correction factors. The counts are sensitive to variations in piloting skill, the time spent over the quadrat, the state of the observer's stomach, and the rapport between pilot and observer. The counts from transects are more robust to these influences."

2. Repeat data

The true count, n say, and the probability P of sighting an animal in a given transect can be estimated by flying over the transect several (= k) times. Several methods of estimation are possible. For example, if $\bar{y}$ and v are the sample mean and variance of the repeated counts, then assuming a binomial distribution, (i.e., random distribution of animals) we have $E[\bar{y}] = nP$ and $E[v] = nP(1-P)$. Thus moment estimates of n and P are (Caughley and Goddard, 1972)

$$\hat{n} = \bar{y}^2/(\bar{y} - v)$$

and

$$\hat{P} = 1 - (v/\bar{y}) .$$

Estimates of P can then be averaged over several such transects to obtain an overall correction factor for the total count. Since

$$E[v] = \frac{nk}{nk-1} E[\bar{y}] - \frac{k}{nk-1} E[\bar{y}^2] ,$$

$$v = a\bar{y} + b\bar{y}^2 + e ,$$

where $E[e] = 0$: Caughley and Goddard (1972) propose a similar quadratic model for handling non-randomly distributed populations. Another method of estimating n is by the bounded counts method (Seber, 1973, 58): $\bar{y}/n$ will then give an estimate of P.

3. Multiple regression method

An interesting regression method for estimating the true density from the "apparent" or observed density is given by Caughley (cf., Caughley et al., 1976). There is clear evidence that sightability goes down as the speed, altitude, and strip width are increased (Pennycuick and Western, 1972). Therefore Caughley suggests regressing apparent density $\hat{D}$ on these factors and then extrapolating to zero. Thus if the model is of the form $E[\hat{D}] = \beta_0 + \beta_1 x_1 + \ldots + \beta_k x_k$, then β_0 represents the true density. This method shows some promise though the validity of the extrapolation needs further investigation. There are also other factors that need to be considered as, for example, fatigue and time of day can affect counts by observers (Larsen, 1972; Norton-Griffiths, 1976): clearly observers need to be properly trained (Sinclair, 1973).

4. Combining data from independent observers

Suppose there are two independent observers and it is possible to map the locations of the animals or their signs so that the numbers seen by observer 1 and not by observer 2, seen by observer 2 and not by observer 1, and seen by both observers are available. Then, by regarding the animals seen by observer i as being "caught" in sample i, a Petersen estimate of the true count can then be made, provided observers are independent. This technique of using several incomplete lists to effectively estimate the number missing from all the lists has a long history and the literature is surveyed by El-Khorazaty et al., 1977. The first application of this method to ecology seems to be that of Magnusson et al. (1978; crocodile nests). If there are several observers then the bounded counts method (Seber, 1973:53) can be used: Bergerud (1971), for example, uses the maximum count of three observers.

5. Use of group sizes

Several models have been proposed by Cook and Martin (1974) and Jolly and Watson (1979) for calculating correction factors and density estimates for populations which tend to cluster in large groups. The main assumption underlying these models is that, conditional on observing at least one member of a group of animals, the entire group is observed with certainty. This assumption could be achieved using a "two level" sampling procedure: on encountering a group of one or more animals the observer counts or photographs in the usual way and then the pilot descends to a very low level so that the observer can re-count or re-photograph until he is satisfied that all the animals in the group have been accounted for. A problem with group of animals is that a group may overlap more than one strip transect. In this case the group count is divided by the number of population strips that contain part of the group (cf., Jolly, 1979, for details).

6. Eberhardt's method

Eberhardt (1978a) introduced a very promising method for estimating P from counts n_1 and n_2 on substrips $(0,\Delta)$ and $(\Delta,2\Delta)$ respectively. The corrected population estimate is

$$\begin{aligned}\hat{N} &= n/\hat{P} \\ &= \frac{A(3n_1-n_2)}{4L\Delta} ,\end{aligned}$$

where L is the length of the strip. For a random population the coefficient of variation has a rough upperbound of $2/\sqrt{n}$, which is double that for quadrat sampling. The choice of Δ is discussed by Eberhardt. A variance estimate is best obtained by replication and not from a theoretical expression for the variance (cf., Seber, 1973, 6).

Aerial survey methods have also been used for counting marine animals such as sirenians, otters, polar bears, seals, dolphins, porpoises, walruses, and whales (cf., Holdgate, 1970; Schevill, 1974; Gilbert et al., 1976; and Eberhardt et al., 1979). However, with both shipboard and aerial counts of marine animals there is an added complication: some of the individuals may be submerged at the time of the count and a correction factor is required for this in addition to the correction for animals which are on the surface but are not seen. Several models have been developed to handle this problem (cf., Eberhardt, 1978a), but further research is needed.

7. Population indices

Another approach to the problem of estimation is to simply recognize that the estimates are biased and treat them as relative, rather than absolute, measures of abundance. If the bias can be held constant by rigorously standardizing the methods (e.g., fixed speed, altitude, and stripwidth), then the indices obtained can be used for monitoring changes in the population size and distribution, and determining preferences for different habitats. If an index is all that is required, then clearly transects are superior to quadrats or blocks. However, the wildlife manager frequently has to know absolute densities so that he can translate a permissible harvest into hunting quotas.

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LINE AND STRIP TRANSECTS

Introduction

The strip transect method, which simply amounts to counting animals or their signs on a strip of prescribed width 2W, is appropriate when the population is fairly numerous and readily visible. The sample survey theory is, of course, the same as for quadrats and this was described briefly in lecture I. When the strips are of different length we saw that more efficient methods than simple random sampling are available.

If measurements such as the right angle distance (y), the radial distance (r), and the angle of sighting (θ) with respect to the center line of the strip, are recorded for each animal, then the counts can be corrected for visibility if not all the animals in the strip are sighted. We mentioned in lecture I that the main requirement for unbiased estimation is that the strip be randomly placed. In this case, if an animal is in the strip then y has a uniform distribution on $[0,W]$. If the population is randomly distributed, then the y's will be statistically independent. However, if the population is not random then the y's may be correlated even though they all have the same marginal distribution. This can be seen by considering the extreme case in which all the animals lie on a line parallel to the transect: y is now the same for all the animals.

In practice the experimenter may choose W after the experiment as W may have been fixed at too large a value, or there may be a few very large values of y which might best be regarded as outliers and ignored.

In contrast to the strip transect, the line transect, which can be regarded conceptually as a strip of infinite width, is perhaps more appropriate when the counts are likely to be low. The observer would then wish to record all the animals seen and not just those out to a distance W.

General Theory

We shall assume to begin with that $y \leq W$. Let N be the total number of animals in the population region of area A. If P is the probability that an animal is seen on the strip and n is the number of animals seen on the strip, then, for a random transect, $E[n] = NP$ (lecture I). Let P_W be the conditional probability of seeing an animal given that it is on the strip, and let P_L be the probability that an animal is on the strip. Then

$$\begin{aligned} P &= \Pr\,[\text{animal seen}] \\ &= \Pr\,[\text{animal seen} \mid \text{animal on strip}]\ \Pr\,[\text{animal on strip}] \\ &= P_W P_L \end{aligned}$$

Now for a random transect $P_L = 2LW/A$, and using the fact (from above) that the random transect implies that y has a uniform distribution, it can be shown that

$$\begin{aligned} P_W &= \underset{y}{E}[g(y)] \\ &= \frac{1}{W}\int_0^W g(y)dy \\ &= \mu_W/W, \text{ say,} \end{aligned}$$

where $g(y)$ is the probability that an animal is seen, given that it is a right angle distance y from the observer. Thus

$$E[n] = NP_WP_L = N \cdot \frac{\mu_W}{W} \cdot \frac{2LW}{A} = 2DL\mu_W \qquad (1)$$

and $D(=N/A)$ can be estimated by

$$\hat{D} = n/(2L\hat{\mu}_W),$$

where $\hat{\mu}_W$ is an estimate of μ_W. It is readily shown that the line transect theory readily follows from the above by letting $W \to \infty$ in (1). Thus D is estimated by $n/(2L\hat{\mu}_\infty)$ where

$$\mu_\infty = \int_0^\infty g(y)dy .$$

It can be shown that the density function of z, the right angle distance of the animal in the strip given that it is seen, is

$$f(z) = g(z)/\mu_W \qquad 0 \leq z \leq W . \tag{2}$$

We use z to distinguish it from the unconditional uniform random variable y (y may not be observed). Thus

$$\frac{1}{\mu_W} = \frac{f(z)}{g(z)} = \frac{f(0)}{g(0)} .$$

Now if we redefine the function g as kg $(0 < k < 1)$, then f(z) is still given by (2) as k cancels out of the ratio. This means that there is an indeterminancy in models which are developed solely in terms of f. This indeterminancy is usually removed by postulating $g(0) = 1$, that is all animals directly in front of the observer are seen. In this case $f(0) = 1/\mu_W$ and

$$\hat{D} = n\hat{f}/(2L) ,$$

where $\hat{f}$ is an estimate of f(0).

Parametric models

The parametric approach described in Seber (1973:29-35) is to postulate a model for g, and hence for f. However, it requires that the animals behave independently of one another so that the z_i $(i = 1,2,\ldots,n)$ (the observed y's) are a random sample with distribution given by f(z). This requirement of independence combined with the fact that f does not depend on the position of the transect amounts to assuming a random distribution of animals. From the data the parameters determining the shape of f(z), and hence f(0), can be estimated using maximum likelihood estimation.

Various models have been postulated for f: for example, the exponential distribution (Gates et al., 1968); the power law distribution (Eberhardt, 1968); the truncated linear model (Järvinen and Väisänen, 1975); the incomplete gamma distribution (Sen et al., 1974, 1978a,b); the logistic model (Eberhardt, 1978, Appendix D); the half-normal distribution (Hemingway, 1971, and Järvinen and Väisänen, 1975); and the family of exponential power series distributions (Pollock, 1978). A number of other estimation procedures are compared experimentally by Robinette et al. (1974). Of particular note is Pollock's model ($W = \infty$):

$$f(z) = \frac{\exp[-(z/\lambda)^p]}{\lambda\,\Gamma(1+1/p)}\,, \quad (z > 0,\ p > 0,\ \lambda > 0)\ .$$

This flexible family of distributions contains several of the above distributions as special cases: for example, the exponential ($p = 1$) and half-normal ($p = 2$). Pollock gives an iterative procedure for finding the maximum likelihood estimate of

$$f(0) = 1/\lambda\Gamma(1+1/p)\ ,$$

and its asymptotic variance. In addition, Pollock gives a useful regression method for handling grouped data which also applies to the strip transect ($W < \infty$).

Assuming that for large n, $E[\hat{f}|n] \approx f(0)$ and $\text{var}[\hat{f}|n] \approx \sigma^2/n$ for some constant σ^2, Burnham and Anderson (1976, 329) show that

$$E[\hat{D}] \approx D$$

and

$$\text{var}[\hat{D}] \approx D^2 \left\{ \frac{\text{var}[n]}{(E[n])^2} + \frac{\sigma^2}{E[n]f^2(0)} \right\}.$$

Since the population is assumed to be random n is approximately Poisson with mean NP (= $2DL/f(0)$) when P is small--the usual case. Then

$$\text{var}[\hat{D}] \approx \frac{Df(0)}{2L} \left\{ 1 + \frac{\sigma^2}{f^2(0)} \right\}$$

and var$[\hat{D}]$ is inversely proportional to L. Thus if we have r sample transects each of length L_i $(i = 1,2,\ldots,r)$, then the appropriate weighted mean is (cf., Seber, 1973, 6, with $w_i = L_i$)

$$\bar{D} = \sum_i L_i\hat{D}_i / \sum_i L_i ,$$

with approximately unbiased variance estimate

$$v[\bar{D}] = \frac{\sum_i L_i(\hat{D}_i - \bar{D})^2}{(r-1)\sum_i L_i} .$$

Non-parametric models

In addition to the parametric models listed above, a number of non-parametric methods have been developed recently (Anderson and Pospahala, 1970; Emlen, 1971; Burnham and Anderson, 1976; Anderson et al., 1978; Eberhardt, 1978; Crain et al., 1978; and G. Patil et al., 1979; and S. Patil et al., 1979).

Eberhardt's Method. This method was described in lecture 1 and consists of estimating f(0) by

$$\hat{f} = \frac{1}{2\Delta}\left(\frac{3n_1-n_2}{n}\right) ,$$

and D by

$$\hat{D} = (3n_1-n_2)/(4L\Delta) ,$$

where n_1 and n_2 are the numbers of animals on either side of the line transect at distances which fall within the intervals $(0,\Delta]$ and $(\Delta,2\Delta]$ respectively.

Log-Linear Model. Anderson and Pospahala (1970) presented data on waterfowl nests which is well described by taking

$$g(x) = \exp(b_0 + b_1x + b_2x^2), \quad 0 \leq x \leq W \quad ,$$

with $b_0 = 0$ as we assume $g(0) = 1$. Suppose that the interval $[0,W]$ is partitioned into k subintervals $I_1 I_2, \ldots I_k$, each of width W/k. Let u_j = midpoint of the jth interval and n_j = number of animals seen on the strip with perpendicular distances lying in I_j. Then

$$\frac{E[n_j]}{E[n_1]} \approx \frac{g(u_j)}{g(u_1)} \approx g(u_j)$$

so that

$$E[\log(n_j/n_1)] \approx b_1u_j + b_2u_j^2 \quad .$$

We can now carry out a weighted least-squares fit, weighted as the n_j are correlated. Finally, using the normal distribution function, we can calculate

$$\hat{\mu}_W = \int_0^W \hat{g}(y)dy = \int_0^W \exp(\hat{b}_1y + \hat{b}_2y^2)dy$$

and $\hat{D} = n/(2L\hat{\mu}_W)$. Full details are given by Anderson et al., 1978.

Ranked Data. Another method of estimating f(0), for the case $W = \infty$, is provided by the theory of S. Patil et al. (1979). If $z_{(1)} < z_{(2)} < \ldots < z_{(n)}$ are the ranked right angle distances then f(0) can be estimated by

$$\hat{f} = k/(nz_{(k)}) ,$$

where k is the integral part of k(n), an appropriate sequence of real numbers satisfying $k(n) \to \infty$ and $k(n)/n \to 0$ as $n \to \infty$. The best choice for k(n) is presently being investigated (Burnham: personal communication). The above method is readily modified to handle the finite W case.

Fourier Series Method. Another very promising method for a fixed width transect (finite W) has been proposed by Crain et al. (1978) who assume a Fourier cosine series for f(z), namely

$$f(z) = \frac{1}{W} + \sum_{k=1}^{\infty} a_k \cos\left(\frac{k\pi z}{W}\right) , \quad 0 \leq z \leq W ,$$

where

$$a_k = \frac{2}{W}\int_0^W f(z)\cos\left(\frac{k\pi z}{W}\right)dz = \frac{2}{W} E\left[\cos\left(\frac{k\pi z}{W}\right)\right] .$$

Then

$$f(0) \approx \frac{1}{W} + \sum_{k=1}^{m} a_k ,$$

where the truncation point m is to be selected (usually $m \leq 6$ is satisfactory).

Unbiased estimates of the a_k are $\hat{a}_k = 2\bar{u}_k/W$, where

$$\bar{u}_k = \frac{1}{n}\sum_{j=1}^{n}\cos\left(\frac{k\pi z_j}{W}\right),$$

and an approximately unbiased estimate of f(0) is given by

$$\hat{f}_m = \frac{1}{W} + \sum_{k=1}^{m}\hat{a}_k .$$

This method is also considered by G. P. Patil et al. (1979).

Choice of Method. Whether one should use a parametric or nonparametric method is still an open question, and the answer will depend to a large extent on the nature of the population. As a general principle, the nonparametric methods are much more robust with regard to the underlying assumptions but are less efficient, that is they give a higher coefficient of variation. For example, if $\hat{C}$ is an estimate of the coefficient of variation of $\hat{D}$, $\hat{C}^2 \approx 2/n$ for Gates' exponential model, while $\hat{C}^2 \approx 4/n$ for Eberhardt's nonparametric method. I believe that these values of $\hat{C}^2$ reflect the general range for randomly distributed populations. Clearly if the exponential model is valid then it should be used in preference to a non-parametric approach. However, Anderson et al. (1976) point out that evidence is gradually collecting that the negative exponential models of Gates are not generally applicable.

Radial distances from a line transect

Circular Flushing Region. Methods of estimation have also been developed which use radial rather than right-angle distances. One such model, which we might call Hayne's circular flushing-region model, is considered by Eberhardt (1978). It is assumed that, for a given survey, an animal is flushed out into the open as soon as the observer crosses the boundary of a circle of radius r centered on the animal. From the line intercept theory (cf. Lucas and Seber, 1977, with $w_i = 2r_i$), it follows that Hayne's (1949) estimator

$$\begin{aligned}\hat{D}_2 &= \frac{n}{2L}\left(\frac{1}{n}\sum_{i=1}^{n}\frac{1}{r_i}\right) \\ &= \frac{1}{2L}\sum_{i=1}^{n}\frac{1}{r_i}\end{aligned} \tag{3}$$

is unbiased; that is, $E[\hat{D}_2|\{r_i\}] = D$. $\hat{D}_2$ is also unconditionally unbiased, so that it is unbiased irrespective of whether we regard the r_i as fixed or random, provided the transect is randomly placed. For this reason I prefer not to use Eberhardt's dichotomy of fixed- and variable-distance models.

Since the transect is randomly placed, the conditional density function of z given r for the above model is

$$f(z|r) = \frac{1}{r}, \quad 0 \leq z \leq r, \tag{4}$$

so that, given r, $\sin\theta = z/r$ has a uniform distribution on [0,1]. Thus θ has density function (cf., Seber, 1973, equation 2.20)

$$f_2(\theta) = \cos\theta, \qquad 0 \leq \theta \leq \pi/2 \tag{5}$$

and, for the above circular model, (5) is true in general, and not just for the exponential model. However, the flushing region need not be circular, and detection may depend on the observer so that other models* have been suggested for the distribution of θ. For example, Robson has suggested that θ is perhaps uniform on $[0,\pi/2]$ when the searching is for inanimate objects. In the case of (5), $E[\theta] = 32.7^\circ$, while for Robson's model $E[\theta] = 45^\circ$. Clearly, $\bar{\theta}$, the average flushing angle, will shed some light on the appropriateness of a given model. For example, Robinette et al. (1974) carried out a number of simulated experiments to compare ten methods of estimation and found that for 11 studies the Hayne esti-

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*See Burnham and Anderson (1976) and Burnham (1979) for an elliptical model.

mator had an average bias of about 41 percent. Burnham and Anderson (1976) point out that this is not surprising as $\bar{\theta}$ ranged from 36.0° to 52.4° with an overall average of 43.6°: this is well removed from 32.7°. Gross et al. (1974) also tested out (4) by comparing their data on jackrabbits with the cosine curve given by (5). The data from one observer seemed to follow the curve fairly well but the data from the second observer was a poor fit. In addition to an observer difference, they found seasonal and yearly differences, and demonstrated a positive relationship between flushing distance and population density.

The validity of equation (4) is best examined by comparing the $\sin\theta_i$ with the uniform distribution. For example, a goodness of fit test for lizard data is given by Eberhardt (1978, table 3). However, a word of caution: although the θ_i will each have the same marginal density function they may not be independent if the population is not randomly distributed.

Up till now we have made no assumptions about the $r_i (i = 1,2,\ldots,N)$ other than that they are constants. Suppose, however, that the r_i are regarded as random sample from a distribution with density function $f_1(r)$. Then, arguing as above, it is readily shown that for the line transect ($W = \infty$), the probability of an animal being seen is

$$P = \frac{2L}{A}\int_0^\infty r f_1(r)dr \qquad (6)$$

$$= \frac{2Ld}{A}\text{, say ,} \qquad (7)$$

and the density function of r for animals <u>actually seen</u> is

$$f_2(r) = rf_1(r)/d\ . \qquad (8)$$

Thus, conditional on n, the <u>observed</u> r_i are independently distributed with density function $f_2(r)$ and

$$E[r^{-1}|\text{animal seen}] = \int_0^\infty r^{-1} r f_1(r)dr/d = \int_0^\infty d^{-1} f_1(r)dr = 1/d \ .$$

Hence, from (3) and (7),

$$\begin{aligned} E[\hat{D}_2] &= \underset{n}{E}E[\hat{D}_2|n] \\ &= \underset{n}{E}[n/(2Ld)] \\ &= NP/(2Ld) \\ &= D \ , \end{aligned}$$

so that Hayne's estimator is unbiased; a fact already noted. Also from the argument leading to (5) we see that the conditional distribution of θ given r does not depend on r; that is, r and θ are independently distributed.

Finally we note that there is an "edge effect" to be considered. As the observer approaches the beginning of the transect a number of animals will be flushed whose flushing regions overlap the beginning of the transect, but these will not be counted. However, these will be compensated for at the other end of the transect as animals will be counted there which are not in the region perpendicular to the transect, that is which do not lie on some perpendicular from the transect and therefore do not, strictly, have an observed y. This situation is identical to the problem of partial chords at the ends of the transect in line intersect sampling: chords are completed at one end and ignored at the other.

Stochastic Flushing Model. Up till now we have not needed any assumptions about the $r_i (i = 1,2,\ldots,N)$ other than that they are constants. An alternative approach, which we shall call the stochastic flushing model, is to assume that the probability of an animal being flushed, given that its distance from the observer lies in the interval $[r, r + dr]$, is $h_1(r)dr$. The density function h_1 is conceptually different from f_1 of (6) as we have made no reference to the notion of a flushing region. Following (8), Burnham and Anderson (1976) develop a joint distribution for z and r, and show that if $f(z|r)$ is the conditional density function of z given r, then

$$\hat{f}_r = \frac{1}{n} \sum_{i=1}^{n} f(0|r_i) \tag{9}$$

is an unbiased estimate of $f(0)$. The estimate of D based on $\hat{f}_r$, namely $n\hat{f}_r/(2L)$, reduces to the Hayne estimate if (4) is true, that is if $f(0|r) = 1/r$. Gates (1969) postulated the exponential models $f(z) = \lambda \exp(-\lambda z)$ and $f(r|z) = \lambda \exp[-\lambda(r-z)]$ which lead to (4) once again so that Hayne's estimate is unbiased for this case.

Following (8) we can define $h_2(r) = rh_1(r)/d$, the density function for an <u>observed</u> r. Gates' models then lead to the gamma distribution

$$h_2(r) = \lambda^2 r \exp(-\lambda r),$$

which provides the (modified) maximum likelihood estimate

$$\hat{\lambda} = (2n-1)/\Sigma r_i \ . \tag{10}$$

Since $f(0) = \lambda$, $\hat{\lambda}$ is an unbiased estimate of $f(0)$. Using Gates' model Kovner and Patil (1974) compared (10) the minimum variance unbiased estimate of λ, with several other well-known estimators.

Eberhardt (1978, Appendix C) also considers the stochastic flushing model and points out the following relationships (see also Burnham and Anderson, 1976, 330):

$$\begin{aligned} g(y) &= 1 - \int_0^y h_1(r)dr \\ &= 1 - H_1(y) \ , \end{aligned}$$

and, using integration by parts,

$$\begin{aligned} \mu_\infty &= \int_0^\infty g(y)dy \\ &= \int_0^\infty rh_1(r)dr \ . \end{aligned}$$

However, he then assumes that once the observer passes the animal the flushing probability drops to zero: this is what happens in the circular flushing region model.

In practice it is not possible to distinguish between $f_1(r)$ and $h_1(r)$ from the data, with the exception that f_1 is violated when the animals flush behind the observer. A basic assumption in both approaches is that the sighting (flushing) of one animal is independent of the sighting (flushing) of any other. However, as pointed out by Eberhardt, "group flushes" only pose a problem if there is a correlation between flushing distance and group size. Otherwise we can assume that the groups flush independently and estimate the number of groups using the above methods; we can then multiply this estimate by the average group size. One approach which has considerable possibility is given by Cook and Martin (1974). They make the reasonable assumption that the probability of an animal being seen depends on the size of the group which flushes with it: the larger the group, the higher the probability. Clearly further research is needed on this problem of group flushing, and any model used should distinguish between any nonrandomness of the population and dependence of flushing distances. For example, it is not clear which is the case in the models suggested by Sen et al. (1974, 338). As already mentioned, nonrandomness need not bias the density estimate if the transect is random, though the theoretical variance will be affected.

Finally, there is one other problem relating to the placing of line transects. It is often convenient, in practice, to have the transect running the full length of the population area so that the length L of the transect is a random variable if the transect is randomly located and the population area is irregular in shape. This problem applies to all transect techniques and appropriate methods of estimation are discussed in Seber (1979).

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THE LINE INTERCEPT METHOD FOR ESTIMATING DENSITY AND GROUND COVER

Introduction

The line intercept method consists of choosing a line of length L at random in a population area and measuring, for example, the length of line intersected by each member of the population. Using this and related measurements we can obtain estimates of population density and the proportion of the ground covered by members of the population (Lucas and Seber, 1977). Clearly the probability that an object is intersected will depend on the two-dimensional size of the object; examples are plant populations, shrub canopies, objects on the seashore or seabed, food fragments under a microscope (Seber and Pemberton, 1979), animal "signs" such as den sites (Eberhardt, 1978a) and geographical features such as lakes, fields and forests (Jolly, 1979). If the population area is irregular in shape, and the transect line runs right across the population area, then the length of a randomly selected transect will be a random variable: this case is considered by Seber (1979).

Line intersect sampling is extensively used in forestry and the reader is referred to De Vries (1979, see also 1973, 1974) for an excellent review. The main technique used there consists of replacing each object by a unique "needle" and the sample then consists of all objects whose needles intersect the transect line. We note that in line transect sampling the probability that an object is sampled is proportional of the size of the object. This kind of sampling leads to the theory of size-biased sampling and weighted distributions (Cox, 1969; Patil and Ord, 1976; Patil and Rao, 1978).

Notation

Suppose we have a planar region R of area A partially covered by N flat uniform particles. A particle is said to be in R if its center of gravity (or some other suitably defined point on the particle) lies in R. Let λ = proportion of R covered by the particles and D = N/A, the population density. When considering λ we are not interested in the amount of overlapping that occurs so that it is convenient to regard a cluster of overlapping particles as a single "clumped" particle. Thus we regard the population as consisting of, say, M nonoverlapping clumped particles of area a_i ($i = 1,2,\ldots,M$): thus

$$\lambda = \sum_{i=1}^{M} a_i/A .$$

Let m be the number of clumped particles and n the number of particles intersecting the transect. For the ith clumped particle ($i = 1,2,\ldots,m$), let y_i be the length of the intercept; and for the jth particle ($j = 1,2,\ldots,n$), let w_j be the maximum perpendicular distance between tangents to the particle that are parallel to the transect (cf., Fig. 1 with R a rectangle). In the case of partial intercepts, a suitable convention is to choose one end of the transect at random and complete partial intercepts at this end; partial intercepts at the other end are ignored. We shall consider three different models:

(i) R is a rectangle of length L and width W: $A = LW$. The transect runs the full length of R and is parallel to the sides of R. It is chosen by selecting a point on the base line at random.

(ii) R is any shape. A base line BC is established and W is now the maximum perpendicular distance between tangents to R that are perpendicular to BC (see Fig. 1). A point Q is chosen at random on BC and the transect is then drawn perpendicular to BC with its extension passing through Q. In this case the transect has random length.

(iii) R is any shape. The transect is located at random by choosing its center at random (for example by choosing a point at random in a rectangle containing R and using this point if it falls in R), and then independently choosing its orientation with respect to some fixed base line: this orientation could be fixed or else chosen at random. In this model we assume that the particles are small compared to L, and L is small compared to the size of R so that boundary problems can be ignored--such as part of the transect lying outside of R.

Theory

Model (i)

Estimation. Although this model is a little artificial it provides the simplest introduction to the basic theory. It does, however, have application to studies involving the comparison of two or more species as for example in some microscope studies (Seber and Pemberton, 1979). Also, because of boundary problems, model (iii) might be best handled by setting out a rectangle within R and using model (i).

We shall now prove that

$$\hat{\lambda} = \sum_{i=1}^{m} y_i/L \tag{1}$$

and

$$\hat{D} = \sum_{j=1}^{n} w_j^{-1}/L \tag{2}$$

are unbiased estimates of λ and D respectively. In words, (1) states that the proportion of R covered is estimated by the proportion of the line covered. The same is true in three dimensions. The proportion of volume occupied by objects is estimated by the proportion of a random plane transect intersected or the proportion of a random line transect intersected.

A heuristic proof that $\hat{\lambda}$ is unbiased is as follows. Divide up the line into very small elements δL such that an element either lies entirely inside a particle or entirely outside a particle; the probability of lying across the boundary is negligible. If the line is randomly placed then each δL is randomly placed and lies within a particle with probability λ. Thus if δy is the observed length of intercept of δL then $E[\delta y] = \delta L.\lambda + 0.(1-\lambda) = \delta L.\lambda$. Since $E[\Sigma y_i] = \Sigma\, E[\delta y] = \lambda\, \Sigma \delta L = \lambda L$, $\hat{\lambda}$ is an unbiased estimate of λ. This intuitive argument applies to both models (i) and (iii), in which L is constant.

Theory. In Fig. 1, on page 39 (with R a rectangle), Q is chosen at random on BC so that u_i has a uniform distribution on $[0,w_i]$. Thus, since y_i is a function u_i,

$$E[y_i \mid \text{intersection}] = \frac{1}{w_i}\int_0^{w_i} y_i du_i = \frac{a_i}{w_i} ,$$

and

$$\Pr[\text{intersection}] = w_i/W = P_i \text{ , say.}$$

For i = 1,2,...,M let

$$\begin{aligned} Y_i &= y_i \text{ with probability } P_i, \\ &\quad 0 \text{ with probability } 1-P_i. \end{aligned}$$

Thus with each clumped particle we associate a random variable Y which is zero if the particle is not intersected, and y if it is. Since

$$\begin{aligned} E[Y_i] &= E[Y_i \mid \text{intersection}]\Pr[\text{intersection}] + \\ &\quad E[Y_i \mid \text{no intersection}]\Pr[\text{no intersection}] \\ &= E[Y_i \mid \text{intersection}]P_i + 0.(1-P_i) \\ &= a_i P_i / w_i \\ &= a_i / W , \end{aligned}$$

and

$$\sum_{i=1}^{m} y_i = \sum_{i=1}^{M} Y_i ,$$

it follows that

$$E[\hat{\lambda}] = \sum_{i=1}^{M} E[Y_i]/L$$

$$= \sum_{i=1}^{M} a_i/LW \tag{3}$$

$$= \lambda \ .$$

Similarly we can define $Z_j = w_j^{-1}$ with probability P_j and zero otherwise so that

$$E[Z_j] = w_j^{-1}P_j + 0.(1-P_j) = 1/W \ ,$$

$$\sum_{j=1}^{n} w_j^{-1} = \sum_{j=1}^{N} Z_j$$

and

$$E[\hat{D}] = \sum_{j=1}^{N} E[Z_j]/L$$

$$= N/LW$$

$$= D \ .$$

Variance estimates. We note that we have not required the particles to be randomly distributed, only that the line transect be randomly sited. If we require variance formulae for the above estimates, then we need to make some assumption about the distribution of the particles. For example, if the particles are randomly distributed then the Z_j are mutually independent and

$$V[\hat{D}] = \sum_{j=1}^{N} V[Z_j]/L^2$$

where

$$
\begin{aligned}
V[Z_j] &= E[Z_j^2] - (E[Z_j])^2 \\
&= w_j^{-2}P_j - W^{-2} \\
&= \frac{1}{w_j W} - \frac{1}{W^2} \quad .
\end{aligned}
$$

Thus

$$V[\hat{D}] = \frac{1}{L^2 W} \sum_{j=1}^{N} w_j^{-1} - \frac{N}{L^2 W^2} \quad , \tag{5}$$

which has unbiased estimate

$$v[\hat{D}] = \frac{1}{L^2} \sum_{j=1}^{n} w_j^{-2} - \frac{\hat{D}}{A} \quad ,$$

However, finding $V[\hat{\lambda}]$ is much more difficult. Assuming the clumped particles are convex*, an unbiased estimate of $V[\hat{\lambda}]$ is (Lucas and Seber, 1977, equation (10)):

$$
\begin{aligned}
v(\hat{\lambda}) &= \frac{1}{L^2} \sum_{i=1}^{m} \left(y_i^2 - \frac{L\pi}{3A} y_i^3 \right) \\
&\approx \sum_{i=1}^{m} y_i^2 / L^2 \qquad (6)
\end{aligned}
$$

---

*This assumption effectively implies no overlap.

as Ly_i/A will be small. However, such formulae tend to be of largely academic interest only as populations are rarely randomly distributed and the Z_j are usually correlated. In this case, variance estimates are best obtained by replication and by using the following result.

Lemma: Let $x_1, x_2, \ldots, x_k$ be independent random variables with common mean θ and variances σ_i^2 $(i = 1,2,\ldots,k)$. Then

$$E[\Sigma(x_i-\bar{x})^2/k(k-1)] = V[\bar{x}] \; .$$

It is not always appreciated that the above result holds for unequal variances σ_i^2. Thus in practice we would use either k transects or perhaps a single transect divided into k segments to give k estimates of each parameter.

Plant cuticles. The above technique can be used for studying plant cuticles from rumen and fecal analyses. For example we may wish to estimate the proportion, by area, of the leaf cuticles that belong to a given species by examining a slide under a microscope. Thus if there are two species, with dashes representing the second species, we would wish to estimate

$$\pi = \sum_{i=1}^{M} a_i \Big/ \left(\sum_{i=1}^{M} a_i + \sum_{i=1}^{M'} a_i' \right) .$$

Several procedures have been suggested and they all involve choosing a line transect on the slide and noting the particle intersections. The most common method, which might be called the "hit or miss" method or the count method, consists of simply counting the number of cuticles of each species that intersect the line (Anthony and Smith, 1974; Anthony, 1976; Staines, 1976). Although this method is quick and easy, it will only work if the size distribution of each species is the same. Another method, which might be called the squared-intercept method, consists of using the squared lengths y_i^2 (cf., Dunnet et al., 1973). However, this method should not be used as it has no theoretical justification and is not supported by empirical investigations (Seber and Pemberton, 1979). The most natural estimate of π is

$$\hat{\pi} = \sum_{i=1}^{m} y_i \Big/ \left(\sum_{i=1}^{m} y_i + \sum_{i=1}^{m'} y_i' \right)$$

$$= \hat{D}/(\hat{D} + \hat{D}') ,$$

though this estimate will be biased as $E[U/V] \neq E[U]/E[V]$ for correlated random variables U and V. However, if K transects are taken, then a jackknife method is available which gives an approximately unbiased estimate of π, together with a variance estimate: for further details see Seber and Pemberton (1979).

Model (ii)

Let $Z = \sum_{j=1}^{n} w_j^{-1}$, then Z and L are now both random variables with means μ_Z and μ_L, variances σ_Z^2 and σ_L^2 , and covariance σ_{ZL}. From (4) $\mu_Z = N/W$ and, since u has a uniform distribution on [0,W] (Figure 1)

$$\mu_L = \frac{1}{W} \int_0^W L du = A/W$$

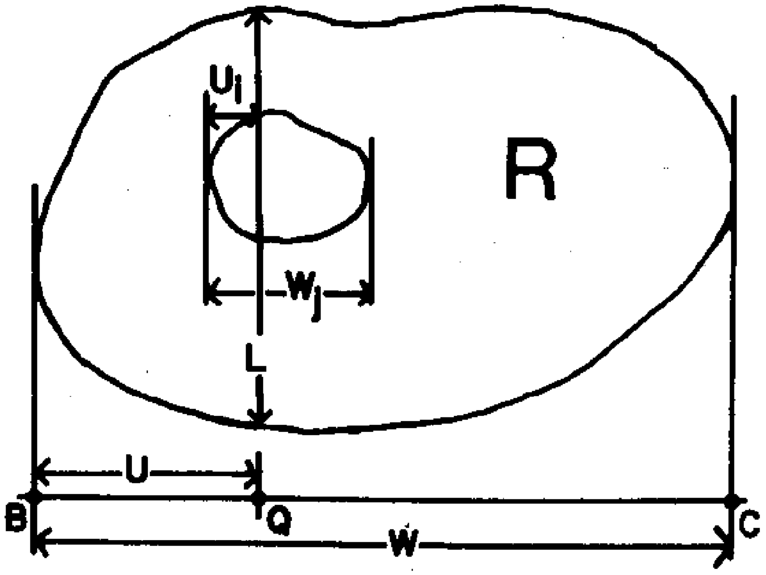

Figure 1 Transect of random length.

Hence, by the δ-method (Seber, 1973:7),

$$\begin{aligned} E[\hat{D}] &= E[Z/L] \\ &\approx \frac{\mu_Z}{\mu_L}\left\{1 + \frac{\sigma_L^2}{\mu_L^2} - \frac{\sigma_{ZL}}{\mu_Z\mu_L}\right\} \\ &= D\{1+b\}\ \text{, say} \end{aligned}$$

and $\hat{D}$ is biased. However, if we use K transects then a jackknife estimate with a small bias can be obtained as follows (Seber, 1979):

Let (L_k,Z_k), $k = 1,2,\ldots,K$, be the observed values of (L,Z) from K transects, and consider the pooled estimate

$$\tilde{D} = \Sigma\, Z_k/\Sigma\, L_k\ .$$

Then, by the δ-method,

$$E[\tilde{D}] \approx D[1 + (b/K)]\ , \tag{7}$$

where the terms neglected are of order K^{-2} if the pairs (L_k,Z_k) are mutually independent, or approximately so. Let $\tilde{D}_{-k}$ $(k = 1,2,\ldots,K)$ be the estimate with the same form as $\tilde{D}$ but based on K-1 transects with the data from transect k omitted. Define

$$D_{(k)} = K\tilde{D} - (K-1)\tilde{D}_{-k}$$

and

$$\tilde{D}_J = \sum_{k=1}^{K} D_{(k)}/K\ .$$

Then $\tilde{D}_J$, the so-called jackknife estimator, has the property that the bias term of order K^{-1} in (7) is now eliminated. Also the variance of $\tilde{D}_J$ can be estimated by

$$s^2 = \sum_{k=1}^{K} (D_{(k)} - \tilde{D}_J)^2/K(K-1) ,$$

and $(\tilde{D}_J - D)/s$ is approximately distributed as the t-distribution with K-1 degrees of freedom.

The jackknife method is reviewed by Miller (1974, mainly theory) and Bissell and Ferguson (1975, practical aspects), and investigated further by Hinkley (1977). Further generalizations, including the so-called "generalized" jackknife, are given by Gray and Schucany (1972) and Sharot (1976 a,b).

If the particles are randomly distributed, then an unbiased estimate of D is available and a regression model can be developed. Thus suppose, for the moment, that L is regarded as fixed and the particles can be moved about at random. Then using the same arguments which led to equations (4) and (5), but with $P_j = Lw_j/A$ (i.e., W is replaced by A/L), we have

$$E[Z|L] = DL$$

and

$$\begin{aligned} V[Z|L] &= \frac{L}{A} \sum_{j=1}^{N} w_j^{-1} - \frac{NL^2}{A^2} \\ &= \frac{L}{A} \sum_{j=1}^{N} \{w_j^{-1} - (L/A)\} \\ &\approx \frac{L}{A} \sum_{j=1}^{N} w_j^{-1} , \end{aligned}$$

since, in practice, $Lw_j << A$. Hence

$$\begin{aligned} E[\hat{D}] &= \underset{L}{E}[Z/L|L] \\ &= \underset{L}{E}[D] \\ &= D , \end{aligned}$$

and $\hat{D}$ is unbiased. If we have K transects, then

$$E[Z_k|L_k] = DL_k$$

and

$$V[Z_k|L_k] \approx \sigma^2 L_k ,$$

where σ^2 is an unknown constant. Thus a plot of Z_k versus L_k should be linear with slope D, and we can obtain a weighted least squares estimate of D, namely

$$\tilde{D} = \Sigma L_k\hat{D}_k/\Sigma L_k = \Sigma Z_k/\Sigma L_k .$$

This has variance estimate

$$v = \hat{\sigma}^2/\Sigma L_k ,$$

where

$$\hat{\sigma}^2 = \Sigma L_k(\hat{D}_k-\tilde{D})^2/(K-1) .$$

Assuming normality, an approximate 95 percent confidence interval for D is given by $\tilde{D} \pm c\sqrt{v}$, where c is the upper 2½ percent point of the t-distribution with K-1 degrees of freedom. The same method can be applied to $\hat{\lambda}$.

Case (iii)

The theory is now complicated by the fact that we have to consider the orientation θ of each object. Here θ could be defined as the angle between the transect and a well-defined chord of the particle as the longest chord. If we treat the angles θ_j as constants and set $P_j = w_j(\theta_j)L/A$, where $w_j = w_j(\theta_j)$ is now a function of θ_j, we find that $E[\hat{D}|\{\theta_j\}] = D$. However, if the transect has a random orientation, that is θ_j has a uniform distribution on $[0,\pi)$, then

$$\begin{aligned} E[\hat{D}] &= \underset{\{\theta_j\}}{E} [\hat{D}|\{\theta_j\}] \\ &= D \ . \end{aligned}$$

Thus for either situation, $\hat{D}$ (and similarly $\hat{\lambda}$) is unbiased: a longer proof, which provides an unbiased estimate of the variance of $\hat{\lambda}$ in a special case, is given by Lucas and Seber (1977).

Forestry applications. Suppose the objects are now needles of length l_j $(j = 1,2,\ldots,N)$ and let x_j be some measurement associated with the jth needle. If the transect is randomly placed with a random orientation, then from the theory of Buffon's famous needle problem (and ignoring boundary effects), the probability that the jth needle intersects the transect is $P_j = 2Ll_j/\pi A)$. Let $X_j = x_j$ with probability P_j and $X_j = 0$ with probability $1-P_j$. Then

$$\begin{aligned} E\left[\sum_{j=1}^{n}(x_j/l_j)\right] &= \sum_{j=1}^{N} E[X_j/l_j] \\ &= \sum_{j=1}^{N} x_j P_j/l_j \\ &= \sum_{j=1}^{N} 2Lx_j/(\pi A) \end{aligned}$$

and

$$\hat{\phi} = \frac{\pi A}{2L}\sum_{j=1}^{n}(x_j/l_j)$$

is an unbiased estimate of

$$\phi = \sum_{j=1}^{N} x_j \ .$$

Thus if the needles represent logs on the forest floor, then possible applications of the above theory are (De Vries, 1979) (i) x_j = volume of jth log so that $\emptyset$ is the total volume in area A, (ii) $x_j = 1$ and $\emptyset = N$, the total number of logs, and (iii) x_j = weight of jth log so that $\emptyset$ is the total weight.

Longest chord. In conclusion, I mention briefly the work of McIntyre (1953) based on the longest chord of a particle parallel to the transect. This method, discussed briefly in Lucas and Seber (1977, 621), requires that all the particles are undistorted magnifications or reductions of a common shape, and is therefore of limited application.

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CAPTURE-RECAPTURE METHODS: CLOSED POPULATION

Introduction

The idea of obtaining information about a population by marking or labelling some of its members can be traced back several centuries. However, two noteworthy applications to ecology were made by Petersen in 1896, using tagged plaice, and Lincoln in 1930, who used band returns to estimate the size of the North American waterfowl population. Since the 1940s the capture-recapture method has been widely used for estimating population numbers and related parameters such as survival and immigration rates. Extensive reviews of the methods are given by Cormack (1968, 1979) and Seber (1973) (referred to as I below), and the technique has been recently considered in relation to estimating the size of a human population from several incomplete lists of the population (cf., Wittes, 1974, for epidemiological applications, and El-Khorazaty et al., 1977, for a general review). A historical overview of the subject is given by Otis et al. (1978).

In discussing the methodology it is convenient to classify populations as either open or closed. A closed population is one which remains unchanged during the experiment so that the population size remains constant and the effects of processes such as migration, mortality, birth, and recruitment are negligible; otherwise the population is said to be open.

Single Recapture

Fixed sample sizes

The simplest mark-recapture experiment, which we shall call the Petersen experiment, for estimating the size N of a closed population consists of catching, marking, and releasing a sample (sample 1) of n_1 animals. After allowing the marked and unmarked to mix, a second representative sample is taken from the population. Equating the proportion of marked in the second sample with the population proportion, n_1/N, of marked leads to an estimate of N. Mathematically, if n_2 is the size of sample 2 and m_2 are found to be marked in this sample, then $m_2/n_2 = n_1/N$ leading to the estimate

$$\hat{N} = n_1 n_2/m_2 \; , \tag{1}$$

the so-called Petersen estimate or Lincoln index (though the term index is misleading). If n_1 and n_2 are regarded as constants and sample 2 is a simple random sample (i.e., a random sample without replacement), m_2 has a hypergeometric distribution with probability function

$$f(m_2\ n_1,n_2) = \binom{n_1}{m_2}\binom{N-n_1}{n_2-m_2} \bigg/ \binom{N}{n_2} \; . \tag{2}$$

It transpires that $\hat{N}$, suitably rounded to an integer, is the maximum likelihood estimate of N for this distribution. However, a modification

$$N^* = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1 \tag{3}$$

is unbiased when $n_1+n_2 \geq N$, and approximately unbiased otherwise. An estimate of the variance of N* with similar properties is also available, and large sample confidence intervals based on N* or $E[m_2]$ $(= n_1 n_2/N)$ can be constructed. Charts are available choosing n_1 and n_2 to achieve a prescribed accuracy of $\hat{N}$ (full details are given in 1, Chapter 3).

In using a Petersen experiment a number of basic assumptions must be satisfied. These can be expressed various ways, but from a practical viewpoint they amount to the following:

(a) The population is closed so that N is constant.

(b) All animals have the same probability of being caught in sample 1.

(c) Marking does not affect the catchability of an animal.

(d) Sample 2 is a simple random sample, i.e., each of the $\binom{N}{n_2}$ possible samples has an equal chance of being chosen.

(e) Animals do not lose their marks between samples.

(f) All marks (or tags) are reported on recovery in sample 2.

The effects of departures from these assumptions on $\hat{N}$ are discussed mathematically in some detail in 1 so we just mention the main points. For example, if (d) is likely to be false, then double tagging can be used to provide a correction factor for the observed number of tagged animals in sample 2: those which have lost one tag can be used to estimate the number losing both. Suppose m_s and m_d are the numbers of animals in sample 2 with single and double tags respectively and let π be the probability of losing a tag (assuming the tags are indistinguishable and independent). Then an estimate of m_2, the (unobservable) number of animals in sample 2 originally tagged in sample 1, is

$$\begin{aligned}\tilde{m}_2 &= m_d/(1-\tilde{\pi})^2 \\ &= (m_s + 2m_d)/2(1-\tilde{\pi}) \\ &= (m_s + m_d)/(1-\tilde{\pi}^2) \ ,\end{aligned}$$

where $\tilde{\pi} = m_s/(m_s + 2m_d)$ and $m_s + m_d$ is the "observed" number of animals tagged in sample 2. This estimate, obtained initially by Chapman et al. (1965, 340), has also been derived independently by Cormack (1968), Caughley (1971), Hubert et al. (1976) and derived theoretically in 1 p. 96 where a large sample variance is also given.

Assumption (f), which is appropriate when the tags are reported by hunters, commercial fishermen, etc., can be tested if part of sample 2 has a 100 percent tag reporting rate--say, by experienced observers. Assumption (d) will depend on (b) and (c) as any variation in the catchability of the animals, whether natural or induced by the handling and marking, will lead to a non-random sample 2. In fact departures from (b) and (c) are difficult to differentiate as a variable catchability means that the more catchable animals are caught in sample 1 and, for a similar method of taking sample 2, the marked will tend to have a higher probability of capture in sample 2: this leads to the underestimation of N. It transpires that in just one case can the effect of variable catchability be eliminated, namely when entirely different methods are used for taking each sample: the catchability in sample 2 is then independent of mark status.

Random sample sizes

Use of the hypergeometric distribution (2) emphasizes the fact that it is basically the activity of the experimenter that brings about random sampling. However, another approach in which randomness is related to the activity of the animals, considers the N animals in the population as N independent multinomial trials, each with the same probability of belonging to a given capture-recapture category. In the Petersen experiment, there are four categories: caught in sample 1 only, caught in sample 2 only, caught in both samples, and caught in neither sample, with respective probabilities P_1, P_2, P_{12} and $Q(= 1-P_1-P_2-P_{12} = 1-P)$. Thus if a_1 $(= n_1-m_2)$, a_2 $(= n_2-m_2)$, $a_{12}(= m_2)$, and $N-a_1-a_2-a_{12}$ $(= N-r$, where r is the total number of different animals caught in the experiment) are the numbers caught in the four categories, then the joint probability function of the random variables a_1, a_2 and a_{12} is

$$f(a_1,a_2,a_{12}) = \frac{N!}{a_1!a_2!a_{12}!(N-r)!} P_1^{a_1}P_2^{a_2}P_{12}^{a_{12}}Q^{N-r} \qquad (4)$$

If $p_i(= 1-q_i)$ is the probability of capture in sample i, and samples are independent so that capture in sample 1 does not affect capture in sample 2, then $P_1 = p_1q_2$, $P_2 = q_1p_2$, $P_{12} = p_1p_2$ and $Q = q_1q_2$. Now the triple (a_{12},a_1,a_2) determines the triple $(a_{12},\ a_1+a_{12},\ a_2+a_{12})$, and vice versa, so that substituting for the P's gives us

$$\begin{aligned} f(m_2,n_1,n_2) &= f(a_1,a_2,a_{12}) \\ &= \frac{N!}{(n_1-m_2)!(n_2-m_2)!m_2!(N-r)!} p_1^{n_1}q_1^{N-n_1}p_2^{n_2}q_2^{N-n_2} \\ &= f(m_2|n_1,n_2) \prod_{i=1}^{2} \left\{ \binom{N}{n_i} p_i^{n_i}q_i^{N-n_i} \right\} \\ &= f(m_2|n_1,n_2)f(n_1,n_2) , \end{aligned} \qquad (5)$$

where $f(m_2|n_1,n_2)$ is given by (2). Thus (5) follows from (2) by simply treating the sample sizes n_i as random variables. If the sample sizes are fixed, (2) is the appropriate model. On the other hand, if the experimenter controls the sampling procedure by the effort he puts in, that is fixes p_1 and p_2, then (5) is the appropriate model. However, under (5), $\hat{N}$ of (1) is still the maximum likelihood estimate with essentially the same asymptotic variance. The fact that sample sizes can be treated as fixed or random with little change in the theory is a common feature of capture-recapture models. It stems from the fact that for large samples, n_i and $E[n_i]$ are essentially interchangeable. Thus if $\underset{\sim}{x}$ represents the set (n_1,n_2) and $E[\underset{\sim}{x}] = \underset{\sim}{\theta}$, then, since $E[\hat{N}|n_1,n_2] \approx N$,

$$\begin{aligned} \mathrm{var}[\hat{N}|n_1] &= \underset{n_1}{E}\{\mathrm{var}[\hat{N}|\underset{\sim}{x}]\} + \underset{n_1}{\mathrm{var}}\{E[N|x]\} \\ &\approx \underset{n_1}{E}\{\mathrm{var}[\hat{N}|\underset{\sim}{x}]\} + \underset{n_1}{\mathrm{var}}\{N\} \\ &= \underset{n_1}{E}\{g(x)\} + 0, \text{ say} \end{aligned}$$

Similarly

$$\begin{aligned} \mathrm{var}[\hat{N}] &\approx \underset{\underset{\sim}{x}}{E}\{g(\underset{\sim}{x})\} \\ &\approx g\{\underset{\sim}{\theta}\} \quad \text{(to first order of approximation)} \\ &= \{\mathrm{var}\ [\hat{N}|x]\}_{\underset{\sim}{x} = \underset{\sim}{\theta}} \end{aligned}$$

In estimating variances we replace expected random variables by random variables so that estimates based on var $[\hat{N}]$ and var $[\hat{N}|\underset{\sim}{x}]$ are essentially equivalent.

In practice, samples are frequently neither completely fixed in advance nor completely random as other factors such as finance, weather, etc., can affect the length of an experiment, once it has started. For this reason there has been some interest in sequential-type experiments in which sample 2 is continued until a prescribed number of marked or unmarked are caught in sample 2 (cf., 1, p. 118). A Bayesian analysis of the problem and a comparison with other schemes is given by Freeman (1973 a,b). Kuno (1977) describes a model in which the second sample if continued until N is estimated with a prescribed coefficient of variation.

Sometimes sample 2 is taken with replacement, for example when the animals are merely observed and not actually captured. In this case $f(m_2|n_1,n_2)$ is binomial with parameters n_2 and $p = n_1/N$. Further details of these modifications are given in 1.

Multiple Recaptures

Maximum likelihood estimation

A natural extension of the Petersen experiment is the so-called Schnabel experiment or multiple recapture census in which $s (s > 2)$ consecutive samples are taken from the population. If n_i animals are caught in sample i, and m_i are the number found to be marked on a previous sampling occasion, then the $u_i (= n_i - m_i)$ unmarked are given a mark and the whole sample returned to the population. If individual numbered marks or tags are used, then animals have to be tagged only once, the first time they are caught. Depending on whether the n_i are regarded as fixed or random both the hypergeometric and multinomial models readily generalize to this case. For example, (4) now becomes

$$f(\{a_w\}) = \frac{N!}{\prod_w a_w!(N-r)!} Q^{N-r} \prod_w p_w^{a_w} \tag{6}$$

$$= \frac{N!}{\prod_w a_w!(N-r)!} \prod_{i=1}^{s} p_i^{n_i} q_i^{N-n_i} , \tag{7}$$

where w is a label describing membership of one of the 2^s-1 capture categories. The maximum likelihood estimate, $\hat{N}$, is close to the unique root, greater than r, of the $(s-1)$th degree polynomial

$$\left(1 - \frac{r}{N}\right) = \prod_{i=1}^{s} \left(1 - \frac{n_i}{N}\right) .$$

This equation is simply an expression of the fact that $Q = q_1 q_2 \ldots q_s$; r is binomial with parameters N and $P (= 1-Q)$. A more accurate procedure is the replace p_i by n_i/N in $f(\{a_w\})$ and then maximize the logarithm of the resulting expression with respect to N (Otis et al., 1978; model M_t).

The corresponding hypergeometric model $f(\{a_w\}|\{n_i\})$ leads to the same maximum likelihood estimate $\hat{N}$ and asymptotic variance. In this case, r is sufficient for N so that $f(\{a_w\}|r)$ contains the same information about N. Using some general theorems about a class of factorial series distributions, of which $f(\{a_w\}|r)$ is a member, Berg (1976) obtains a ratio type estimate $\tilde{N}$ which is minimum variance unbiased if $N \leq \Sigma n_i$. He provides a useful recurrence relation for overcoming some of the computational difficulties in finding $\tilde{N}$ and its variance estimate. When $s = 2$, $\tilde{N}$ reduces to (3).

Log-linear models

Another method of estimating N from a Schnabel census which shows some promise is to use the theory of incomplete contingency tables. Since there are s samples, the number of different capture histories is 2^s which can be arranged in an s-dimensional contingency table. However the number of animals in one of the cells, namely the N-r animals not caught at all, is unobservable so that the contingency table is incomplete. By fitting a suitable log-linear model to the rest of the table, N can be estimated. A variety of models can be fitted depending on how many interaction terms are included. These interaction terms correspond to dependencies between various samples and for brief readable discussions of the problem see Bishop et al. (1975, chapter 6) and Cormack (1979). When the samples are independent so that all the interactions are zero, the estimate of N obtained is simply $\hat{N}$.

Modelling catchability

We note that the assumptions underlying the Petersen method must apply to all the samples in a Schnabel census so that any departures from these assumptions can seriously affect the validity of $\hat{N}$. Since variation in catchability seems to be a fact of life, a general package of models has been developed by Otis et al. (1978), which allows this variation to be modelled in various ways. They present six models: M_t (variation with trapping occasion or _t_ime, given by (7)), M_b (variation by _be_havioural responses, e.g., trap shyness or addiction), M_h (variation by individual response or _h_eterogeneity, e.g., size selectivity in electrofishing) and various combinations M_{tb}, M_{bh}, M_{th} and M_{tbh}. The authors also include the model M_0 in which there is no variation (i.e., (7) with $p_i = p$), and a generalized removal model in which removal corresponds to tagging.

If p_{ij} is the probability that the ith animal ($i = 1,2,\ldots,N$) is caught in the jth sample ($j = 1,2,\ldots,s$), and we can assume that the animals are independent of one another as far as catching is concerned, then the likelihood function is

$$\prod_i \prod_j p_{ij}^{x_{ij}} \cdot (1 - P_{ij})^{1-x_{ij}} ,$$

where $x_{ij} = 1$ if the ith animal is caught in the jth sample and $x_{ij} = 0$ otherwise. The various models can now be described mathematically by specifying p_{ij}, for example $M_t(p_{ij} = p_j)$, $M_h(p_{ij} = p_i$ where the p_i are a a random sample from some distribution), M_{bh} ($p_{ij} = p_i$ for any first capture and $p_{ij} = c_i$ for any recapture) etc. A standard algorithm is used to calculate the maximum likelihood estimates for the models M_0, M_t, M_b and M_{bh}, the last model being regarded as the most realistic and the most useful. The method used for analysing M_{bh} can also be applied to so-called "removal" experiments in which animals are removed from the population on capture. Suitable estimation procedures are not yet available for M_{bt}, M_{th} and M_{tbh}, but a generalized jackknife estimator due to Burnham (cf., Burnham and Overton, 1978) is available for M_h. This method utilizes the data on frequency of capture and largely replaces various other ad hoc frequency of capture models which have been shown to be unreliable for estimating the number (N-r) with zero frequency (cf., Cormack, 1979). Otis et al. (1978) discuss the robustness of these estimates and the usual confidence intervals estimate ± 1.96 standard deviation. They give a procedure for selecting a model and discuss the important aspects of design relating to number of traps, trap spacing and number of samples s. The authors also discuss various tests of closure, including one of their own, and conclude from the general insensitivity of these tests that the best evidence for closure is biological rather than statistical. The experiment should be designed to approximate closure, otherwise more general methods such as those described in I chapter 5 should be used.

Converting Totals to Densities

A major problem in population studies which has received insufficient attention in the literature is the conversion of total counts, or counts on sample plots, to density estimates. If grid trapping is used, then simply dividing the total count (N) on the grid by the area enclosed (A) by the grid will generally lead to a severe overestimation of the population density. This problem is due to what is commonly known as "edge effect"; that is, traps on the boundary of the trapping area tend to catch more animals than inner traps. This edge effect is due to immigrants, and animals living outside the trapping area which have home ranges overlapping the trapping region.

Following Dice (1938), a common technique for calculating the effective trapping area is to add to A a strip of width W, where 2W (= R) is some linear measure such as the average diameter of the home range of an animal.

Home range estimation

Circles or ellipses. Although numerous methods of estimating the shape and area of the home range from recapture data have been suggested, particularly for small mammals, they are generally unsatisfactory as they are basically ad hoc and the results tend to vary with trap spacing (Faust et al., 1971), number of captures (see below), species, season (Briese and Smith, 1974), and size of study area (Wierzbowska, 1975, 17). The concept of the center of activity has also been criticized on the grounds that it may not have any biological significance (Siniff and Jessen, 1969; Wierzbowska, 1972; Smith et al., 1973; Koeppl et al., 1975, 86): it is simply an average of points of contact (Hayne, 1949). In the past, circular home ranges were widely used, though ellipses now appear to be more popular (cf., Jennrich and Turner, 1969; Tanaka, 1972; and, for further references, Mazurkiewicz, 1971 and Wierzbowska, 1975). However, Metzgar (1973a), using smoked-paper tracking and the Kolmogorov-Smirnov test, judged that 10 of his 22 home ranges were circular. Also Maza et al. (1973) "failed to find evidence to indicate that the home range is other than circular." A number of authors effectively assume a circular home range by their use of the term recapture radius (Burge and Jorgensen, 1973).

Bivariate distributions. As the probability of capture tends to decrease with increasing distance from the "center" of the home range, various bivariate distributions have been fitted to the distribution of probability: this concept has recently been extended to three-dimensional home ranges (Koeppl et al., 1977; Meserve, 1977). Although the bivariate normal provides a reasonable model in many situations (e.g., circles--Calhoun and Casby, 1958; Maza et al., 1973; circles and ellipses, Van Winkle, 1975: ellipses--Mazurkiewicz, 1971; Koeppl et al., 1975; Dunn and Gipson, 1977; Randolph, 1977; Hawes, 1977), there are cases when it is not appropriate (e.g., Metzgar, 1972, 1973a) and a more general bivariate model is required. For example, for a nonhomogeneous habitat such as an ecotone, Van Winkle et al. (1973) present a non-normal model with independent marginal distributions. However, several authors (Tanaka, 1974, 126) feel that the above bivariate models are inappropriate for mammal populations, particularly small rodents, and recommend methods which do not require the concept of center of activity, or any assumptions about the shape of the home range; for example, the method of Wierzbowska (1972). In comparing various methods Wierzbowska (1975) concludes that her own 1972 method and a method of Tanaka (1972), who proposes using $W = \sqrt{ab}$ where 2a and 2b are the observed range length and width (ORL and ORW respectively), are the most versatile methods. Wierzbowska uses the concept of a random walk which also forms the basis of further, but laborious, methods proposed by Morisita (cf., Tanaka, 1974). However, the assumption of random walking over a home range may be unrealistic (Ambrose, 1969; Siniff and Jessen, 1969). A further problem is that there may be parts of the grid area which are seldom or never entered by animals (Wallin, 1971).

Trap-revealed range. One of the difficulties of the trapping method is that the home range of an animal may change during the course of an experiment. This could lead to an animal visiting more different traps with a consequent overestimate of the home range area (Andrzejewski and Wierzbowski, 1970). Even if the home range remains unchanged there will be a tendency for the trap-revealed range to grow as the number of captures increases, but it will level off after a certain number of captures. Some authors put this figure at 10; others at 6, 5, or even 2 if the population is large enough (Wierzbowska, 1975, 56). It is clear that stochastic methods are needed for assessing trapping data rather than using such simple expedients as joining up outermost points (and possibly adding a strip of width equal to half the trap spacing) to obtain a map of the home range. Another problem in home range studies is to distinguish between the permanent resident and the immigrant. At present there seems to be a lack of objective methods for distinguishing the occasional sally from the normal home range movements.

We conclude that it is not easy to get an accurate picture of the shape and size of the home range using trapping as trapping can affect animal behavior. For this reason the home ranges of small mammals have also been studied using radio telemetry (e.g., Doebel and McGinnes, 1974; Trent and Rongstad, 1974;

Banks et al., 1975; and, for a mathematical analysis, Dunn and Gipson, 1977); remote censusing (Marten, 1972, 1973); radioactive tracers (Ambrose, 1969, 1973); Gentry, Smith, and Beyers, 1971); footprints on smoked paper (Metzgar, 1973a) or in the sand (Sarrazin and Bider, 1973); and bait with fluorescent pigment (Franz, 1972) or colored wool (Ryszkowski, 1971). An interesting comparison of trap- and track-revealed home ranges in *Peromyscus* is given by Metzgar (1973b): see also Metzgar (1973c). An index of home range size based on an exponential model is given by Metzgar and Sheldon (1974).

Radio telemetry

In recent years telemetry has been used extensively for studying the movements and behavior of animals. At present I have a bibliography of over 80 articles published in the 1970s describing the application of radio tracking to many species of birds, mammals and fish (for a review of the latter see Stasko and Pinock, 1977). Although the bibliography is incomplete it does at least indicate the considerable possibilities of such a method. Some of the papers refer to the design and monitoring aspects of a radio transmitter (e.g., design - Kolz et al., 1972, 1973; Corner and Pearson, 1972; Luke et al., 1973; Bray and Corner, 1972; Pedersen, 1977; monitoring - Gilmer et al., 1971, 1973; Lund, 1974; Hutton et al., 1976; Hoskinson, 1976, Whitehouse and Steven, 1977; Wolcott, 1977), and transmitters are sometimes used to relay other physiological information such as body temperature and heart rate (Lonsdale et al., 1971, Skutt et al., 1973, Kolz et al., 1973, Langman, 1973). However, transmitters should be properly designed for the particular species being investigated as they can modify the behavior of an animal. This has been demonstrated clearly in the case of birds (cf., Gilmer et al., 1974) where a package which appears satisfactory for one sex or one avian species may not be tolerated by the other sex or another even closely related species. Unfortunately, there do not appear to be many articles on the effects of radio packages and comparing them with other forms of tagging: some of these studies are Boag (1972), Boag et al. (1973), Gilmer et al. (1974), Brand et al. (1975), McCleave and Stred (1975), Lance and Watson (1977), and Facey et al. (1977).

Assessment lines

Even if the home range is known accurately there is still the problem of choosing W, some appropriate linear measure of the home range. Clearly the simplest approach is to treat W as an unknown parameter and devise a model for the joint estimation of N and W. One such approach involves the use of assessment lines which are generally lines of equally spaced traps cutting the sides of the trapping grid (usually at right angles) and extending from within the grid to out beyond the effective trapping area. An assessment line can hopefully be used to "calibrate" the trapping rate across the boundary of the grid, and the points of discontinuity of this rate along the line provide an estimate of W (Smith et al., 1971; O'Farrell et al., 1977; it is also used for the removal method). However, this method is somewhat subjective and an alternative method of estimating the effective trapping area is given by Swift and Steinhorst (1976). They make use of the plausible assumption that the marked proportion of animals caught in a segment of an assessment line falls off to zero as the edge of the effective trapping area is approached.

A different assessment method is given by H. D. Smith et al. (1972), who surround the grid by a dense band of traps, which they call a dense line. These traps provide information on other parameters, such as mortality and migration numbers, as well as population size. An extension of this method which is supposed to apply even if the band is omitted is given by Jorgensen et al. (1975). These various methods are also surveyed in Smith et al. (1975). However, the above methods of determining the effective trapping area are rather subjective and depend very much on trial and error. Several authors (Hagen et al., 1973; Tanaka, 1974; Barbehenn, 1974; and Tanaka and Murakami, 1977, 118) do not support the use of assessment lines on the grounds of unrealistic assumptions and the labor involved in the field.

Method of selected grids

An alternative approach to the problem is to estimate W directly from a series of selected grids. The key assumption is that W is independent of the grid size so that for the kth grid (k = 1,2,...,K)

$$N_k = D(A_k + P_k W + \pi W^2) , \qquad (8)$$

where D is the population density, and N_k, A_k and P_k are the "effective" population size, the area and perimeter respectively of the kth grid. MacLulich (1951) suggested using two such grids and solving the pair of equations for D and W, with each N_k replaced by its estimate $\hat{N}_k$.

Hansson (1969) suggests using a single grid and assumes that there is an inner subgrid for which the edge effect is negligible. However, Tanaka (1972) gives evidence that the edge effect, although decreasing as you move into the center of the trapping grid, does not vanish for some central area.

Another method which avoids much of the subjectivity associated with the previous method is described by Otis et al., 1978. They suggest using a single large grid and selecting K subgrids nested within each other inside the grid. If $y_k = \hat{N}_k/A_k$ then we have a nonlinear regression model of the form

$$y_k = D(1 + a_k W + b_k W^2) + e_k , \quad k = 1,2,\ldots,K ,$$

where the a_k and b_k are known constants (cf., eqn.(8)), and $E[e_k] = 0$ if $\hat{N}_k$ is unbiased. As the grids are nested, the y_k, and therefore the "errors" e_k, will be correlated. The authors suggest putting the correlation between y_j and y_k equal to the proportion of overlapping area between grids j and k (including their boundary strip), and carrying out a generalized nonlinear least squares to estimate D and W. The estimates $\hat{N}_k$ can be based on either removal trapping or capture-recapture data. Useful practical details about the design of such an experiment with regard to choosing the number of traps, trap-spacing, etc., are given in Otis et al. (1978).

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THE MULTI-SAMPLE SINGLE RECAPTURE CENSUS

General Model

We shall consider a particular capture-recapture model that has wide applications to exploited open populations. In this model the animals are removed on capture and tagged animals are released into the population from outside as, for example, in birdbanding and fisheries. We therefore have several samples, but animals are only recaptured once: for this reason, I call the model the multi-sample single recapture census (Seber, 1962 and 1973, called *I* below). Contrary to the usual capture-recapture models for open populations, we shall allow the possibility of releases and recapture samples being made at different times.

Suppose that releases are made at times $t_1, t_2, \ldots, t_s$ and recapture samples are taken at times $t'_1, t'_2, \ldots, t'_s, \ldots, t'_{s+k}$ where $t_1 < t'_1 \leq t'_2 \leq \ldots \leq t_s < t'_s < t'_{s+1} \ldots < t'_{s+k}$. We are allowing for the possibility of k further recapture samples at times $t'_{s+1}, \ldots t'_{s+k}$ without corresponding releases. The following assumptions are now made:

(a) Every marked individual has the same probability p_i $(= 1-q_i)$ of being caught in the ith sample at time t'_i, given that it is alive and in the population just before time t'_i $(i = 1,2,\ldots,s+k)$.

(b) For $i = 1,2,\ldots,s$, every marked individual has the same probability $1-\phi_i$ of dying or permanently emigrating in the time interval t_i to t'_i, given that it is alive and in the population just after the ith release at time t_i.

(c) For $i = s+1, s+2, \ldots, s+k$, every marked individual has the same probability $1-\phi_i$ of dying or permanently emigrating in the time interval t'_{i-1} to t'_i, given that it is alive and in the population just after the ith release time t'_{i-1}.

(d) Every marked individual has the same probability $1-\varphi_i$ of dying or permanently emigrating in the interval t'_{i-1} to t_i, given that it is alive and in the population just after the sample at time t'_{i-1} $(i = 2,\ldots,s)$.

(e) Either there is no emigration, or the emigration is permanent, so that emigrants can be regarded as being "dead."

Thus if m_{ij} is the number from release i caught in sample j, the joint distribution of the m_{ij} is proportional to (see Figure 5.1)

$$\prod_{i=1}^{s}\left\{\beta_i^{m_{ii}}(\alpha_i\beta_{i+1})^{m_{i,i+1}}\cdots(\alpha_i\alpha_{i+1}\cdots\alpha_{t-1}\beta_t)^{m_{it}}\,(1-\theta_i)^{R_i-r_i}\right\} = \tag{1}$$

$$\prod_{i=1}^{s-1}\left\{\alpha_i^{T_i-m_i}\beta_i^{m_i}(1-\theta_i)^{R_i-r_i}\right\}\beta_s^{m_s}\,(1-\theta_s)^{R_s-r_s}\gamma_s^{m_{s+1}}\cdots\gamma_t^{m_t}\ ,$$

where

$$t = s+k\ ,$$

$$\beta_i = \phi_i p_i\ (i = 1,2,\ldots,t)\ , \tag{2}$$

$$\alpha_i = \begin{cases}\phi_i q_i \varphi_{i+1} & (i = 1,2,\ldots,s-1)\\ \phi_i q_i & (i = s,\ldots,t)\ ,\end{cases} \tag{3}$$

$$\gamma_j = \alpha_s\alpha_{s+1}\cdots\alpha_{j+1}\beta_j\ (j = s+1,\ldots,t)\ ,$$

and

$$\theta_i = \beta_i + \alpha_i\beta_{i+1} + \ldots + \alpha_i\alpha_{i+1}\cdots\alpha_{t-1}\beta_t\ ,$$

where θ_i is the probability of recapture from the ith release. Here R_i is the

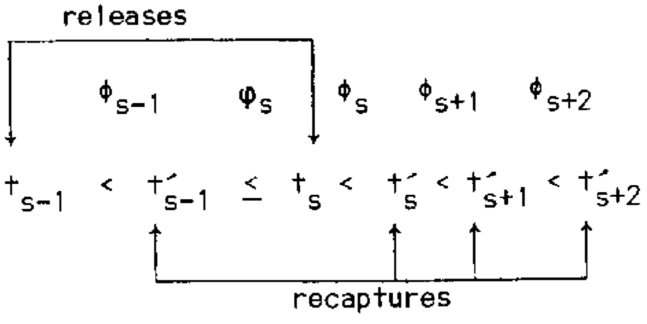

Figure 5.1 Pattern of survival probabilities.

number in the ith release, r_i is the number recovered from R_i, m_i is the number of recaptures (marked) in the ith sample, and T_i is the number of different individuals recaptured in the ith sample or later from releases made prior to the ith sample. Thus $T_i - m_i$ (= $T_{i+1} - r_{i+1} = z_{i+1}$) is the number recovered after the ith sample from releases made prior to the ith sample or, expressed another way, the number recovered after the (i+1)th release from releases prior to the (i+1)th release. (For this latter reason I have denoted this number by z_{i+1} in 1 rather than z_i as the theory also applies to bird-banding models.) The maximum likelihood estimates for the estimable parameters in (1) are:

$$\hat{\alpha}_i = \frac{T_i - m_i}{T_i} \cdot \frac{r_i}{R_i} \cdot \frac{R_{i+1}}{r_{i+1}} \ , \ (i = 1,2,\ldots,s-1), \tag{4}$$

$$\hat{\beta}_i = \frac{m_i}{T_i} \cdot \frac{r_i}{R_i} \ , \ (i = 1,2,\ldots,s) \ , \tag{5}$$

$$\hat{\gamma}_j = \hat{\beta}_s \frac{m_j}{m_s} \ , \ (j = s+1,s+2,\ldots,t) \ ,$$

and

$$\hat{\theta}_i = \frac{r_i}{R_i} \ .$$

Now Robson and Youngs (1971) show that the conditional distribution of m_i, given r_i and T_i, is binomial, namely

$$f(m_i | r_i, T_i) = \binom{T_i}{m_i} \left(\frac{\beta_i}{\theta_i}\right)^{m_i} \left(1 - \frac{\beta_i}{\theta_i}\right)^{T_i - m_i} \ ,$$

which indicates that m_i is independent of r_i. Thus, since $E[r_i] = R_i \theta_i$,

$$\begin{aligned} E[\hat{\beta}_i] &= \underset{r_i}{E}\, E[\hat{\beta}_i | r_i] \\ &= \underset{r_i}{E}\left[\frac{\beta_i}{\theta_i} \cdot \frac{r_i}{R_i}\right] \\ &= \beta_i \quad , \end{aligned}$$

and $\hat{\beta}_i$ is unbiased. Similarly, writing

$$\hat{\alpha}_i = \left(\frac{r_i}{R_i} - \hat{\beta}_i\right) \Big/ \left(\frac{r_{i+1}}{R_{i+1}}\right) ,$$

and noting that the numerator and denominator are statistically independent, leads to

$$E[\alpha_i] = (\theta_i - \beta_i)R_{i+1}\, E[r_{i+1}^{-1}] .$$

Since r_{i+1} is binominal with parameters R_{i+1} and θ_{i+1} we can make the usual adjustment for bias based on the binomial distribution, namely

$$\alpha_i^* = \frac{T_i - m_i}{T_i} \cdot \frac{r_i}{R_i} \cdot \frac{R_{i+1} + 1}{r_{i+1} + 1} .$$

Since $\theta_i - \beta_i = \alpha_i\theta_{i+1}$ we have

$$\begin{aligned} E[\alpha_i^*] &\simeq \alpha_i \left\{1 - (1 - E[r_{i+1}/R_{i+1}])^{R_{i+1} + 1}\right\} \\ &= \alpha_i \left\{1 - (1 - \theta_{i+1})^{R_{i+1} + 1}\right\} . \end{aligned}$$

and α_i^* is approximately unbiased. The large sample variances and covariances of the α_i^* will be the same as those of the $\hat{\alpha}_i$, namely

$$V[\hat{\alpha}_i] \simeq \alpha_i^2 \left\{ \frac{1}{E[r_i]} + \frac{1}{E[r_{i+1}]} + \frac{1}{E[T_i - m_i]} + \frac{1}{E[R_i]} - \frac{1}{E[R_{i+1}]} - \frac{1}{E[T_i]} \right\} ,$$

$$\mathrm{cov}[\hat{\alpha}_i, \hat{\alpha}_{i+1}] \simeq \alpha_i \alpha_{i+1} \left\{ \frac{1}{E[r_{i+1}]} - \frac{1}{R_{i+1}} \right\}$$

and

$$\mathrm{cov}[\hat{\alpha}_i, \hat{\alpha}_j] \simeq 0 , \quad j > i+1 .$$

A general goodness of fit test of the model is given by

$$T = \sum_{i=1}^{s} \sum_{j=1}^{t} (m_{ij} - E_{ij})^2 / E_{ij} ,$$

which is approximately distributed as chi-squared with $(s-1)(t-1)-\frac{1}{2}s(s-1)$ degrees of freedom when the model is true. Here

$$E_{ii} = R_i \hat{\beta}_i \quad (i = 1,2,\ldots,s) ,$$

$$E_{ij} = \begin{cases} R_i \hat{\alpha}_i \hat{\alpha}_{i+1} \ldots \hat{\alpha}_{j-1} \beta_j & (j = i+1,\ldots,s) \\ R_i \hat{\alpha}_i \hat{\alpha}_{i+1} \ldots \hat{\alpha}_{s-1} \hat{\gamma}_j & (j = s+1,\ldots,t) \end{cases} ,$$

and the terms involving $R_i - r_i$ are not included in T as their contribution is zero (since $R_i - r_i - R_i(1-\hat{\theta}_i) = 0$).

Unfortunately, the basic parameters ϕ_i, p_i, and φ_i (cf., (2) and (3)) are not estimable unless some constraints are applied to reduce the number of free parameters. In Seber (1962), we assumed that releases are made immediately after recaptures so that $t_i' = t_{i+1}$ and $\varphi_{i+1} = 1$.

Manly (1974), however, assumed that the survival probability per unit time is constant for the interval between any two releases (though it may vary from interval to interval). This implies that for the time interval (t_i, t_{i+1}) we have

$$\phi_i = \psi_i^{1-\Delta_i} \quad \text{and} \quad \varphi_{i+1} = \psi_i^{\Delta_i}, \quad (i = 1,2,\ldots,s-1)$$

where $\Delta_i = (t_{i+1} - t_i')/(t_{i+1} - t_i)$, and $\psi_i = \phi_i \varphi_{i+1}$ may be interpreted as the probability of "natural" survival (that is, ignoring the recapture sample). Since we now have a one-to-one correspondence between the parameters (α_i, β_i) and (ψ_i, p_i), the maximum likelihood estimates $\hat{\psi}_i, \hat{p}_i$ satisfy $\hat{\alpha}_i = \hat{\psi}_i \hat{q}_i$ and $\hat{\beta} = \hat{\psi}_i^{1-\Delta_i} \hat{p}_i$. Thus for $i = 1,2,\ldots,s-1$,

$$\hat{\psi}_i - \hat{\beta}_i \hat{\psi}_i^{\Delta_i} = \hat{\alpha}_i$$

and

$$\hat{p}_i = \hat{\beta}_i \hat{\psi}_i^{\Delta_i - 1}$$

which can be solved for $\hat{\psi}_i$ and $\hat{p}_i$. Using the delta-method Manly shows that, asymptotically,

$$V[\hat{\psi}_i] = \psi_i^2 \left\{ \frac{p_i^2}{E[m_i]} + \frac{(1-p_i)^2}{E[z_{i+1}]} - \frac{1}{E[T_i]} + \frac{1}{E[r_i]} - \frac{1}{R_i} + (1-p_i)^2 \left(\frac{1}{E[r_{i+1}]} - \frac{1}{R_{i+1}} \right) \right\} / (1 - \Delta_i p_i)^2 ,$$

$$\text{cov}[\hat{\psi}_i, \hat{\psi}_{i+1}] = \frac{-\psi_i \psi_{i+1} (1-p_i)}{(1-\Delta_i p_i)(1-\Delta_{i+1} p_{i+1})} \left(\frac{1}{E[r_{i+1}]} - \frac{1}{R_{i+1}} \right)$$

and

$$\mathrm{cov}[\hat{\psi}_i,\hat{\psi}_j] = 0 , \qquad j > i + 1 .$$

Estimates are obtained by replacing expectations by random variables.

Manly (1974) describes an application of the above theory to a moth population where it was found convenient to make releases in the mornings and recapture samples in the evenings. He also considers a special case of the above model in which $p_i = p$ and $\psi_i = \psi$ (Manly, 1975a,b, 1977).

Exploitation Model

Estimation. In I we showed that the multi-sample single recapture census could be applied to the situation where the sampling (exploitation) is continuous and tag releases are made at the beginning of each year. Here α_i is now the probability of an individual surviving the ith year, and, as it refers to survival from both natural and exploitation mortality, is sometimes called the total survival rate for year i. The parameter β_i is the probability that an individual is caught and its tag recovered in year i : β_i is sometimes referred to as the observed exploitation rate for year i. As the model for this new situation is still given by (1) estimates of α_i and β_i are given by equations (2) and (3). Noting the equivalences $z_{i+1} = T_i - m_i$ and $r_i + z_i = T_i$, approximate expressions for the variances and covariances of the $\hat{\alpha}_i$ are given above. In fisheries the observed exploitation rate is an important parameter in its own right so we include the following results:

$$V[\hat{\beta}_i] \approx \beta_i^2 \left\{ \frac{1}{E[r_i]} - \frac{1}{R_i} + \frac{1}{E[m_i]} - \frac{1}{E[T_i]} \right\}$$

and

$$\mathrm{cov}[\hat{\beta}_i,\hat{\beta}_j] \approx 0 \quad \text{for} \quad i \neq j .$$

If we use the notation $\alpha_i \rightarrow S_i$ and $\beta_i \rightarrow E_i^*$, and replace expected random variables by the random variables, the above variance and covariance expressions for the $\hat{\alpha}_i$ and $\hat{\beta}_i$ lead to the estimates given by Youngs and Robson (1975). These authors also give a number of useful graphs for planning such studies, and the following discussion is based on their paper, with the above changes in notation.

Experimental design. Assuming $\alpha_i = \alpha$, $\beta_i = \beta$ and $R_i = R$ for $i = 1,2,\ldots,s$, it can be shown that

$$RV[\hat{\alpha}_i] \simeq \frac{\alpha^2}{\beta}\left[\frac{1-\alpha^2}{\alpha(1-\alpha^{s-i})} - \frac{(1-\alpha)^2(1-\alpha^{i-1})}{(1-\alpha^i)(1-\alpha^{s-i})(1-\alpha^{s-i+1})} - 2\beta\right]$$

$$(= R\sigma^2[\hat{\alpha}_i] \text{ , say) ,}$$

and the authors give graphs of $\sqrt{R}\,\sigma[\hat{\alpha}_1]$ versus α for $\beta = 0\cdot01$, $0\cdot1$ and $0\cdot3$, and different s (= k in their notation). Suppose that a fishery manager wishes to estimate the survival probability for the first year of study of a three-year release program and be within $\pm\ 0\cdot1$ with 95 percent confidence. Then using the approximate confidence interval $\hat{\alpha}_1 \pm 2\sigma[\hat{\alpha}_1]$, we have that $2\sigma[\hat{\alpha}_1] = 0.1$ or $\sigma[\hat{\alpha}_1] = 0\cdot05$. Suppose further that preliminary studies have indicated $\alpha \simeq 0\cdot6$ and $\beta \simeq 0\cdot1$. Then entering Figure 5.2 with $\alpha = 0\cdot6$ and $s = 3$ we have $\sqrt{R}\sigma[\hat{\alpha}_1] = 2\cdot3$ or $R = (2\cdot30/0\cdot05)^2 = 2116$ so that 2116 tags must be released at the beginning of each of the three years. If a graph is not available for a particular β then, for a conservative R (i.e., too many tags), we would choose the nearest value below β which is graphed. Now the maximum value of $\sigma[\hat{\alpha}_i]\sqrt{R}$ is a function of β and occurs when $i = 2$ and $s = 3$ with α at its maximum value. This relationship is shown graphically in Figure 5.3 and gives an upper bound on the number of tags that need to be released each year in order to have at least the desired level of confidence.

Hypothesis testing. Youngs and Robson (1975) also give a number of test procedures for testing the above model (1). As pointed out by Robson and Youngs (1971), a test of the model can be obtained from the distribution of the $\{m_{ij}\}$ conditional on the sufficient statistics $(r_1,r_2,\ldots,r_s,T_2,\ldots,T_s)$. This conditional distribution has "rank"

$$s(s+1)/2 - (2s-1) = (s-1)(s-2)/2 = 1 + 2 + \ldots + s - 2 \qquad (6)$$

and may be expressed as a product of multi-hypergeometric distributions of successively smaller "ranks" $s-2$, $s-3,\ldots,1$. Each distribution leads to an

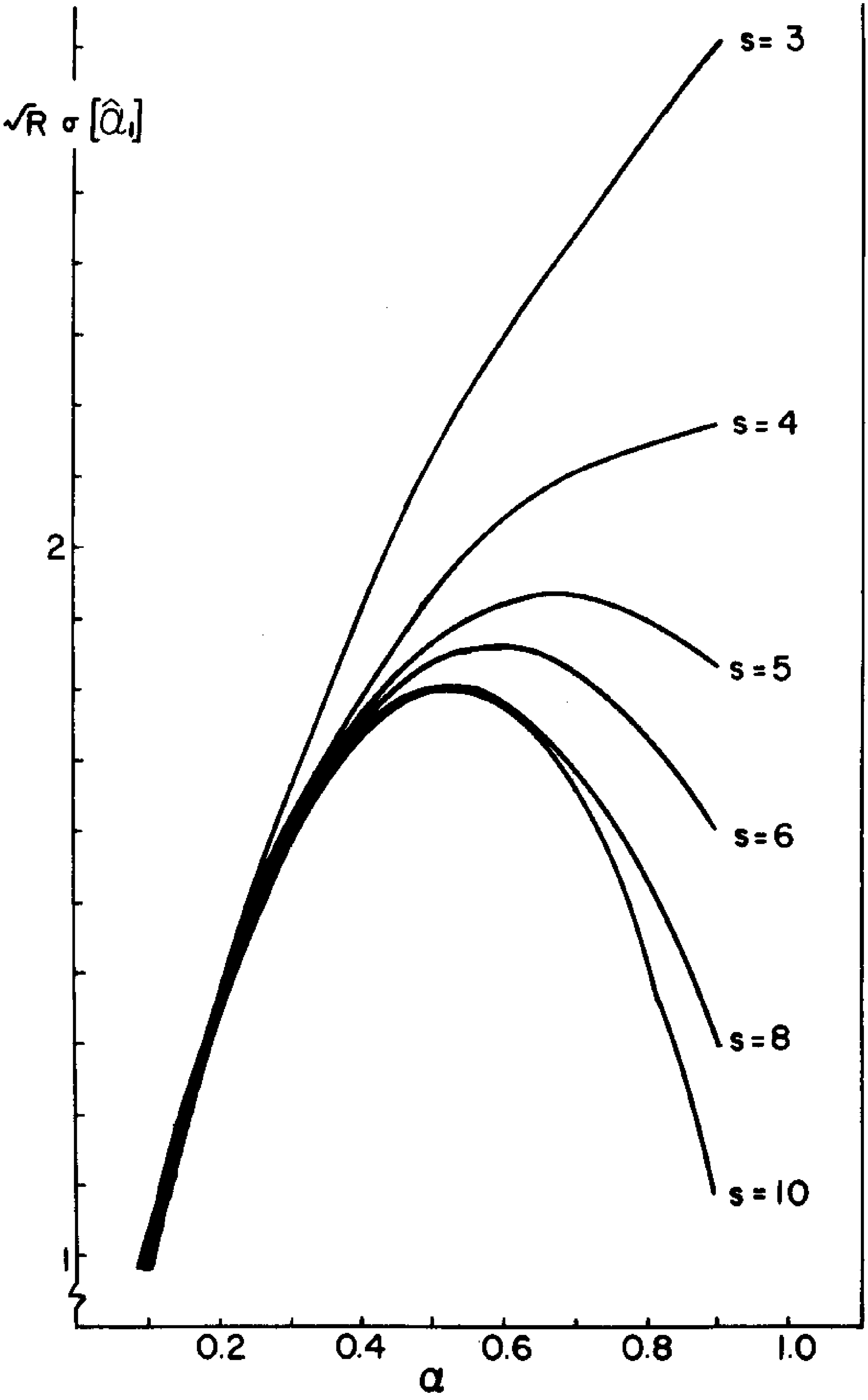

Figure 5.2 Relationship of $\sqrt{R}\,\sigma[\hat{\alpha}_1]$ as a function of survival (α) and number of years of tag releases (s) with a reported exploitation rate (β) equal to 0.1: from Figure 2, Youngs and Robson (1975).

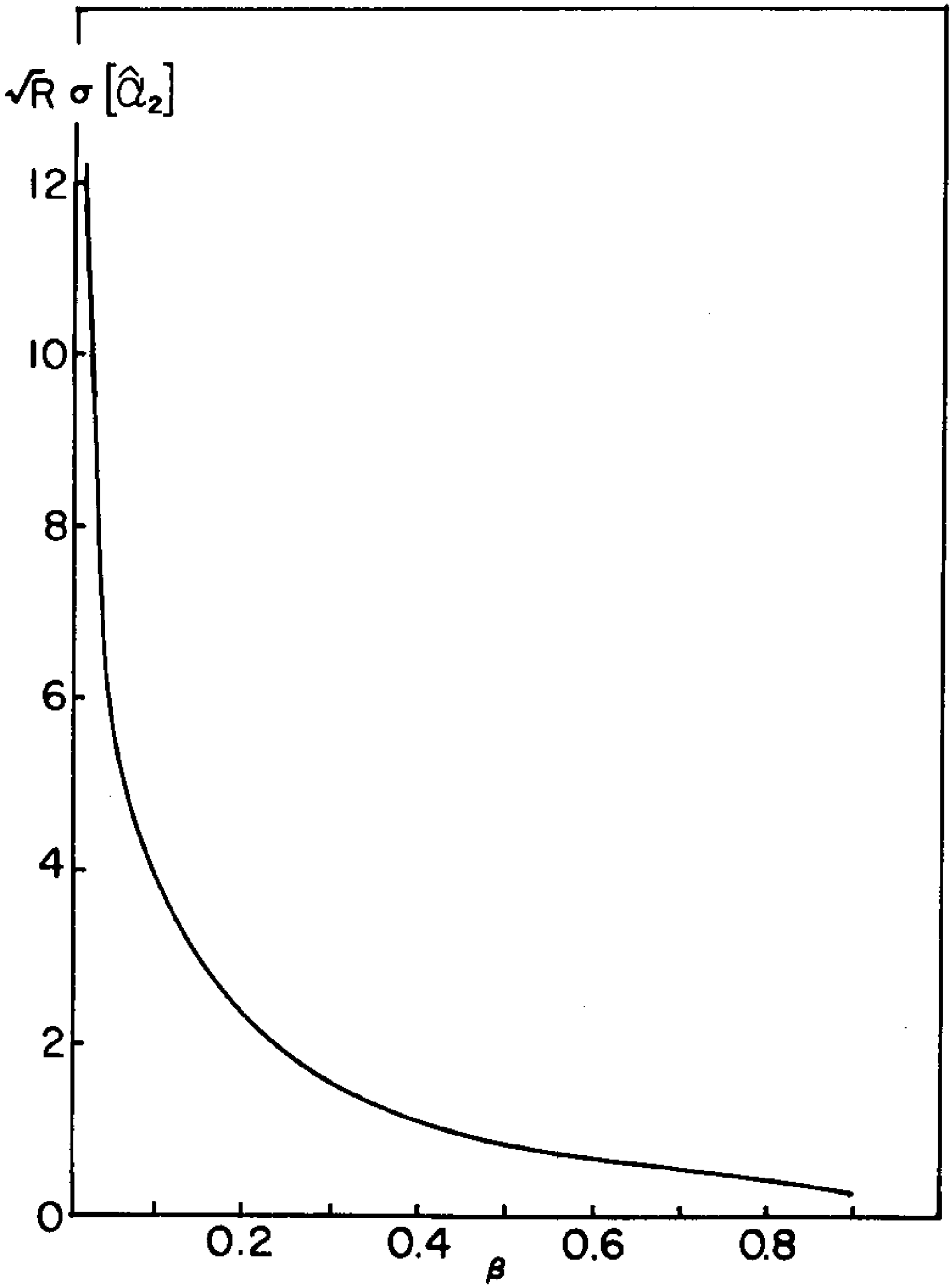

Figure 5.3 Relationship between $\sqrt{R}\,\sigma[\hat{\alpha}_2]$ and β for $s=3$ years of tag releases: from Figure 5, Youngs and Robson (1975). (My thanks to Douglas Robson for providing the original photos of Figs. 2 and 3.)

(asymptotically) independent chi-squared test based on a contingency table. The first table is Table 5.1, and the usual test statistic for homogeneity based on this table is approximately χ^2_{k-2}, when the model is true. The second table is Table 5.2, and the test statistic is asymptotically χ^2_{k-3}. This statistic is approximately independent of the previous test statistic so that the two chi-squared statistics are additive. The (i-1)th such table is given by Table 5.3, and the chi-squared statistic for this table is approximately independent of the previous chi-squared statistics. Proceeding in this manner we end up with (s - 2) independent chi-squared statistics which may be added to give one combined test of the model with (s - 1) (s - 2)/2 degrees of freedom (cf., (6)).

Certain alternatives to the model can be tested by partitioning each of the above chi-squares. An important alternative is the possibility of a type I loss or initial tagging mortality (1, p. 231). A test against this alternative is obtained by partitioning each 2 x (s - i + 1) table, Table 5.3 ($m^*_{ij} = m_{1j} + m_{2j} + \ldots + m_{ij}$), into the two tables, Table 5.4 and 5.5. We thus have a partition of χ^2_{s-i} into χ^2_1 and χ^2_{s-i-1}, respectively. The sum of the s - 2 χ^2_1 statistics provides a test against short-term tagging effects.

Table 5.1 Contingency table for testing the goodness of fit of model (1): from Youngs and Robson (1975).

Year tagged	Year of recapture				Total
	2	3	···	s	
1	m_{12}	m_{13}	···	m_{1s}	$T_2 - r_2$
2	m_{22}	m_{23}	···	m_{2s}	r_2
Total	m_2	m^*_{23}	···	m^*_{23}	T_2

Table 5.2 Contingency table for testing the goodness of fit of model (1): from Youngs and Robson (1975).

Year tagged	Year of recapture				Total
	3	4	···	s	
1 or 2	m^*_{23}	m^*_{24}	···	m^*_{2s}	$T_3 - r_3$
3	m_{33}	m_{34}	···	m_{3s}	r_3
Total	m_3	m^*_{34}	···	m^*_{3s}	T_3

Table 5.3 Table to be partitioned for testing type I loss: from Youngs and Robson (1975).

Year tagged	Year of recapture i	 $i+1$	 $\cdots$	 s	Total
$1,2,\cdots,i-1$	$m^*_{i-1,i}$	$m^*_{i-1,i+1}$	$\cdots$	$m^*_{i-1,s}$	$T_i - r_i$
i	m_{ii}	$m_{i,i+1}$	$\cdots$	$m^*_{i,s}$	r_i
Total	m_i	$m^*_{i,i+1}$	$\cdots$	$m^*_{i,s}$	T_i

Table 5.4 Contingency table for detecting type I losses; all the columns of Table 5.3, but the first are pooled. From Youngs and Robson, 1975.

$m^*_{i-1,i}$	$T_i - r_i - m^*_{i-1,i}$	$T_i - r_i$
m_{ii}	$r_i - m_{ii}$	r_i
m_i	$T_i - m_i$	T_i

Table 5.5 A partition of Table 5.3 involving all the columns but the first. From Youngs and Robson (1975).

$m^*_{i-1,i+1}$	$\cdots$	$m^*_{i-1,s}$	$T_i - r_i - m^*_{i-1,i}$
$m_{i,i+1}$	$\cdots$	$m_{i,s}$	$r_i - m_{ii}$
$m^*_{i,i+1}$	$\cdots$	$m^*_{i,s}$	$T_i - m_i$

Youngs and Robson (1975) demonstrate the above theory and tests on some data for lake trout.

Instantaneous mortality rates. Let μ_i, μ_{Ei} and $Z_i = \mu_i + \mu_{Ei}$ be the instantaneous natural, exploitation, and total mortality rates respectively in year i (1, p. 3). Suppose that a proportion $1 - \nu_i$ of those tagged and released at the beginning of year i die immediately after release, and a proportion ρ_i of the tags recaptured in year i are actually reported. Then, if the time unit is one year,

$$\alpha_i = e^{-Z_i} \quad (= S_i \text{ of } \underline{6.2} \text{ in } \underline{1}) \tag{7}$$

and, from p. 272 equation (6.2),

$$\beta_i = c_i\mu_{Ei}(1 - \alpha_i)/Z_i \quad (= c_i u_i, \text{ say}) , \tag{8}$$

where $c_i = \rho_i\nu_i$ is usually assumed to be constant (= c, say). Then from the maximum likelihood estimates $\hat{\alpha}_i$ and $\hat{\beta}_i$ given by equations (4) and (5), we can use (7) and (8) to obtain the maximum likelihood estimates $\hat{Z}_i = -\log \hat{\alpha}_i$ of Z_i and $\hat{G}_i = -\hat{\beta}_i \log \hat{\alpha}_i /(1 - \hat{\alpha}_i)$ of $G_i = c_i\mu_{Ei}$. Also using the delta method (1, p. 7), we have

$$V[\hat{Z}_i] \approx V[\hat{\alpha}_i] / \alpha_i^2 \tag{9}$$

and

$$\text{cov}[\hat{Z}_i,\hat{Z}_j] \approx \text{cov}[\hat{\alpha}_i,\hat{\alpha}_j]/\alpha_i\alpha_j . \tag{10}$$

If an estimate of c_i is available, then μ_{Ei}, and hence μ_i, can be estimated. A number of special cases will now be considered.

Suppose that $c_i = c$ and $\mu_i = \mu$, then using the approximation

$$(1 - e^{-w}) / w \approx e^{-\frac{1}{2}w} ,$$

we have

$$\frac{e^{-\mu} - e^{-(\mu+\mu_{Ei})}}{1 - e^{-(\mu+\mu_{Ei})}} \cdot \frac{\mu_{Ei} + \mu}{\mu_{Ei}} \approx e^{-\frac{1}{2}\mu} ,$$

or

$$\begin{aligned} e^{-\mu} - e^{-Z_i} &\approx e^{-\frac{1}{2}\mu}(1 - \alpha_i)\mu_{Ei}/Z_i \\ &= e^{-\frac{1}{2}\mu}\beta_i/c . \end{aligned}$$

Then rearranging the above equation, and setting $\phi = e^{-\mu}$ and $k = c^{-1}e^{-\frac{1}{2}\mu}$, we have from (7)

$$\alpha_i \approx \phi - k\beta_i . \tag{11}$$

Thus a regression of $\hat{\alpha}_i$ versus $\hat{\beta}_i$ will be approximately linear with the intercept estimating ϕ, the natural mortality rate. This model, (11), was proposed by Youngs (1972), although he used a less efficient estimate of β_i, namely $\beta_i^* = m_{ii}/R_i$ in his example. If the exploitation is seasonal then it transpires that the only change is in the constant k.

Now if just $c_i = c$ we have, for large releases,

$$E[\hat{G}_i] \approx G_i = c\mu_{Ei}$$

so that

$$\begin{aligned} E[\hat{Z}_i] &\approx Z_i \\ &= \mu_i + \mu_{Ei} \\ &\approx \mu_i + (\frac{1}{c})E[\hat{G}_i] . \end{aligned}$$

Thus if $\mu_i \approx \mu$ or $\mu_i = \mu + \varepsilon_i$, where $E[\varepsilon_i] = 0$, we have the regression model

$$\hat{Z}_i = \mu + (\frac{1}{c})\hat{G}_i + e_i , \tag{12}$$

where e_i is the "error" satisfying $E[e_i] \approx 0$, and c can be estimated from the slope of the fitted line. This model, together with an example, was proposed by Youngs (1974) with the following changes in notation: $\hat{G} \to R$, $\alpha \to S$ and $\beta \to f$. It should be noted that some care is needed in fitting (11) and (12) as they both are, so-called, "functional relationships" (cf., Seber, 1977, 210, and Ricker, 1973). Equation (12) is discussed further by Youngs (1976, see his equation (2)) from the point of view of μ_{Ei} varying throughout the year.

If $\mu_i = \mu$ and effort data are available then we have the model

$$E[\hat{Z}_i] \approx Z_i = \mu + k\overset{o}{f}_i ,$$

where $\overset{o}{f}_i$ is the total effort in year i, and least-squares estimates of μ and k, the Poisson catchability coefficient, can be readily calculated. Although the $\hat{Z}_i$ are correlated, the (unweighted) least-squares estimates will still be approximately unbiased. However, the usual variance formulae for the least-squares estimates will not be correct unless the covariances are small and the variances approximately equal. A more appropriate procedure would be to use a generalized or weighted least-squares analysis (I, p. 11) using an estimated variance-covariance matrix of the $\hat{Z}_i$ obtained from (9) and (10).

If $\mu_i = \mu$, $\mu_{Ei} = \mu_E$ and $c_i = c$, then $\alpha_i = \alpha$, $\beta_i = \beta$ and the maximum likelihood equations must be solved iteratively. Also μ and μ_E can be estimated if an estimate of c is available. Alternatively, we note that

$$E[m_{ij}] = R_i\alpha^{j-i}\beta = R_i e^{-Z(j-i)}cP_1 \text{ , say,}$$

where $P_1 = \beta/c$, and this leads to the model

$$E[\log(R_i/m_{ij})] \approx -[Z + \log(cP_1)] + Z(j - i + 1).$$

This model is considered in I, p. 239, equation (5.34), but with a change in notation for the m_{ij} so that $(j - i + 1)$ becomes j.

Bird-Banding Models

Time-specific model

Band returns have been used extensively for estimating survival rates for birds for many years but it is only recently (cf., Brownie et al., 1977) that proper statistical models, together with their associated goodness of fit tests, have been developed. The choice of model depends on whether the survival rate and band recovery rate are time and/or age dependent. Invariably the recovery rate is at least time-dependent as the recovery of a band depends on such factors as the mortality rate and the probability that a band is returned, given that it is found. If survival is allowed to be completely age- and time-dependent, then there are too many parameters in the model with a consequent lack of identification, and some constraints on the parameters are needed. These are provided by the fact that the survival rates (and hence the recovery rates) of adult birds tend to become age-independent and depend only on the calendar year. Thus, if just adults are banded, then survival is time-dependent only. If we also assume that the band recovery rate does not depend on age, then we arrive once again at the basic model (1), which can be best described by the equation

$$E[m_{ij}] = R_i \alpha_i \alpha_{i+1} \ldots \alpha_{j-1} \beta_j \quad (i = 1,2,\ldots,s;\ j = 1,2,\ldots,t) \qquad (13)$$

or, in the notation of Brownie et al. (1977) which is given in brackets below,

$$E[R_{ij}] = N_i S_i S_{i+1} \ldots S_{j-1} f_j \ .$$

Here $R_i (N_i)$ is the number released at the beginning of the ith calendar year, $m_{ij} (R_{ij})$ is the number from $R_i (N_i)$ recovered in the jth calendar, $\alpha_i (S_i)$ is the probability of survival in the ith year ("survival rate" in year i) and $\beta_j (f_j)$ is the probability that a band is recovered in year j (the so-called band recovery rate or reported exploitation rate in year j). We note that Figures 5.2 and 5.3 can be used for designing such an experiment.

The above model was originally developed independently by Robson and Youngs (1971) and Seber (1970) and is described in the context of bird-banding in

1, pp. 240-3. Further numerical examples of this model are given in Anderson and Sterling (1974), Anderson (1975) and Brownie et al. (1977, chapter 2, model 1). In my approach on page 240 I emphasized the case of non-game birds for which $\beta_j = (1 - \alpha_j)\lambda_j$ (with $\alpha_j \equiv \phi_j$), λ_j being the probability that banded bird is found and its band returned in year j. For game birds, where bands are returned by hunters, β_j can be expressed in the form $\beta_j = H_j\delta_j$, where H_j is the so-called harvest rate and δ_j is the band reporting rate, that is the probability that a hunter will report the band given that he has killed and retrieved a banded bird in year j. Clearly H_j and δ_j cannot be separately estimated unless further information is available; for example, δ_j is estimated using reward bands (Henny and Burnham, 1976). We note that $H_j < 1 - \alpha_j$ as $1 - \alpha_j$ also includes natural mortality as well as hunting mortality. The relationships between the various parameters are discussed in detail by Anderson and Burnham (1976) and Brownie et al. (1977, 14). The estimate $\hat{\beta}_j$ has been used as an index of hunting pressure in preference to the proportion of bands recovered in the first season after a band release (Anderson and Sterling, 1974). The special cases of constant survival rate (α) and/or constant recovery rate β are considered by Brownie et al. (1977, models (2) and (3)). These models should be fitted where possible as the estimation of fewer parameters leads to more efficient estimates (e.g., Raveling, 1976). However, explicit solutions of the maximum likelihood equations do not exist and the equations need to be solved iteratively.

Time- and age-specific models

For a number of reasons the recovery rates for newly banded birds may be different from those of birds banded in previous years. The above model (13) has been modified by Brownie et al. (1977, 30) to deal with this generalization. Further adaptions have been given by Brownie (1973), Brownie and Robson (1976), and Brownie et al. (1977, chapter 3), which allow for the survival and recovery rates to be age-dependent with respect to the two groups young-adults (adults being birds older than one year) or the three groups young-subadults-adults (more than two years old). These models assume that only two groups, young and adults, are distinguishable--the usual situation in practice--and that separate records are kept for the numbers released and recovered from the two groups. Models where the three age groups are recognizable are given by Brownie (1973) and discussed in detail by Brownie et al. (1977, Chapter 4). A two-group model which imposes some constraints on the parameters for the young birds is given by Johnson (1974): he assumes that two proportionality factors relating young to adult parameters are constant over time.

For many species it is easier to band the young than band adults so that there is a strong temptation to band only the young. However, Brownie et al. (1977, 112-3) demonstrate that this is a pointless practice as the parameters are no longer identifiable (that is uniquely determined from the model) and therefore cannot be estimated. This lack of identifiability is due to the fact that young generally have a lower survival rate than adults and that the first-year band recovery rate for young is typically higher than for adults.

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THE USE AND MISUSE OF ANIMAL LIFE TABLES

Introduction

A life table is simply a table that one can look up to determine the mortality rate and the life expectancy of an individual at a given age. The use of such tables for human populations goes back to the 17th century. For example, Ludwig Huyghens writes to his brother Christian in 1669: "I have just been making a table showing how long people of a given age have to live...Live well! According to my calculations you will live to be about 56½ and I to 55." Techniques for the construction and analysis of human life tables have been developed in considerable detail and have been largely used for determining insurance premiums. The success of such methods is due to the fact that human populations are large and stable, and information on various categories such as age, occupation, etc., is readily obtainable by census, sample survey, records, etc.

In recent years, attempts have been made to develop valid life tables for animal populations, with the hope that such tables will throw some light on the dynamics of a population or lead to realistic policies in population management. However, in contrast to human populations, animal populations tend to fluctuate with changes in the environment, and methods of aging animals are often of limited accuracy. Also, data for such tables is generally obtained from free ranging populations and this can lead to sampling problems as samples may not be representatives.

There are two basic types of animal life tables: the age-specific or dynamic life table, and the time-specific table. These are discussed below.

Age-Specific Table

Notation

The age-specific table is based on the fate of a "cohort" of l_0 animals, that is l_0 animals born at the same time. The table usually contains the following columns:

(i) age x, measured in some convenient unit of time such as day, month, year etc.

(ii) l_x, the number of l_0 surviving to age x. The usual convention of scaling l_x so that $l_0 = 1000$ or 1, although useful in standardizing the table, is not recommended when samples are small as it can give a false impression of the accuracy of the table. If scaling is used, the raw data should also be quoted.

(iii) $d_x = l_x - l_{x+1}$, the number of deaths in the age-class $[x,x+1)$. This notation, which follows actuarial practice, differs from that commonly used in the construction of animal life tables. Usually, x denotes the class interval $[x-1,x)$, and l_x is defined to be the number surviving at the beginning of this interval, i.e., of age x-1. One reason for the popularity of the latter notation is that in applying, or should I say misapplying, life table methods to birdbanding experiments it is convenient to think of d_x as the number of banded birds recovered in their xth year of life. Since both notations are used they can, in practice, be combined by the simple expedient of labelling the age-intervals 0-1, 1-2, etc.--instead of 0,1,2, etc. or 1,2,3, etc. In this case, the first entry in the d_x column refers to the number dying in the interval $[0,1)$, irrespective of whether we call it d_0 or d_1. Personally, I feel it would be best if the notation of (ii) was universally adopted.

(iv) $q_x = d_x/l_x$, the observed mortality rate at age x.

(v) e_x , the observed mean expectation of life remaining for individuals of age x.

If w is the last age in the table, then

$$\begin{aligned} l_x &= (l_x - l_{x+1}) + (l_{x+1} - l_{x+2}) + \dots + (l_w - 0) \\ &= d_x + d_{x+1} + \dots + d_w , \end{aligned}$$

and

$$e_x = \tfrac{1}{2} + (l_{x+1} + l_{x+2} + \dots + l_w)/l_x .$$

When the observed mortality rates q_x are fairly constant, we can combine the q_x in several ways to give a mean mortality rate. One possibility is

$$q_{ave} = \frac{1}{w} \sum_{x=0}^{w-1} q_x ,$$

or the more popular estimate

$$\begin{aligned} q_{pool} &= \sum_{x=0}^{w-1} d_x \Big/ \sum_{x=0}^{w-1} l_x \\ &= \sum_{x=0}^{w-1} d_x \Big/ \left[\sum_{x=0}^{w-1} (x+1)\, d_x + w d_w \right] \end{aligned}$$

In both cases the last age class w is <u>not</u> included as $d_w = l_w$ and $q_w = 1$.

Data for an age-specific table can be collected in two ways: (1) by recording the ages at death of animals in the cohort, thus giving a d_x series, or (2) by recording the number of animals still alive at various times, thus giving an l_x series. The age-specific method is most readily applied to laboratory populations of relatively short-lived species such as voles (Leslie et al., 1955), or to zoo populations (Comfort, 1957), though such tables are of limited value. In the case of natural populations, the initial cohort can be identified by tagging, and either of the above methods for collecting the data can be used. For example, a cohort can be followed up using radio telemetry (Trent and Rongstad, 1974, cottontail rabbits; Brand et al., 1975, snowshoe hares; and Mech, 1977, voles).

Unfortunately, the stochastic aspects of life tables have been largely ignored and variance estimates are seldom given. However, a stochastic theory is available from Chiang (1960a,b).

Theory

Suppose that all individuals of age x from the cohort have the same probability P_x (= $1-Q_x$) of surviving to age x+1. Then the joint distribution of $d_0, d_1, \ldots, d_w$ is

$$f(d_0,d_1,\ldots,d_w|l_0,w) = \frac{l_0!}{\prod_{x=0}^{w} d_x!} Q_0^{d_0}(P_0Q_1)^{d_1}\ldots(P_0P_1\ldots P_{w-2}Q_{w-1})^{d_{w-1}}(P_0P_1\ldots P_{w-1})^{d_w} \tag{1}$$

For $x = 0,1,\ldots,w-1$, the maximum likelihood estimate of Q_x is the unbiased estimate

$$\hat{Q}_x = d_x/(d_x + \ldots + d_w) = d_x/l_x ,$$

which is q_x again, with variance estimate

$$v[\hat{Q}_x] = \frac{(1 - \hat{Q}_x)\hat{Q}_x}{l_x}\left\{1 + \frac{1}{l_x} - \frac{1}{l_0}\right\}$$

(cf., Seber, 1973, 408-9). We note that x could refer to the coded age so that the above theory can be applied to any group of l_0 individuals of the same age. Also, the above theory applies to the situation where some members of the cohort are still alive at the end of the experiment. In this case, w is the time taken by the experiment so that there are l_w animals of age w alive at the end of the experiment and d_w (= l_w) is the number dying after the experiment has finished and not just the number dying in the interval $[w,w+1)$.

If Q_x is assumed to be constant, say $Q_x = Q$, then the likelihood function is proportional to

$$P^{l_1+l_2+\ldots+l_w} Q^{l_0-l_w} , \tag{2}$$

and the maximum likelihood function of Q turns out to be q_{pool} with asymptotic variance estimate

$$v[q_{pool}] = \left(\sum_{x=1}^{w} l_x\right)(l_0 - l_w)/\left(\sum_{x=0}^{w-1} l_x\right)^3 .$$

As q_{pool} is biased, the less efficient but unbiased estimate q_{ave} with unbiased variance estimate

$$v[q_{ave}] = \sum_{x=0}^{w-1} (q_x - q_{ave})^2/w(w-1)$$

may be preferred. Regression estimates are also available and the reader is referred to Seber (1973, 413) for details.

It would appear that q_{pool} is the same as Lack's estimate of mortality rate commonly used in birdbanding. This is not the case as Lack's estimate

$$q_{Lack} = \sum_{x=0}^{w} d_x / \sum_{\lambda=0}^{w} l_x$$

includes an extra d_w and l_w (= d_w) in the numerator and denominator. Lack's method makes the assumption that there are no animals left at the end of the experiment and that the likelihood function is approximately proportional to

$$Q^{d_0}(PQ)^{d_1} \ldots (P^{w-1}Q)^{d_{w-1}}(P^wQ)^{d_w} = P^{l_1+\ldots+l_w}Q^{l_0} ,$$

which may be compared with (2). The similarity of q_{pool} and q_{Lack} has caused some confusion in the literature because several authors have used the life table approach simply as a means of calculating Lack's estimate. I recommend that this use of the life table be dropped.

An interesting application of q_{pool} was given by Trent and Rongstad (1974) who worked with adults only (i.e., x is a coded age) and used a time unit of one day; the experiment lasting n (=w) days. Assuming a constant daily survival rate of S (= 1-Q), they used $S_{pool} = 1 - q_{pool}$ (cf., their equation (2) with $y_i = d_{i-1}$, $x_i = l_{i-1}$) as their estimate of S. As the d_x were usually 0 and occasionally 1, the daily mortality rate was small (q_{pool} = 0.0037), so that Σd_x was approximately distributed as Poisson with mean $(1-Q)\Sigma l_x$. Tables of the Poisson distribution were used to obtain a confidence interval for S and S^n (the survival rate for n days).

Birdbanding

With reference to lecture 5 there is one further birdbanding model which merits special reference, because of its misuse rather than its usefulness and its connection with life tables. This model assumes that (i) the survival and band recovery rates are age-dependent only (that is, they are unaffected by year to year changes in the hunting regulations, habitat, weather, etc.) and (ii) the age-specific band recovery rate is a constant fraction (λ) of the age-specific mortality (cf., Anderson and Burnham, 1976, Appendix B). Thus if ϕ_j (equivalent to P_{j-1} above) is the probability that a bird aged j-1 survives for one year, then $\lambda(1-\phi_j)$ is the probability that a band is recovered from a bird in the age range $[j-1,j)$. An analysis of this model, which requires one constraint on the ϕ_j's for the purposes of identifiability, has been carried out by Seber (1971) using a conditional likelihood approach, that is he considers the joint distribution of the band recoveries conditional on the total numbers of bands recovered from each release. A goodness of fit test for this model which, as might be expected, does not depend on the choice of identifiability constraint, is given by Burnham and Anderson (1979). They also give a contingency table statistic to test whether the first year recovery rates are constant. If the unconditional likelihood is used, then the maximum likelihood equations for ϕ_j and λ do not have explicit solutions and must be solved iteratively. When $\phi_j = \phi$ (all j), the conditional approach leads to a generalization of Haldane's method (Seber, 1973, 246).

However, the above assumptions are demonstrably invalid for game bird studies, e.g., mallard (Anderson, 1975; Burnham and Anderson, 1979) and are questionable for non-game species. For instance, the band recovery rates of nearly all waterfowl species vary significantly by both age and year (Anderson, 1975, 13). In addition to the problem of time-dependent survival, harvest rate depends on the hunting regulations which may change with time (e.g., Hopper et al., 1975, 63), and the band reporting rate tends to fall off with time as hunters lose interest in the program (Henny and Burnham, 1976). Not only are the basic assumptions generally invalid, but the estimators obtained from the above model are also very sensitive to departures from the assumptions.

As well as the maximum likelihood approaches, there is another time-hallowed method of analyzing the above model called the composite dynamic method (Hickey, 1952; Geis and Taber, 1963; Geis et al., 1971; Geis, 1972 a,b). This method, which is frequently set out in the form of a life table with the band recoveries from each age group being treated like a d_x series (cf., Seber, 1973, 252), makes the additional assumption (iii) that the experiment is continued for a sufficient number of years after the last release so that all the banded birds are dead by the end of the experiment. When $\phi_j = \phi$ then Lack's method is usually used for estimating ϕ. However, assumption (iii) is not very practical in the case of birdbanding studies where estimates are needed immediately after the last band release, and not several years later. If (iii) is not met, which is often the case, then the survival estimates will be too low (Seber, 1972, table 2; see also Burnham and Anderson, 1979). Clearly the composite dynamic method, along with the various ad hoc life table methods associated with it, should be dropped. As far as birdbanding experiments are concerned we quote the following from Brownie et al. (1977, 115, see also 184): "We cannot emphasize too strongly that, based on our current knowledge, there is no valid way to estimate age-specific survival rates from only the banding of young."

Time-Specific Table

Underlying assumptions

If N_x, the number of animals of age x in a population, remains constant with respect to time for each x, then the population is said to be stationary and the age structure of the population at any time t will reflect the fate of a cohort of N_0 animals born at time t. Thus the cohort will reduce to N_1 animals at time t+1, to N_2 at time t+2 etc., and the sequence $\{N_x\}$ forms an l_x series. This series can then be used to construct a life table as in the age-specific case. Such a life table, determined from the age structure of a stationary population at a given point in time, is called a time-specific table. In practice, the age structure must be determined by a sample, so that time-specific tables involve sampling errors. Although a time-specific table is usually easier to obtain (particularly for long-lived animals), it is less accurate than an age-specific table. Also, its two basic assumptions need to be checked (Murphy and Whitten, 1976); namely, (i) the sample age structure reflects the population age structure, and (ii) the population is stationary. Assumption (i) may not hold because of variable catchability: for example, juveniles are sometimes under-represented as they have a lower catchability (e.g., Wilbur, 1975, turtles). Gill-net selectivity in fisheries can also lead to a violation of (i) (e.g., Healey, 1975, 430). Frequently assumption (ii) does not hold, or may hold only for certain years (e.g., Nellis and Keith, 1976, 395). Spinage (1972) constructed life tables for several African ungulates using age data from skulls. Unfortunately, skulls of different sizes may deteriorate at different rates, though sometimes correction factors can be made using data from live populations.

Theory

Let $S_x = N_{x+1}/N_x$ $(x = 1,2,\ldots,w-1)$, the actual proportion surviving from age x to age x+1 (we use S_x to distinguish this proportion from the probability P_x). Suppose that in a random sample of n animals n_x are of age x (some of the n_x may be zero). Then, by considering the joint distribution of the n_x given n, Chapman and Robson (1960) obtained the maximum likelihood estimates

$$\hat{S}_x = n_{x+1}/n_x \qquad (x = 0,1,\ldots,w-1: \ n_x \neq 0)$$

along with asymptotic variances and covariances. If we regard the $\{n_x\}$ series as an $\{l_x\}$ series we see that $1 - \hat{S}_x$ is just q_x once again. However, because of sampling variation in the n_x, $\hat{S}_x$ is now biased and Chapman and Robson suggested the almost unbiased modification

$$S_x^* = n_{x+1}/(n_x+1) \ .$$

These estimates will have the same asymptotic variances and covariances as the $\hat{S}_x$. In practice w will be unknown so that the data will be truncated as some <u>prechosen</u> age $K(K \leq w)$, where K is chosen so that (hopefully) $n_x > 0$ $(x = 0,1,\ldots,K)$.

If S_x is assumed to be constant (= S, say), then the underlying distribution for the age x of a randomly chosen animal is the truncated geometric distribution; truncated at age w. The maximum likelihood estimate of S is then the solution of

$$X/n = [S/(1-S)] - (w+1)\, S^{w+1}(1-S^{w+1}) \ , \tag{3}$$

where

$$X = \sum_{x=0}^{w} x n_x \ .$$

This solution is called $\hat{S}_{seg}$ in Seber (1973, 421) and a table is available for solving (3): an asymptotic variance formula is also given there. When $S^w \approx 0$, which is usually the case, the second term on the right-hand side of (3) can be neglected and the maximum likelihood estimate is now $\tilde{S} = X/(n+X)$ $(= 1-\tilde{q})$. In this case the underlying model is the (non-truncated) geometric distribution and

$$\hat{S} = X/(n+X-1)$$

is a minimum variance unbiased estimate for this model with

$$v[\hat{S}] = \hat{S}\left(\hat{S} - \frac{X-1}{n+X-2}\right)$$

a minimum variance unbiased estimate of the <u>exact</u> variance of $\hat{S}$ (Chapman and Robson, 1960).

Although the life table format is a convenient method of summarizing time-specific data, the use of life table methods in this context has led to a great deal of confusion. This confusion is usually caused by practitioners being uncertain as to whether a sample of ages is an $\{l_x\}$ or a $\{d_x\}$ series (Seber, 1973, 401-2). Clearly the $\{n_x\}$ must be a sample of the <u>live</u> population if we are to treat the $\{n_x\}$ as an $\{l_x\}$ series and obtain the correct estimates $\hat{S}_x$ and S^*_x. However, when $S_x = S$, several estimates of q $(= 1-S)$ have been proposed. For example, setting $n_x = l_x$ we have the following contenders:

$$\tilde{q} = n/(n+X) = \sum_{x=0}^{w} l_x \Big/ \sum_{x=0}^{w} (x+1) l_x \ ,$$

$$q_{pool} = \sum_{x=0}^{w-1} d_x \Big/ \sum_{x=0}^{w-1} l_x \ ,$$

$$q_H = \sum_{x=0}^{w} d_x \Big/ \sum_{x=0}^{w} l_x$$

$$= \sum_{x=0}^{w} d_x \Big/ \sum_{x=0}^{w} (x+1) d_x$$

$$= l_0 \Big/ \sum_{x=0}^{w} l_x \ ,$$

and

$$q_1 = d_0/\ell_0$$

$$= d_0/\sum_{x=0}^{w} d_x \ .$$

where w is now the maximum observed age in the sample. Here $1-\tilde{q}$ $(= \tilde{S})$ is the maximum likelihood estimate of S, $1-q_{pool}$ $(= (n_1+\ldots+n_w)/(n_0+\ldots+n_{w-1}))$ is simply Jackson's (1939) survival estimate, $1-q_H$ $(= (n-n_0)/n)$ is an estimate due to Heinke (1913), and q_1 is a simple estimate of mortality based on the first entry in the d_x column. All four estimates are used and will all generally give reasonable (and similar) answers as $d_x \simeq (1-S)\ell_x$. However, if the $\{n_x\}$ series is incorrectly treated as a $\{d_x\}$ rather than an $\{\ell_x\}$ series, then using q_H and q_1 is equivalent to using $\tilde{q}$ and q_H: also $\tilde{q}$ will still provide a reasonable estimate (being similar to using q_H). Thus ecologists can freely confuse ℓ_x and d_x and still get a reasonable estimate of S.

Stage-Specific Survival Rates

As insects pass through various stages of development (egg, larval instar, etc.) it would seem appropriate to estimate survival rates for each stage. If a cohort of eggs can be followed through the various stages then the stochastic model of (1) can be used to estimate the P_x, where P_x is now the probability that an insect entering stage number x survives to enter stage number x + 1. Examples where cohort and related information is available are given by Beaver (1966), Berryman (1968) and McLaren and Pottinger (1969). However, in practice, information about the stages is usually obtained by taking a sequence of samples from the population and noting the proportions of insects in the different stages for each sample. Unfortunately, such data is not easy to analyse as the time when an insect enters the cycle of stages is random so that the insects get out of phase and the various stages overlap. A number of attempts have been made to set up an adequate model and obtain estimates of stage-specific survival, average duration of each stage, numbers entering each stage and daily survival rates. Manly (1974b) compared five such methods due respectively to Richards and Waloff (1954), Richards et al. (1960) (though see Manly, 1975, for a stochastic justification), Dempster (1961), Kiritani and Nakasuji (1967), and Manly (1974c) under a variety of conditions using simulation. All the methods require fairly strong assumptions and are listed for comparison by Manly (1974b). For example, four of the methods assume a constant daily survival rate throughout, and all the methods assume that the durations of the stages are the same for all insects. Kiritani and Nakasuji's (K-N) method requires the sampling to be carried out at equal intervals of time until almost all the insects are dead, while Manly's method assumes a normal distribution for entry times. Manly concluded that the K-N method should be used for estimating stage-specific survival provided the conditions about sampling are satisfied. Otherwise, Manly's method should be used, particularly if it is desired to estimate the actual number of insects entering each stage. In later papers Manly (1976, 1977) extended the K-N method so that it could be used with populations that have been sampled at irregular intervals of time. He also gave procedures for estimating various other parameters in addition to age-specific survival rates and demonstrated that Tukey's jackknife method for variance estimation is reliable. Since Manly's extension seems to be the best of the above methods, the basic equations are summarized as follows using Manly's (1977) notation. For a <u>given</u> stage let:

M = number of insects that enter the stage,

a = duration of the stage (measured, say, in days and assumed to be the same for all insects),

$e^{-\theta}$ = daily survival rate (the probability of surviving for one day),

$\phi(u)$ = probability density function for the distribution of time of entry to the stage ($\phi(u) \rightarrow f(x)$ in Manly's notation),

μ = mean time of entry to the stage, and

σ^2 = variance of the time of entry to the stage.

Now the expected number, $N(t)$ say, of the insects in this stage at time t will be those individuals that entered in the time interval $(t - a, t)$ and survived to time t, that is

$$N(t) = M \int_{t-a}^{t} \phi(u) e^{-\theta(t-u)} du \, . \tag{4}$$

We require the following expressions:

$$A = \int_{-\infty}^{\infty} N(t)dt = M(1 - e^{-\theta a})/\theta ,$$

$$B = \frac{1}{A}\int_{-\infty}^{\infty} tN(t)dt = \theta^{-1} + \mu - ae^{-\theta a}/(1 - e^{-\theta a}) ,$$

and

$$C = \frac{1}{A}\int_{-\infty}^{\infty} t^2N(t)dt - B^2$$

$$= \theta^{-2} + \sigma^2 - a^2e^{-\theta a}/(1 - e^{-\theta a})^2 .$$

Suppose that the insects start to enter the stage being considered just after t_1 and that all insects have left the stage by some time t_n. Suppose also that the population is sampled at times $t_1, t_2, \ldots, t_n$ so that we have estimates $\hat{N}(t_i)$ of $N(t)$ at these times ($\hat{N}(t_1) = \hat{N}(t_n) = 0$). Then using the trapezoidal rule for estimating the areas under the curves $N(t)$, $tN(t)$ and $t^2N(t)$, estimates of A, B, and C are

$$\hat{A} = \tfrac{1}{2}\sum_{j=1}^{n}(h_j + h_{j+1})\hat{N}(t_j) ,$$

$$\hat{B} = \tfrac{1}{2}\sum_{j=1}^{n}(h_j + h_{j+1})t_j\hat{N}(t_j)/\hat{A} , \text{ and}$$

$$\hat{C} = \tfrac{1}{2}\sum_{j=1}^{n}(h_j + h_{j+1})t_j^2[\hat{N}(t_j)]^2/\hat{A}^2 - \hat{B}^2 ,$$

where $h_j = t_j - t_{j-1}$. As we have five unknown parameters for each stage, namely M, θ, a, μ and σ^2 we cannot estimate these parameters by equating A, B, and C to their estimates. However, by assuming θ is constant for all stages, Manly shows how the data from the different stages can be pooled to provide "moment-type" estimates of all the parameters. Finally, there is the important problem of finding estimates $\hat{N}(t_i)$ of $N(t_i)$. If $n(t_i)$ is the number sampled from a given stage at time t_i, and a proportion p_i of the populations is sampled, then $N(t_i)=n(t_i)/p_i$. Usually p_i is kept constant throughout the experiment and is equal to the proportion of the population area (or population volume, as in the case of trees) sampled.

Birley's method. An alternative approach to stage-specific survival is given by Birley (1977) who uses the more realistic discrete version of (4) (since sampling is discrete), namely

$$N_t = M \sum_{j=0}^{a} \phi(t - j)\alpha_j ,$$

where N_t is the expected number in a given stage on day t, $\phi(t - j)$ is the fraction of the population entering the stage on day $t - j$, and α_j is the probability of an insect in the stage surviving j days. Setting $\ell_0 = M$ and $\ell_j = M\alpha_j$ (= s_j in Birley's notation), we have for that stage a life table series $\{\ell_j\}$, where the time unit is one day. If $\phi(u)$ can be estimated (for example, from emergence traps, cage experiments, or from visible differences between old and new), and estimates $\hat{N}_{t_i}$ are available at times t_i, then the ℓ_j can be estimated by minimizing

$$\sum_i [\hat{N}_{t_i} - \sum_{j=0}^{a} \phi(t_i - j)\ell_j]^2$$

subject to $\ell_0 \geq \ell_1 \geq \cdots \geq \ell_a \geq 0$. Basically this is a so-called constrained multiple linear regression and can be solved using quadratic programming. Alternatively, the ℓ_j could be modelled in terms of a smooth function with fewer parameters. For example, if the survival rate is constant, we can assume

$$\ell_j = Me^{-\theta j} = M\phi^j , \text{ say.}$$

One advantage of Birley's model is that it can be modified to take care of catastrophes, for example sudden changes in survival due to the application of an insecticide. However, an objective method of determining a is not given, though a general plot of ℓ_i against i for a guessed a will give further information about a.

Method of Read and Ashford. A very general method, showing considerable potential, has been given by Read and Ashford (1968) and Ashford et al. (1970). The main advantage of this approach over the above method is that it allows for a random stage length. If X_i is the time that an individual is in stage i ($i = 1,2,\ldots,k$), then $X_i = \min(Y_i,Z_i)$ where Y_i would be the time spent in stage i if there were no mortality and Z_i would be the time an individual lives in stage i assuming no transition to stage i + 1. Let f_i, g_i, h_i and F_i, G_i, H_i be the respective density and distribution functions of X_i, Y_i, Z_i. Then, assuming the independence of Y_i and Z_i, $\Pr[X_i > X] = \Pr[Y_i > x]\Pr[Z_i > x]$ or $1 - F_i(x) = [1 - G_i(x)][1 - H_i(x)]$. Thus differentiating we have

$$f_i(x) = g_j(x)[1 - H_i(x)] + h_i(x)[1 - G_i(x)] .$$

Now if $p_i(t)$ is the probability that an individual is alive in stage i at time t, it follows that

$$p_i(t) = \int_0^t \phi_{i-1}(u_{i-1})[1 - F_i(t - u_{i-1})]du_{i-1}$$

where ϕ_{i-1} is the density function of the time of entry to stage i from stage i-1. Also

$$\phi_i(u_i) = \int_0^{u_i} \phi_{i-1}(u_{i-1})k_i(u_i - u_{i-1})du_{i-1}$$

where

$$k_i(u) = g_i(u)[1 - H_i(u)] ,$$

the probability density function of the time spent in stage i given that it enters stage i + 1. Ashford et al. (1970) assume that death is a Poisson process so that

$$h_i(z_i) = \theta_i e^{-\theta_i z_i} , \qquad (5)$$

which leads to

$$k_i(u) = g_i(u)e^{-\theta_i u} .$$

They also consider modelling g_i by a one parameter Erlangian distribution, namely a scaled Gamma distribution with 2 or 3 degrees of freedom and an unknown scale factor, and then estimate all the parameters using maximum likelihood estimation. Unfortunately, considerable computations are required and some of the equations are not given, which will unfortunately preclude the use of the method by some ecologists.

If the generation length is constant (= a_i) rather than random, and $h_i(z_i)$ is given by (5), then

$$1 - F_i(x) = \begin{cases} e^{-\theta_i x} & 0 \leq x < a_i \\ 0 & \text{otherwise,} \end{cases}$$

and

$$p_i(t) = \int_{t-a_i}^{t} \phi_{i-1}(u_{i-1})e^{-\theta_i(t-u_{i-1})}du_{i-1} ,$$

which is the same as the expression for N(t)/M given by (4). Also $\phi_i(u_i) = \phi_{i-1}(u_i + a_i)$.

Other methods. One approach to the above type of problem is to model the population by a continuous time Markov chain with transition states corresponding to the various stages and an absorbing state corresponding to death. Moon (1976) developed such a model for a mosquito population and obtained an expression for the expected number of adult mosquitoes, N(T), alive at time T.

Finally, a number of rather specialized models have been considered by Ruesink (1975).

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