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A Systematic-encounter-sampling Design for Nesting Studies

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Encounter-sampling designs are data-collection procedures in which population units are included in the sample as they are detected, or "encountered." Perhaps the most familiar examples of encounter-sampling designs are line-transect (e.g. Burnham et al. 1980) and line-intercept (e.g. De Vries 1979) procedures. One characteristic of encounter-sampling designs is that a sampling frame (e.g. Cochran 1977) of population units is not required. When individuals are mobile, elusive, or possess other characteristics that make it difficult to construct a sampling frame, encounter-sampling designs often provide the only effective means of sampling a population. A second characteristic of encounter-sampling designs is that they lack control over the subset of the population comprising the sample. As a result, data collected by these procedures often are not representative of the population of interest (i.e. a biased sample), and are best viewed as a probability sample. If variables of interest are correlated with the probability of inclusion, the data cannot be treated as a simple random sample, and estimators based upon random sampling theory are biased (Rao 1965). In these cases, design-specific estimators or bias corrections dependent on the probability structure of the data must be employed.

A population of bird nests is one example of a population whose study requires the use of an encounter-sampling technique. In addition to the obvious lack of a sampling frame, the population is demographically open in that nests are initiated and fail through time. The usual sampling design consists of conducting searches for viable nests, including all detected nests in the sample. Data collected under such a design are biased because longer-lived nests are included in the sample with higher probability than are shorter-lived nests (Mayfield 1961). However, the method by which searches are conducted, typically, is not structured and is not helpful in deriving estimators.

The parameter most often of interest is the nest-survival rate (i.e. probability a nest survives to "success"). Success is often defined as the production of at least one offspring, though other definitions are equally appropriate. Nest-survival rates may be estimated using a number of models. Mayfield (1961, 1975), Johnson (1979), and Bart and Robson (1982) modeled nest survival after detection. Hensler and Nichols (1981), Pollock and Cornelius (1988), and Bromaghin and McDonald (1993) modeled the entire existence of nests by incorporating probabilities of inclusion and partial information of the total lifetime of detected nests in the model. While all of these models attempt to treat the probability structure of the data, only the Pollock-Cornelius and Bromaghin-McDonald models do so fully and correctly. Although Heisey and Nordheim (1990) indicated that the Pollock-Cornelius model produces biased estimates of nest survival, recent information (Pollock and Cornelius unpubl. data) suggests that the bias decreases as the time between visits to nests decreases.

All of the nest-survival models are designed to produce estimators of a single parameter, the probability of nest-success, while acknowledging the biased nature of the data. To some extent, they have all been successful. However, any number of additional parameters may also be of interest, and their estimation, which is also complicated by the biased nature of the data, has received little attention. We present a sampling design and estimation procedures that directly utilize the unequal probabilities with which nests are included in the sample. The method is developed from a classical sampling approach in that all characteristics of the population of nests are considered as fixed; randomness observed in the data is due solely to the sampling design. The design consists of temporally systematic searches for nests, and nests are included in the sample as they are detected. The model assumes that nests are (approximately) aged at the time of detection and monitored until they either fail or are successful. The systematic design permits probabilities of inclusion to be estimated. The estimates are employed in modified Horvitz-Thompson estimators (Horvitz and Thompson 1952) to obtain estimates of any parameter that can be expressed as a total or a ratio of totals. Such parameters include the probability a nest survives to success, the number of nests which survive to success, and the numbers of nests initiated.

The sampling model.—Consider a fixed geographic area in which birds are nesting. Nests are initiated and survive for some period of time. The population of interest consists of all nests which exist within the area for any portion of a specified time frame. For example, the time frame might be constructed to contain all or some interesting portion of the nesting season of the species under consideration. Thus, a geographic area and a time frame are used to define the population. The population size is denoted N and the number of time units in the time frame of interest is denoted D.

The time frame of D time units is divided into a

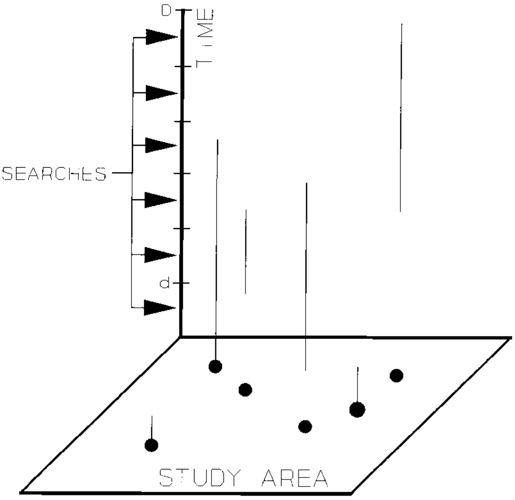

Fig. 1. Schematic diagram of systematic-encounter-sampling design. Circles represent physical location of nests within study area; vertical lines above circles indicate lifetime of nests within time frame; and arrows on time axis indicate temporal location of searches.

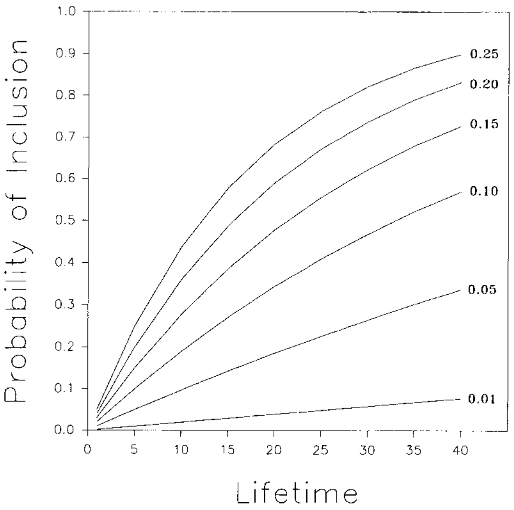

Fig. 2. Graphs of probability of inclusion versus lifetime for d of 5 and several values of probability of detection.

number of periods, each consisting of d time units. One time unit is selected at random from the first period. A search is conducted for active nests during the selected time unit and every dth time unit thereafter throughout the time frame (i.e. a systematic search with a random starting point). All detected nests are included in the sample. Figure 1 conceptually illustrates the sampling design.

The number of time units a nest has existed within the time frame is determined at the time of detection. Nests are then monitored until they fail, are successful, or the end of the time frame is reached. Note that it may be necessary to monitor nests past the end of the time frame in order to observe some types of variables, such as the fate of a nest. The total number of time units a nest exists within the time frame is termed its lifetime, denoted as x. Other variables of interest, denoted as y's, may be recorded at any time.

Estimation procedure.—Let β be the probability a nest is detected during an individual search given it is in existence at that time. Assuming that β is equal for all nests and constant through time and that nests are independently detected, the probability of inclusion for a nest with lifetime x is given by

$$\pi(x) = 1 - (1 - \beta)^{\theta}\{1 + \beta[\theta - (x/d)]\}, \qquad (1)$$

where θ is the largest integer in x/d (Bromaghin 1991). A derivation of $\pi(x)$ is presented in the Appendix.

As D and d are specified by the systematic design and x is recorded for each nest, an estimate of β provides an estimate of $\pi(x)$. Graphs of $\pi(x)$ are presented in Figure 2 for several values of β. We now present a maximum-likelihood procedure for estimating β.

Given the time units on which searches were conducted, knowledge of the time unit each nest was detected, and knowledge of the lifetime of each detected nest, two additional quantities can be determined. Let s be the number of searches conducted during the lifetime of a nest and let m be the number of searches during which the nest was not detected prior to inclusion in the sample. For the ith nest, s_i is a fixed quantity, conditioned on x_i, D, and d, and m_i is a realization of a random variable. Given s_i, m_i contains information concerning β; large values of β will tend to result in small values of m_i. This relationship may be exploited to obtain a maximum-likelihood estimate of β.

Under the assumptions of the systematic design, the probability of observing $\{m_1, m_2, \ldots, m_n\}$ is given by the conditional-likelihood function

$$L(\beta) = \prod_{i=1}^{n} \left[\frac{(1 - \beta)^{m_i}\beta}{1 - (1 - \beta)^{s_i}}\right], \qquad (2)$$

where n is the number of detected nests. The ith term of the likelihood function is the probability the ith nest was detected on the $(m_i + 1)$st search, given it was detected on one of the s_i searches conducted during its lifetime. The maximum-likelihood estimate of β, denoted $\hat{\beta}$, is that value which maximizes $L(\beta)$ (Hogg and Craig 1978). As an estimator cannot be expressed in closed form, the likelihood function must be maximized using numerical techniques (e.g. Luenberger 1984).

An estimator of the asymptotic variance of $\hat{\beta}$, denoted as $\hat{v}(\hat{\beta})$, can be obtained through the information limit (Rao 1973). This estimator can be easily derived and is given by

$$\hat{v}(\hat{\beta})=\left(\frac{n}{\hat{\beta}^2}+\sum_{i=1}^{n}\left\{\frac{m_i}{(1-\hat{\beta})^2} - \frac{s_i(1-\hat{\beta})^{s_i-2}[s_i-1+(1-\hat{\beta})^{s_i}]}{[1-(1-\hat{\beta})^{s_i}]^2}\right\}\right)^{-1}. \tag{3}$$

When either n or β is small, the estimator of the maximum of the likelihood function may not be stable. In these cases, Bromaghin and McDonald (1992) recommended that bootstrap estimates of β and $v(\hat{\beta})$ be employed (Efron 1982, Gleason 1988) since bootstrap estimates are likely to be less sensitive to influential observations. In any event, the remainder of this discussion assumes that $\hat{\beta}$ and $\hat{v}(\hat{\beta})$ have been obtained in some appropriate manner.

We now present estimation procedures for any parameter that can be expressed as a total or a ratio of totals. A modified Horvitz-Thompson estimator (Horvitz and Thompson 1952), with the probabilities of inclusion being estimated rather than known, is recommended for the estimation of population totals. This estimator is given by

$$\hat{Y} = \sum_{i=1}^{n} y_i/\hat{\pi}(x_i), \tag{4}$$

where $\hat{\pi}(x_i)$ is equation (1) evaluated at $x = x_i$, and $\beta = \hat{\beta}$. Note that equation (4) produces an estimate of the population size, N, if y is defined as 1 for all nests. This special case is denoted $\hat{N}$. An estimate of the variance of equation (4) can be obtained using the delta method (Seber 1982) and is given by

$$\hat{v}(\hat{Y}) = v(\hat{\beta})\left(\sum_{i=1}^{n}\left[\frac{y_i}{\hat{\pi}(x_i)^2}\right]\left\{\left(\theta_i - \frac{x_i}{d}\right)(1-\hat{\beta})^{\theta_i} - \theta_i[1-\hat{\pi}(x_i)](1-\hat{\beta})^{-1}\right\}\right)^2. \tag{5}$$

A ratio of totals is a functional statistic and can be estimated using a jackknife procedure (Efron 1982). Let z_i be the value of an additional characteristic of interest possessed by the ith unit and let Z be the population total of the z characteristic. Also, let the ratio of population totals, Y/Z, be denoted τ. Then, defining

$$\tilde{\tau} = \sum_{i=1}^{n}\left[\frac{y_i}{\hat{\pi}(x_i)}\right]\Big/\sum_{i=1}^{n}\left[\frac{z_i}{\hat{\pi}(x_i)}\right], \tag{6}$$

$$\tilde{\tau}_i = \sum_{j=1,\,j\neq i}^{n}\left[\frac{y_j}{\hat{\pi}(x_j)}\right]\Big/\sum_{j=1,\,j\neq i}^{n}\left[\frac{z_j}{\hat{\pi}(x_j)}\right], \tag{7}$$

and

$$\tilde{\tau}_\mu = \frac{1}{n}\sum_{i=1}^{n}\tilde{\tau}_i, \tag{8}$$

the estimators of the ratio and the variance of the estimator are given by

$$\hat{\tau} = n\tilde{\tau} - (n-1)\tilde{\tau}_\mu, \tag{9}$$

and

$$\hat{v}(\hat{\tau}) = \left(\frac{\hat{N}-n}{\hat{N}}\right)\left(\frac{n-1}{n}\right)\sum_{i=1}^{n}(\tilde{\tau}_i - \tilde{\tau}_\mu)^2, \tag{10}$$

respectively, where the first term of equation (10) is an estimated finite population correction factor.

An example.—The estimation procedures presented in the previous section were applied to data collected during a study of nesting waterfowl in North Dakota (Klett and Johnson 1982). Weekly searches for roadside nesting waterfowl were conducted using a cable-chain drag in 1976 and 1977. Detected nests were revisited at weekly intervals until nests either failed or were successful. A nest was considered successful if at least one nestling survived to leave the nest. Considered here are 1976 and 1977 observations of Mallard (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*) nests that were either successful or destroyed. Following Klett and Johnson (1982), abandoned nests were excluded from the analysis.

Although the searches were not initiated on a randomly selected day and the weekly search schedule was not strictly followed, these data may be approximately analyzed under the systematic-encounter-sampling design. Defining y as 1 for all nests which survived to success and 0 for all nests that failed, and defining z as 1 for all nests, equation (9) estimates the probability a nest survives to success, denoted Φ. Under the same condition of y, equation (4) estimates the total number of successful nests, denoted S. The estimates obtained under the naive model (proportion of nests that were successful), by Klett and Johnson (1982) using the Mayfield (1975) model, and under the systematic-encounter-sampling design are presented in Table 1. The estimates obtained under the systematic-encounter-sampling design were computed using the program ENCOUNTR, which is available from the authors.

The estimates of nest survival rates obtained under the systematic-encounter-sampling design compare quite favorably with the estimates obtained using the Mayfield method. In all cases, the estimated coefficients of variation are substantially smaller under the systematic-encounter-sampling design. These estimates are not based on the assumption that the probability of surviving a single time unit is equal for all nests and constant through time, as are the estimates obtained under the Mayfield model. In addition, the procedures presented here permit the population size and the number of successful nests, parameters of interest in most applications, to be estimated.

Discussion.—The systematic-encounter-sampling design is appropriate for the study of any population of nesting birds in which the age of nests can be determined at the time of detection. An important

Table 1. Point estimates and estimated coefficients of variation ($\widehat{CV}$), expressed as percentages, obtained under the naive model, the Mayfield model, and the systematic-encounter-sampling model.[a]

Quantity	Naive	Mayfield	Systematic
		Mallard (1976)	
$\hat{\Phi}$	0.315	0.207	0.260
$\widehat{CV}(\hat{\Phi})$	*	16.70	6.63
$\hat{\beta}$	*	*	0.483
$\widehat{CV}(\hat{\beta})$	*	*	8.00
$\hat{S}$	*	*	43
$\widehat{CV}(\hat{S})$	*	*	1.62
$\hat{N}$	*	*	165
$\widehat{CV}(\hat{N})$	*	*	4.13
		Mallard (1977)	
$\hat{\Phi}$	0.663	0.559	0.610
$\widehat{CV}(\hat{\Phi})$	*	10.99	2.67
$\hat{\beta}$	*	*	0.651
$\widehat{CV}(\hat{\beta})$	*	*	7.04
$\hat{S}$	*	*	56
$\widehat{CV}(\hat{S})$	*	*	0.39
$\hat{N}$	*	*	91
$\widehat{CV}(\hat{N})$	*	*	1.92
		Blue-winged Teal (1976)	
$\hat{\Phi}$	0.446	0.307	0.352
$\widehat{CV}(\hat{\Phi})$	*	10.86	4.55
$\hat{\beta}$	*	*	0.411
$\widehat{CV}(\hat{\beta})$	*	*	7.30
$\hat{S}$	*	*	104
$\widehat{CV}(\hat{S})$	*	*	2.07
$\hat{N}$	*	*	293
$\widehat{CV}(\hat{N})$	*	*	3.99
		Blue-winged Teal (1977)	
$\hat{\Phi}$	0.736	0.639	0.685
$\widehat{CV}(\hat{\Phi})$	*	8.46	2.17
$\hat{\beta}$	*	*	0.603
$\widehat{CV}(\hat{\beta})$	*	*	6.06
$\hat{S}$	*	*	79
$\widehat{CV}(\hat{S})$	*	*	0.62
$\hat{N}$	*	*	115
$\widehat{CV}(\hat{N})$	*	*	1.65

[a] Asterisk (*) indicates quantity could not be estimated under the model.

data requirement is that detected nests be monitored until the data of interest is observed, which is until either success or failure occurs for estimation of survival rates. However, given these restrictions, the design requires relatively few assumptions. While the design requires the implicit assumption that searches cover the entire study area, this assumption can be dealt with through a stratification of the study area. Although, strictly speaking, the design assumes that the lifetime of detected nests is determined without error, simulation results indicate the design is robust to modest violations of this assumption (Bromaghin and McDonald 1992). In particular, if the lifetimes of nests can be determined accurately on average, the statistical quality of the estimators appears to suffer little. If nest lifetimes are estimated with bias, it is preferable to overestimate lifetimes than to underestimate them. This is apparent from an examination of Figure 2; overestimation of x produces a smaller change in the estimation of the probability of inclusion than does underestimation by an equal amount.

The estimators presented here assume that the probability of detection, β, is equal for all nests and constant through time. Although this assumption appears reasonable in the example, it would be violated in many applications. However, the estimators are undoubtedly robust to some violations of this assumption. For example, if β is heterogenous but not correlated with variables of interest, $\hat{\beta}$ produces an estimate of the population mean β. In this case, the statistical quality of the estimators would not suffer greatly, although some increase in variability would be expected. In many studies, β would be expected to vary as a function of such factors as time, weather, age of nesting birds, habitat differences within the study area, and the differing abilities of searchers. Since such factors are likely to vary greatly between nesting studies, we have made no attempt to develop procedures to incorporate them. However, the basic approach used here could easily be modified to incorporate most, or all, such situations.

Bromaghin and McDonald (1992) summarized a simulation study undertaken to investigate the properties of these estimators under general conditions. Although the simulation was not specifically designed to model nesting studies, many of the conclusions are applicable. The results indicated that the estimators have desirable statistical properties under many conditions. In general, ratios, such as survival rates, are estimated with little bias and small variance under nearly all scenarios, primarily because violations of assumptions influence both the numerator and denominator of the estimator to a similar degree. Estimates of totals tend to be positively biased and have larger variance. As might be expected, the primary factor influencing the quality of estimates of totals is the search effort (i.e. an interaction of the magnitude of the probability of detection and the frequency with which searches are conducted). However, the tendency of estimates of totals to be positively biased can be greatly reduced or even made negligible by increasing the search effort.

The example illustrates a number of differences between traditional nest-survival models and this procedure and merits further discussion. In particular, the coefficients of variation are uniformly smaller and estimates of nest-survival rates are uniformly larger under the systematic-encounter-sampling design than under the Mayfield (1975) model. The reduction in variance is easily explained. Strictly speaking, traditional nest-survival models, including the Mayfield

(1975) model, require sampling with replacement, although such models often may be applied without concern when the sample is small with respect to the population. However, the population was relatively small, and since the method used to detect nests was quite efficient, a large proportion of the population was observed (Klett and Johnson 1982). Use of a classic sampling approach and an estimated finite population correction (Cochran 1977) in the variance estimator of equation (10) provides a much more realistic picture of the variability of the estimator under repeated sampling. Also, since simulation results indicated that estimates of population size tend to have positive bias, the estimated finite population correction will tend to be conservative.

The observed difference between the estimates of nest survival is more difficult to explain conclusively. With the exception of the Pollock and Cornelius (1988) model, nest-survival models assume that the probability a nest survives a single unit of time is equal for all nests and constant through time. This assumption may have been substantially violated in the example, perhaps because of the unnatural stress of nesting near roadways. In addition, the Mayfield model, like all traditional nest-survival models, is a likelihood function, although Mayfield (1961, 1975) did not express the model in those terms. Maximum-likelihood estimation requires a number of assumptions (Rao 1973), including an assumption of identically distributed observations. The systematic manner by which the data were obtained would violate this assumption if the probability of surviving a unit of time were not constant. Although a third possibility arises from the fact that the systematic-encounter-sampling design was only approximated in the example, the deviations from the design were slight and unlikely to produce differences of the magnitude observed. Although other possibilities exist, these are perhaps most likely to have produced the observed differences.

In summary, we propose the systematic design for the study of nesting bird populations in which nests can be approximately aged at the time of detection. Although the design requires restrictive assumptions in comparison to models specifically designed to estimate nesting success, assumptions regarding the survival rate over time are not required. The design is intuitive and permits two general classes of parameters to be estimated, including survival rates. The number of parameters that can be estimated is limited only by the number of variables observed on each nest and the researcher's ingenuity in constructing indicator variables. Prior to this work, estimates of parameters other than nest survival were subject to the type of bias addressed by nest-survival models.

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APPENDIX

Derivation of the probability of inclusion.—Let P(*S*) represent the probability of the event *S*, let *E* represent exclusion from the sample, and let *t* represent the randomly selected time unit on which the first search will be conducted. Then

$$\begin{aligned}\pi(x) &= 1 - \mathrm{P}(E)\\ &= 1 - \sum_t \mathrm{P}(E \cap t)\\ &= 1 - \sum_t \mathrm{P}(E \mid t)\mathrm{P}(t)\\ &= 1 - \frac{1}{d}\sum_t \mathrm{P}(E \mid t), \qquad (11)\end{aligned}$$

since $\mathrm{P}(t) = 1/d$. Now, $d(\theta + 1) - x$ choices of t result in θ searches being conducted during the x time units a nest is in existence and $x - d\theta$ choices of t result in $\theta + 1$ searches being conducted. As the searches are assumed independent and the probability of detecting a nest on any one search is β if it is in existence and 0 if it is not,

$$\pi(x) = 1 - \frac{1}{d}[(d(\theta + 1) - x)(1 - \beta)^{\theta} + (x - d\theta)(1 - \beta)^{\theta+1}]. \qquad (12)$$

This function can easily be written in the form given in equation (1).

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Application of Computed Tomography to Morphological Study of Emperor and Adélie Penguins

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Computed tomography (CT) has been commonly applied to medical science and clinics. This scanning technique also has been applied to the functional physiology of human muscle. Häggmark et al. (1978), Schantz et al. (1983) and Borkan et al. (1983) used CT for measuring the cross-sectional area of muscle and subcutaneous fat. Through these studies it was revealed that CT provides a rapid and accurate measuring method without sectioning of material.

Using CT, we first attempted to measure the body and organ cross-sectional area of one male Emperor Penguin (*Aptenodytes forsteri;* the largest penguin) and one female Adélie Penguin (*Pygoscelis adeliae;* a medium-sized penguin), which were initially collected for measuring heavy-metal concentrations. We calculated the body and organ volumes from the serial measurements of cross-sectional area as part of a morphological analysis of internal organ size. Here we report the preliminary results of our study.

Methods.—We collected the Emperor and Adélie penguins from Riiser-Larsen Peninsula (68°50'S, 34°40'E) and Langhovde (69°13'S, 39°39'W), Antarctica on 19 September 1990 and 18 January 1991, respectively. The birds were euthanized by intermuscular injection of Ketamine hydrochloride and kept frozen at −20°C. The frozen materials were laterally scanned by a Yokogawa CT scanner (ImageMax II). CT images were obtained at 10-mm intervals, perpendicular to the longitudinal body axis from top of the beak to end of the foot extended caudad. Images were filmed

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