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A Review of Estimating Animal Abundance

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SUMMARY

During the past 5 years there have been a number of important developments in the estimation of animal abundance and related parameters such as survival rates. Many of the new techniques need to be more widely publicised as they supplant previous methods. The aim of this paper is to review this literature and suggest further avenues for research.

1. Introduction

Since the manuscript of my book (Seber, 1982, hereafter referred to as *Sb*) was submitted in 1979, there have been several important developments in capture-recapture methods and related topics. We shall review the literature during this period and suggest some areas where further research is needed. The terminology and notation will follow that of my book. With these new developments it is now possible to give clearer guidelines in many of the topics. Some of the methods in *Sb* are now largely of historical interest only. Earlier reviews have been given by Youngs and Robson (1978), Begon (1979), Cormack (1979), Ralph and Scott (1981), Blower, Cook, and Bishop (1981), White et al. (1982), Sen (1982), and North and Morgan (1985).

Before proceeding, we mention four important technological advances that are relevant to population estimation. The first is the development of very small radio transmitter tags (Amlaner and MacDonald, 1980). Although transmitter failure is still a problem, one can foresee the day when these tags will be so small, cheap, and reliable that they can be used in large numbers [e.g., Thomas (1980) describes a 1-gm transmitter]. The second development is in remote sensing such as thermography, where animals are detected by the heat they radiate (Wyatt, Trivedi, and Anderson, 1980; Best and Fowler, 1981). The third development relates to the use of underwater acoustics (*Sb*, p. 453; MacNeill and Dowd, 1975; Orr, Hays, and Hess, 1978; Dickie, Dowd, and Boudreau, 1983; Kieser and Mulligen, 1984). The fourth and most important advance is the widespread availability of computers with associated statistical techniques such as simulation, Monte Carlo inference (Buckland, 1984), the jackknife, and the bootstrap (Parr, 1983). Computers have also made it possible to examine the robustness of many techniques. Some of the standard estimation methods have been found to be very sensitive to certain departures from their underlying assumptions so that there has been a renewed emphasis on developing more robust nonparametric procedures.

2. Closed Populations: Sample Units

A closed population is one that remains unchanged during the period of investigation: the effects of migration, mortality, and recruitment are negligible. We now consider the problem

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of estimating the density of an animal population (or its signs) using various sampling units such as plots, strips, lines, and points.

2.1 *Quadrats and Strip Transects*

The most common method of estimating population density is to count the numbers on a random sample of plots. Quadrats are frequently used, though the term also refers loosely to rectangles, circles, and so forth, as well as to squares. As populations tend to be very patchy, stratified sampling seems to be the most appropriate method (Sb, pp. 26, 451). Systematic sampling with a random starting point (equivalent to cluster sampling) is preferred in many ecological situations as it ensures a more even coverage of the population area (Lenarz and Adams, 1980; Scherba and Gallucci, 1976). There needs to be a greater emphasis on the use of efficient sample survey methods (Otis and Bowden, 1979, ratio estimates; Sen, 1981a, 1981b, bird surveys; Geissler and Noon, 1981; Couling, Sen, and Martin, 1982; Schweigert and Sibert, 1983, 1984; Bowden, Anderson, and Medin, 1984, age and sex ratios). Insect populations, for example, require careful multistage designs (Kuno, 1976; Yano, 1983). Transformations sometimes improve a statistical analysis (Sen, 1981b). Data from marine surveys often contain a large proportion of zeros and treating the zeros separately can lead to more efficient estimators of abundance (Pennington, 1983).

In an initial study of a population, the spatial distribution is frequently unknown so that post-stratification (Holt and Smith, 1979) may be a useful aid in the analysis. If the population is very patchy and the population area is very large (e.g., sampling for plankton or krill in the sea), then it is difficult to design an adequate sampling scheme because of the high coefficient of variation. A more appropriate design would be an adaptive scheme (Thompson, 1982) in which the sampling intensity used in a given area depends on the density found in the previous area(s). Sampling is then more concentrated in the higher-density areas. More research is needed on this topic.

The negative binomial distribution has been found to be a useful model for a wide range of clustered populations (Sb, pp. 25, 450), as, for example, trawl catches (Lenarz and Adams, 1980), mosquitoes (Nedelman, 1983), and pellet groups (White and Eberhardt, 1980). This distribution has probability function

$$f(x) = \frac{k(k+1) \cdots (k+x-1)}{k!} \left(\frac{\mu}{k}\right)^x \left(1 + \frac{\mu}{k}\right)^{-x-k}, \quad x = 0, 1, 2, \dots, \quad (1)$$

representing the probability of finding x animals or signs on a sample plot. The population mean μ is related to the variance σ^2 by the standard equation

$$\sigma^2 = \mu + \mu^2/k. \quad (2)$$

The smaller the value of k , the greater the clustering. However, the use of the negative binomial has been questioned on several counts. First, it does not contain a regular spatial distribution as a special case. Second, although k is often described as a measure of aggregation, it does not appear to have a clear-cut ecological property (Taylor, Woiwood, and Perry, 1979). By contrast, the well-known Taylor's power law

$$\sigma^2 = \alpha\mu^\beta, \quad (3)$$

or $\log \sigma^2 = \log \alpha + \beta \log \mu$, is remarkably universal for a given species (Taylor, Woiwood, and Perry, 1980). The parameter β , frequently between 1 and 2, seems fairly constant over time and space for many species. The estimation of α and β is discussed by Perry (1981). If (2) and (3) are both true for a population, then

$$\frac{1}{k} = -\frac{1}{\mu} + \alpha\mu^{\beta-2},$$

and k is density-dependent and unstable in relationship to μ (Taylor et al., 1979; Nachman, 1981). One problem is that the negative binomial can arise with both apparent and true contagion (Sb, pp. 479, 483; Cliff and Ord, 1973, p. 59; Freeman, 1980, p. 261). With apparent contagion k is constant and independent of μ , while with true contagion $p (= k\mu)$ could be constant so that k varies with μ (and therefore with quadrat size). The estimation of k and μ for the negative binomial and its truncated version are discussed by White and Eberhardt (1980) and Schenzle (1979), respectively (see also Pieters et al., 1977; Willson, Folks, and Young, 1984). Methods of estimation when k or p is constant over several data sets are discussed by White and Eberhardt (1980); see also Freeman (1980) for two-parameter discrete distributions in general. Related to this subject of clustered populations is the problem of finding confidence intervals for indices of spatial aggregation based on counts (Reed, 1983).

Strip transects are generally easier to locate and sample than quadrats, though they are more affected by boundary effects (for example, movement of animals on the boundary). Strips are used extensively in aerial censusing (see §2.2) and in counting pellet groups. Freddy and Bowden (1983) discuss the merits of temporary versus permanent transects for pellet counts. Although temporary transects are cheaper to use, care is needed in distinguishing between old and new pellet groups. On permanent transects all pellets are cleared off after the sampling. Converting pellet densities to animal densities is fraught with difficulties because of the variability of conversion factors. Pellet densities may not even give an accurate representation of relative habitat use (Collins and Urness, 1981).

The efficiency of any sampling scheme can be increased by making use of any highly correlated "auxiliary" variables such as previous estimates, number of ponds for waterfowl, and so forth (Sen and Beznacuk, 1982).

2.2 Aerial Censusing

When sampling is done from the air, strips are preferred to quadrats as they are easier to locate and easier to standardize for calculating visibility factors (Sb, pp. 454–458). However, quadrats are useful in censusing difficult terrain using helicopters, though helicopter flying is harder to standardize (Kufeld, Olterman, and Bowden, 1980). Helicopters are also useful for surveying low, densely brush-covered areas because they can be flown at lower speeds and less height (Besom, 1979). Marine surveys present their own set of problems (Sb, p. 459; Estes and Gilbert, 1978; Powers, 1982; Reilly, Rice, and Wolman, 1983; Briggs, Tyler, and Lewis, 1985).

Important research in aerial censusing has been carried out in Australia (see Australian National Parks and Wildlife Service, 1979, for practical details). For example, a helpful comparison of ground, helicopter, and fixed-wing aircraft counts is made by Ridpath et al. (1983). When making area comparisons using analysis of variance, Caughley et al. (1980) found the square root transformation (appropriate for Poisson data) helpful in homogenising variances.

The most important problem is that of providing a correction factor for lack of visibility. If the objects are stationary and can be mapped by two independent observers, then the Petersen capture–recapture method can be used (Bergerud, 1971, caribou; Henny et al., 1977, osprey nests; Magnussen, Caughley, and Grigg, 1978, crocodile nests; Grier et al., 1981, bald eagle nests; Maxim, Harrington, and Kennedy, 1981, objects on aerial photographs). When the population density is low, the method can also be applied to mobile populations by two observers viewing simultaneously and independently (Caughley and Grice, 1982). Unfortunately, not all animals are equally sightable, though this does not bias estimates if the observers' abilities to sight animals are independent of each other (Sb, p. 86). However, animals that are hard to see by one observer are usually hard to see by the other. To allow for this, Caughley and Grice (1982) suggested a modification of the

method based on the observer average probability of sighting. Another method of obtaining a correction factor is to use radio-tagged deer on test plots similar to the census plots (Floyd, Mech, and Nelson, 1979). One of the correction methods of Caughley and Goddard (1972), based on repeat data, has been criticised by Routledge (1981). Clearly further research is needed on correction factors; radiotelemetry will no doubt become more useful here (Packard, Summers, and Barnes, 1985).

A further problem with aerial censusing is the counting of animals in groups (Cook and Martin, 1974; Jolly and Watson, 1979). Models for dealing with this have been proposed by Cook and Jacobson (1979) and Samuel and Pollock (1981). A different approach, also used in line transects (see §2.3), is to treat the groups as single units and then multiply the number of groups by the average group size; aerial photography could be used effectively here. Caughley and Grice (1982) found that they could use a presence-absence method (Sb, p. 56) for counting the number of emu groups as the groups were sparse and fitted a Poisson distribution satisfactorily. If \hat{q} is the proportion of empty transects, each of area a , then the density D can be estimated by $\hat{q} = \exp(-\hat{D}a)$, or

$$\hat{D} = -\frac{1}{a} \log \hat{q}. \quad (4)$$

This presence-absence method is considered further by Swindel (1983) and Oakenfull, Salbe, and Zehnwirth (1984).

One other method that has been proposed for aerial censusing is the bounded counts method (Regier and Robson, 1967; Cook, 1979). However, Routledge (1982) studied the method in detail and concluded that it is not appropriate unless the average proportion seen exceeds .8; this rules out its use in many surveys.

2.3 Line Transects

Strip transects are generally inappropriate for birds because of lack of visibility (Burnham, Anderson, and Laake, 1981). However, a useful method for studying mobile animals such as birds is the so-called line transect or variable-width transect (Sb, p. 461; Burnham, Anderson, and Laake, 1980; Gates, 1980; Quinn and Gallucci, 1980; Franzeb, 1981). An observer moves along the line and, for every animal observed or flushed into the open, estimates the perpendicular distance y of the animal from the line. Alternatively, one can measure the radial distance r and the angle θ ; then $y = r \sin \theta$. Hayes and Buckland (1983) examined models based on r using hazard-rate analysis and concluded that methods based on y are better. These latter methods hinge on finding a suitable estimate of $f(0)$, where f is the density function of observed y . Elliptical flushing models using both r and y are discussed by Otten and de Vries (1984).

A number of parametric models are available (Sb, p. 462; Ramsey, 1979; Buckland, 1985), though estimates from such models are often very sensitive to departures from the underlying assumptions (Gates, 1980, p. 660). The use of incorrect models can lead to erroneous estimates (Hildén, 1981). If animals can be seen with probability 1 in a given subarea, usually referred to as the basal area, then a method due initially to Emlen (1971) can be used (Ramsey and Scott, 1981). However, the nonparametric Fourier model of Burnham et al. (1980) seems superior as it satisfies a number of sensible criteria for robust estimation (Burnham, Anderson, and Laake, 1979; 1981, p. 469) and gives reasonable estimates for a wide range of "visibility" functions, f . Recent applications include Ratti et al. (1983, gray partridges) and T. D. Smith (1983, aerial censusing of dolphins). Buckland (1982a) also found that the Fourier method gave reliable estimates but analytic confidence intervals tended to be too narrow with, at best, 90% confidence for 95% intervals. He compared three techniques—namely, replicate lines, jackknifing, and Monte Carlo—and recommended the last one. Unfortunately, the Fourier methods can be very dependent on

the number of terms and Buckland (1985) proposed a Hermite polynomial model that is less sensitive. A promising nonparametric method based on shape restrictions has been proposed by Johnson and Routledge (1985). The line transect method can also be extended to sequential sampling in which sampling continues until a prescribed number is sighted (Rao, Portier, and Ondrasik, 1981). As sampling may not terminate in a reasonable period of time, Rao (1984) also gave a combined method in which sampling stops when either a prescribed number of objects is sighted or a prespecified length of transect is traversed.

The search for other methods of estimating $f(0)$ continues. The function f has also been approximated by polynomials (Gates and Smith, 1980); kernel methods for estimating probability density functions may also have a role to play (Fryer, 1977; Wertz, 1978). The problem of left-truncated data is considered by Alldredge and Gates (1985). When a population is made up of groups (e.g., schools, flocks, or herds) of varying sizes, the above methodology can still be used, but with some modification (Burnham et al., 1980; Quinn, 1981). A new parametric model for handling randomly distributed groups is proposed by Rao et al. (1981). Further extensions are discussed by Rao and Portier (1985).

Unfortunately, transect methods do not always work because dense shrub and rough terrain make it difficult for the observer to walk quietly and simultaneously look for birds. Ramsey and Scott (1979, 1981) and Reynolds, Scott, and Nussbaum (1980) suggested using a "variable circular plot" technique in which stations are located along the transect and some time is spent at each station observing bird distances. Such a procedure has several advantages: (i) there is time for the observer to see most of the birds close to the station; (ii) different species can be studied at the same time, including rare species; and (iii) between stations the observers have the luxury of looking where they are going! The theory behind the procedure is analogous to that for line transects (cf. Burnham, Anderson, and Laake, 1980, p. 195) and, for the same reasons, does not require the assumption of random distribution. Provided the stations are located in a random or semirandom fashion, the location of each bird will have a uniform distribution. Any dependency among the birds due to clustering will not affect arguments based on expected values, but variances will be affected. Sample variance estimates from replicates are preferred, in this case, to model-based variances. As with the line transect method, the birds can be repulsed by the observer and may be counted more than once. DeSante (1981) found that the method gave useful results, though with a tendency toward underestimation when the species is dense and overestimation when the species is sparse. However, Anderson and Ohmart (1981) found considerable daily variation with the method. Pyke (1983) suggested using ladders as well but found that repulsion was still a problem. Unfortunately, the movement of the birds affects all the methods of estimation (Granholt, 1983). Some practical details for large surveys are given by Scott, Jacobi, and Ramsey (1981).

A closely related technique that is sometimes useful is the line-intercept method, in which the length of intercept of each object covering the line transect is recorded (see Kaiser, 1983, for a good survey). Although its main application is to habitat sampling, it can be used for sampling large animal signs such as den sites (Eberhardt, 1978). Under the title of linear intercept density estimation, the method has also been extended to estimating fish density using hydroacoustics (Kimura and Lemberg, 1981).

2.4 Distance Methods

Instead of lines one can focus on points. A number of interpoint-distance methods are available for estimating density and testing for randomness in populations of animal signs such as termite mounds or almost stationary organisms such as slugs and snails. Several types of distance can be measured, namely (Byth, 1982): (i) x_r , the distance from a randomly selected point P to the r th nearest object Q_r ; (ii) y_r , the distance from Q_1 to the r th nearest object in a direction away from P , the so-called "T square" distance; and (iv)

w , the distance from Q_1 to the nearest object. Originally the theory was developed for x_r and y_r on the basis that both P and Q_0 were randomly selected and the population was randomly distributed according to a homogeneous Poisson model. Unfortunately, populations are rarely random and tend, on the whole, to be clustered and occasionally regular. Furthermore, subsequent research has shown that the older methods are not robust to departures from randomness (Sb, p. 473; Warde and Petranka, 1981). This nonrobustness tends to get worse as r increases so that usually $r = 1$. Recent theoretical extensions to n dimensions are given by Clark and Evans (1979), Stauffer (1979), and Cox (1981).

In order to choose an object Q_0 at random, it must be possible to label every member of the population and then choose a label at random using, for example, random numbers. As this is generally out of the question, another method was used, namely selecting P at random and then choosing Q_1 , the nearest object. Unfortunately, it was erroneously thought that y_1 and w had the same distribution. However, there have been two important developments which have helped to get around this problem. The first was the introduction of z_r , which replaces the role of y_r in density estimation. The second was the introduction of semisystematic sampling by Byth and Ripley (1980), which enabled y_r to be used; it seems that x_1 and y_1 are essential ingredients of a good test of randomness. New robust density estimates are given by Byth (1982). She prefers semisystematic sampling to random sampling as the former avoids oversampling (Byth and Ripley, 1980, p. 281) and, for nonhomogeneous spatial point processes, it also tends to give smaller variances without causing large increases in absolute biases; the bias is often reduced.

Patil, Burnham, and Kovner (1979) showed that, for a wide range of homogeneous spatial point processes, the population density D is given by $D = f(0)$, where f is the density function of $u = \pi x_1^2$. They proposed a nonparametric estimate of $f(0)$ based on ranked values of u . However, this approach has some disadvantages (Byth, 1982, p. 128). In particular, $D = f(0)$ holds only for homogeneous processes.

The above methods need to be extended to the case when an object can no longer be regarded as a point but its size must be taken into account. Some steps in this direction, in the provision of tests for nonrandomness, have been made by Pielou (1962), Simberloff (1979), and Cook (1981).

A further adaption of the distance method, in which the points are chosen from a thin strip, is given by Parker (1979). He uses a negative binomial model (Eberhardt, 1967) with parameter k independent of area sampled: in his formula (23) there should be no n inside the bracket.

2.5 Removal Method

The removal method consists of sequentially removing samples from the population and using the decline in catch size to provide an estimate of population number (Sb, pp. 309, 500). Usually at least three samples are required, though in special circumstances one can do with fewer (Sb, p. 318; Keller and Burnham, 1982). The two-sample case, for small samples, is considered further by Harding et al. (1984). Good et al. (1979) proposed a model in which the probability of capture depends on the number of unoccupied traps. However, the effects of home range, trap response, and heterogeneity will almost certainly swamp any proportional trapping effect. Also, the model has serious numerical problems. At present it appears that the best estimators of N are the generalised removal estimator of Otis et al. (1978, p. 44) and, possibly, the new jackknife estimator of Pollock and Otto (1983) for model M_{bh} , yet to be tried on removal data. The problem of point and interval estimation of the ratio of two population sizes using separate removal experiments is discussed by Skalski, Simmons, and Robson (1984). A regression method is considered by Soms (1985).

In converting size estimates from grid trapping to density estimates, we run into the problem of determining the effective trapping area (mentioned in §3.2). The edge effect is more serious with removal trapping as the gradual depletion of the grid area will encourage migration into the area. As the home range and population density will tend to vary from grid to grid, the method of MacLulich (1951) for simultaneously estimating density and home range is no longer recommended. Stenseth and Hansson (1979) proposed a method based on the assumption that the rate at which the number of animals caught per trap station changes with the distance from the edge is inversely proportional to the number of "borderers." A promising method is the method of nested subgrids suggested by Otis et al. (1978). Finally, the use of assessment lines does not seem appropriate (Sb, p. 504).

2.6 Relative Density

The density of animal signs can often provide a useful index of population density provided the index is relatively stable under a variety of environmental conditions (Sb, pp. 52, 452; see also Bull, 1981, for a good review relating to birds). A method of estimating hare numbers from lengths of snow tracks is given by Hayashi, Komazawa, and Hayashi (1979). A useful technique for converting an index to population density, proposed by Davis (1963), consists of calculating the index before and after a known number of animals are removed. Following Eberhardt (1982), who discusses this method in detail, we can call the technique the index-removal method.

The presence-absence method described in Section 2.1 has been used in New Zealand for estimating deer pellet group density over rugged terrain. Referring to equation (4), \hat{q} is an unbiased estimate of q , the probability of finding an empty plot. Setting $q = f(0)$ in (1), we see that \hat{D} is an asymptotically unbiased estimate of

$$\begin{aligned} -\frac{1}{a} \log q &= \frac{k}{a} \log \left(1 + \frac{Da}{k} \right) \\ &= D - D^2 a / 2k + \dots \\ &= D(1 - Da / 2k) + \dots \end{aligned}$$

Although the method is specifically designed for Poisson distributions, it will also give reasonable estimates for clustered populations if $Da/k < .1$. For example, if $k = .1$, representing a highly clustered population, then the average number per plot ($= Da$) must be less than .01.

3. Closed Populations: Capture-Recapture Methods

3.1 Single Recaptures

Suppose a population of unknown size N has M marked individuals and $U = N - M$ unmarked. A random sample of size n from the population yields m marked and $u (= n - m)$ unmarked. Assuming marked and unmarked are equally represented in the sample, we can write

$$\frac{m}{M} = \frac{u}{U} \left(= \frac{m + u}{M + U} = \frac{n}{N} \right),$$

which leads to the well-known Petersen estimate (Sb, Chap. 3) $\hat{N} = Mn/m$. This principle of equating proportions caught from similar subgroups underlies many of the more complex capture-recapture models. Various probability functions have been used for modelling the

above experiment. Defining $\pi = M/N$, we can write three of these as

$$f(m | M, N) = \binom{M}{m} \binom{U}{u} / \binom{N}{n}, \quad (5)$$

$$f(m | \pi) = \binom{n}{m} \pi^m (1 - \pi)^{n-m}, \quad (6)$$

and

$$f(m | \pi) = \exp(-n\pi)(n\pi)^m / m!. \quad (7)$$

If we assume that the marking sample is random, and p_i is the probability of capture in the i th sample ($i = 1, 2$), we also have the multinomial distribution

$$f(\{a_w\} | N) = \frac{N!}{\prod_w a_w!(N-r)!} (p_1 q_2)^{a_{10}} (q_1 p_2)^{a_{01}} (p_1 p_2)^{a_{11}} (q_1 q_2)^{N-r} \propto \frac{N!}{(N-r)!} \prod_{i=1}^2 p_i^{n_i} q_i^{N-n_i}. \quad (8)$$

Here a_w is the number with recapture history w (e.g., a_{01} are caught in sample 2 but not in sample 1, a_{11} are caught in both samples, etc.), n_i is the number caught in the i th sample, and r is the number of different animals caught all together. We find that the maximum likelihood estimate of N is \hat{N} for (6) and (7), $[\hat{N}]$ for (5), and close to \hat{N} for (8). Another potentially useful model, particularly when m is small, is the Bayesian model

$$f(N | m) \propto f_1(m | M, N) f_2(N), \quad (9)$$

where $f_2(N)$ is the prior distribution of N and $f(N | m)$ is the posterior distribution. The main problem is the choice of prior, and several have been suggested (Gaskell and George, 1972; Johnson, 1977). However, if f_2 is uniform, the so-called vague prior, then the mode of (9) is \hat{N} ; one can also use the posterior mean.

The binomial model (6) may be regarded as an approximation for the hypergeometric model (5) when sampling is without replacement, or it can be used in its own right when sampling is with replacement (for example, animals sighted but not recaptured) (Sb, p. 61; Henzell and McCloud, 1984). The design procedures of Robson and Regier (1964) for the hypergeometric distribution have also been applied to the binomial model by Jensen (1981) with simpler equations being obtained. The multinomial model was considered by McDonald et al. (1983), who gave an exact test of $p_1 = p_2$ and discussed point and interval estimation of the parameters. In particular, they gave useful results for the model M_0 ($p_1 = p_2$, see Sb, p. 323), though this model is of limited application.

Although several applications of the Petersen method have appeared in the literature, the example by Bowen and Sergeant (1983) on harp seal pups is worth singling out because of the careful examination of underlying assumptions. They allow for tag loss, incomplete tag reporting, and age cohorts in their analysis. The effect of tag loss and the use of double tagging are discussed in detail by Seber and Felton (1981). A number of authors have independently derived the same tag loss estimates, though their formulae appear to be different (Sb, p. 489; Eberhardt, Chapman, and Gilbert, 1979). Some of the problems of nonreporting in sports fishing are highlighted by Matlock (1981). Inference relating to comparing two Petersen estimates is considered by Skalski, Robson, and Simmons (1983); see also Sb, pp. 122–125. The Petersen method has also been combined with age-length data to estimate fish production rates (Newman and Martin, 1983). For a good review of the Petersen method for estimating bird numbers see Nichols et al. (1981).

A useful extension of the Petersen method is to the case where the second sample consists of a sequence of samples, each sample being permanently removed from the population (De Lury, 1958; Paloheimo, 1963). This model, which can be appropriately called the mark-removal model, is studied in detail by Skalski and Robson (1982). Combining the

mark–recapture method with a removal model provides various estimates and tests of underlying assumptions (see also Skalski and Robson, 1979).

3.2 Multiple Recaptures

We now consider the Schnabel census (Schnabel, 1938), in which a series of samples is taken from a closed population. The unmarked animals in each sample are given individual tags and are returned to the population. One group of models for estimating N , which are particularly useful for open populations (see later), are the loglinear models (Bishop, Fienberg, and Holland, 1975, Chap. 6; Cormack, 1979; Heckel and Roughgarden, 1979). Another important set of models was introduced by Otis et al. (1978)—see also White et al. (1982)—to cope with variations in the catchability of the animals. These models are designated M_0 , M_b , M_h , M_t , M_{bh} , M_{th} , and M_{tbh} . The subscript “b” represents behavioral (trap) response; “h” represents heterogeneity, in which each animal has the same probability of capture in any sample but the probability varies from animal to animal; and “t” represents temporal changes in which the probability of capture is the same for all animals but the probability varies from sample to sample. The model M_0 assumes a constant probability of capture for all animals and all sampling occasions. Otis et al. (1978) gave estimation procedures for the first five models only; the other models have identifiability problems. Heterogeneity and trap response seem to be a fact of life (e.g., Tanaka, 1980, pp. 42–52) so that the most useful models appear to be M_h and M_{bh} . Otis et al. proposed a jackknife estimator \hat{N}_h of N for M_h , and a so-called generalised removal estimator for M_{bh} . These models were originally considered by Pollock (1974, 1975a, 1981a) and studied further by Pollock and Otto (1983). They confirmed that \hat{N}_h was the best on the market for M_h , and introduced a new jackknife estimate for M_{bh} . Recently Pollock, Hines, and Nichols (1984) proposed the use of logistic auxiliary variables (e.g., relating to environment and size) in modelling the probability of capture in M_t and M_b . An application of the above methodology is given by Lefebvre, Otis, and Holler (1982).

Model M_t was the first model to be exploited, and Darroch (1958) and Otis et al. (1978) investigated the maximum likelihood estimate \hat{N}_t of N in some detail. Several approximations were considered by Sen and Sen (1981), but these are not preferred. Darroch (1958) also considered the special case of samples of size 1 and later (Darroch and Ratcliff, 1980) provided a simpler estimate with high asymptotic efficiency. For interval estimation, Sprott (1981) suggested constructing a confidence interval for N based on the approximate normality of $\hat{N}_t^{-1/3}$. A Bayesian analysis of models M_t and M_0 is given by Castledine (1981).

Model M_0 has been used as a basis for two models, the truncated binomial and the truncated Poisson, for estimating N from recapture frequencies (Sb, pp. 169–170). If there is heterogeneity or trap response, several truncated parametric models such as the geometric, negative binomial, and Skellam’s model have been proposed (Sb, pp. 170–179; North, 1981). The geometric model has the advantage of having an associated regression model, but see Romesburg and Marshall (1979). However, there is now sufficient evidence from the literature (Sb, p. 496; Zarnoch, 1979; Guthery, 1980; Nichols et al., 1981, p. 127) and work done at Auckland University by Mr R. Felton to indicate that these models are inappropriate and should be abandoned. It is usually difficult to distinguish between the models even though they give widely different estimates. Goodness-of-fit tests do not seem to help much, as it is not uncommon for several models to fit the data well. The models are also sensitive to heterogeneity, including those specifically designed to allow for heterogeneity. The Poisson model has recently been adapted to allow for heterogeneity amongst birds caught only once (North, 1981). Whether this model will fare any better remains to be seen. In general, nonparametric models are preferred and the estimation procedures associated with models M_h and M_{bh} (Pollock and Otto, 1983) are recommended.

In some situations (for example, grid trapping of small mammals), the recapture experiment is carried out on sample areas only so that estimates of total numbers have to be converted to density estimates. This raises two long-standing problems: (i) determining the actual area sampled by the traps (the so-called edge effect), and (ii) identifying the "transient" animals that are only temporarily in the area during the experiment. Various procedures have been suggested to delineate the trapping area (Wilson and Anderson, 1985). One method that merits further investigation is the method of nested subgrids suggested by Otis et al. (1978). Perhaps the most popular method, proposed by Dice (1938) and advocated by Tanaka (1980, pp. 17–18), is to add a strip of width half the "home range" of the animal to the outermost line of traps. The inference is that animals in this strip will come in contact with traps on the grid. Home range is a somewhat nebulous concept and is difficult to measure. It not only varies for different species but it also varies with respect to location, sex, and density (Abramsky and Tracy, 1980) within a species, and can change with time. Some of the earlier methods (and their shortcomings) are described in Sb (pp. 446–449), Tanaka (1980), Mares, Willig, and Bitar (1980), Getty (1981a), Anderson (1982), Jones and Sherman (1983), and W. P. Smith (1983), and are based on capture frequencies at each trap. The concept of centre of activity has also been debated (Sb, p. 446; Tanaka, 1980, p. 27; Dixon and Chapman, 1980). Prebaiting has often been recommended but there is now some doubt about its value. It can cause an inflow of transients into the trapping area (see Tanaka, 1980, pp. 52–55). Apart from density estimation, home range can be a useful concept when linked with ecological and behavioural information (Getty, 1981b; Bowen, 1982; Slade and Swihart, 1983). Grid trapping can also be utilised for studying social behaviour such as pairing (Novak, 1983). However, the presence of traps can also affect foraging and social activities.

A common model for range activity is the elliptical bivariate normal (Madden and Leslie, 1978). A test for this is given by W. P. Smith (1983), and Dunn and Gipson (1977) allow for the dependence of successive observations (see also Swihart and Slade, 1985). However, Don and Rennolls (1983) criticise the elliptical model because of its symmetry. Sometimes there are certain "nuclei" or biological points of attraction (e.g., nest sites) and the authors give a model based on a mixture of several bivariate normals with *known* nuclei. Rather than specify a particular probability distribution for range utilisation, a nonparametric fitting method would seem preferred. Three such methods are given by Ford and Krumme (1979) (see also Ford and Myers, 1981) and Anderson (1982). However, to apply Dice's recommendation, a crude linear measure of home range may be all that is required. Tanaka (1980, p. 24) and Jones and Sherman (1983) suggest that the observed range length (maximum distance between recaptures) is the most reliable linear measurement.

Various procedures using assessment lines have also been suggested for assessing edge effect both in capture–recapture experiments and removal trapping (Sb, pp. 448, 504; Tanaka, 1980, for references; Schroder, 1981). Along with others, however, I do not support their use on the grounds of unrealistic assumptions and the labour involved. Clearly radiotelemetry will help resolve some of the problems (Amlaner and MacDonald, 1980, pp. 375–424). A simulation model for grid trapping is given by Zarnoch and Burkhart (1980) and although edge effect is not mentioned, it could no doubt be investigated.

In the light of the above difficulties, we need a method that avoids the question of edge effect altogether. Anderson et al. (1983) propose such a method based on a radial trapping "web" and the nonparametric distance sampling technique of Burnham et al. (1980) described above. Their density estimate takes the form $\hat{D} = n\hat{f}(0)$, where n is the total number of different animals caught and $f(x)$ is the probability density that an animal caught during the study is caught for the first time at distance x from the centre of the web. The authors suggest that their web design can be regarded as an extension of assessment lines whereby (i) the rectangular trapping grid is not employed, (ii) trap density near the centre

is very high to allow all animals near the centre to be captured with certainty, and (iii) rigorous methods of analysis are available. The problem of transients is not considered and the method of Manly (1977) is not readily applicable as the probability of capture decreases with trap distance from the web centre. However, the technique of Anderson et al. (1983) is very promising and the simulation study of Wilson and Anderson (1985) indicates that it deserves further study. In conclusion we note an interesting capture–recapture model by Macdonald and Smith (1980) for estimating salmon migration, and a Petersen-type model for comparing subpopulation survival rates by Geramita and Smith (1985).

4. Open Populations

4.1 Multiple Recaptures

The J–S model, developed independently by Jolly and Seber (Sb, Chaps 5 and 13; Seber and Manly, 1985), has found to be a useful model for populations in which there is death, permanent migration, and recruitment (Hightower and Gilbert, 1984; Loery and Nichols, 1985). Goodness-of-fit tests for the model are given by Pollock, Hines, and Nichols (1985). Unfortunately, there are still few guidelines for designing such a multiple-recapture experiment (Nichols et al., 1981, pp. 128–129; Pollock and Mann, 1983). A number of comprehensive programs (see Brownie and Pollock, 1985) for carrying out the analysis are available. One problem associated with the model that seems hard to avoid is the high correlations between estimates and variance estimates for population size (Seber and Manly, 1985). However, one solution to this problem is given by the transformation method of Manly (1984). The effects of trap response, heterogeneity of capture, and tag loss are well documented from various studies (Sb, pp. 506–509; Arnason and Mills, 1981; Nichols and Pollock, 1983a; Nichols, Hines, and Pollock, 1984). Heterogeneity produces negative-biased estimates of population size N_i and, in most cases, of the survival probability ϕ_i , though the survival estimates are much less affected (Carothers, 1979). Temporary trap response also produces bias, the direction depending on the type of response. Permanent trap response (Nichols et al., 1984) seems common in small mammals as they apparently tend to become trap-happy—that is, their probability of capture increases after initial capture. This leads to negative bias in population estimates. However, survival estimates are not biased by permanent trap response, though their variance estimates are affected. Variances for both population size and survival estimates tend to increase with trap-shy response and decrease with trap-happy response. As survival estimates are less affected by the above departures, Pollock (1982) proposed a special sampling design to take advantage of this. The design should be seriously considered by all workers in this topic.

If only survival estimates are important, then the usual J–S model can be used but with sightings instead of recaptures (Cormack, 1964; see also Richardson, Patterson, and Dunnet, 1979, and Keen and Hitchcock, 1980, for further examples). Buckland, Rowley, and Williams (1983, p. 567) found by simulation that variable sightability introduces a negative bias in the estimation of ϕ_1 and the last few ϕ_i 's, but leaves the remaining estimates approximately unbiased. This finding is supported by Carothers (1979, Table 2), who shows that the usual test for variable catchability (sightability) is not very useful in indicating when variable sightability can be ignored. Cormack's model has been generalised by Sandland and Kirkwood (1981) to allow for dependence between sightings using a two-state first-order Markov chain. Another generalisation is given by Brownie and Robson (1983), which allows for the animals to be affected by tagging for one period only; live recaptures can also be incorporated. Applications with constraints on the parameters are discussed by Clobert et al. (1985).

Enumeration estimators of population size and survival rate based on the “minimum

number known alive" (the so-called "calendar of captures" method, are still widely used in small mammal capture-recapture studies. However, the J-S estimators are superior to enumeration estimators (Nichols and Pollock, 1983a) and I recommend that the latter be dropped.

The J-S model has now been extended in a number of directions. First, Buckland (1980) showed how to modify the analysis to include tags recovered from dead animals, and introduced a smoothing method to handle out-of-range estimates (e.g., survival probabilities greater than unity). As asymptotic variances were difficult to obtain algebraically, he used the Monte Carlo method for finding confidence intervals. He also applied his method to estimating survival rates when different cohorts have different catchabilities, and gave several pooling procedures for estimating a survival curve (Buckland, 1982b; Buckland et al., 1983). A second extension of the J-S model, which also gives explicit estimates, is given by Crosbie (1979) and Crosbie and Manly (1985), who proposed a simple model for recruits. A simple model for trap-shyness is discussed by Buckland and Hereward (1982).

Further generalisations of the J-S model were provided by Robson (1969) and Pollock (1975b). These allowed for survival and capture probabilities to depend on past capture histories. Adaptions of these models to age-dependent survival and capture, along with suitable contingency table tests for dependence are given by Pollock (1981b) and Pollock and Mann (1983, with emphasis on fisheries). A two-age-class model is given by Stokes (1984).

The J-S model and its extensions have been developed using likelihood functions that are products of multihypergeometric or multinomial distributions such as (5) and (8), respectively, depending on whether sample sizes are regarded as fixed or random, and whether sampling is (approximately) with or without replacement. In some cases, such as the death-only model, a single multinomial distribution is obtained. The multihypergeometric approach is particularly useful for formulating exact tests for nested hypotheses based on sufficient statistics. However, a fruitful development that uses independent Poisson distributions such as (7) has been initiated by Cormack (1979) and Jolly (1979). The model consists of a "hyperpopulation" that includes all members of the population alive at present or to be born during the experiment. Each individual has a specific history of birth, survival, and capture, and the numbers in the various possible history classes are assumed to be mutually independent Poisson variables. As in the Petersen experiment, we find that we obtain the same J-S estimates as before. The Poisson model, however, has several advantages. First, standard large-sample maximum likelihood theory is more readily applicable. Second, large-sample variance estimates are easier to construct as the variance equals the mean and covariances are zero for independent Poissons. Third, we have the important application of loglinear models to open populations developed by Cormack (1980, 1981, 1985). He shows how the statistical package GLIM, which uses a different structure than the usual one for defining main effects and interactions, can be adapted for model selection; a model for trap response is also included in the family of possible models. However, variance estimates are not yet available for most of the possible models. Some populations (for example, the closed population, the death-only open population, and Crosbie's (1981) extension), can all be modelled by a single multinomial distribution. This type of model bears a close resemblance to the above Poisson model (Sandland and Cormack, 1984).

A major problem with the above complex models is that a large amount of data is required for estimating the large number of unknown parameters. In practical terms this means that high probabilities of capture are needed; otherwise, variances are large. To overcome this problem it is sometimes possible to reduce the number of parameters by restricting the model. For example, Crosbie (1979) (see also Crosbie and Manly, 1985) considered fitting a Weibull distribution to survival probabilities and a beta distribution to entry probabilities. He gives a FORTRAN package called CMR for selecting a suitable model

with fewer parameters than his generalised J–S model. Using the Poisson formulation, Jolly (1982) gives four models: A (the standard J–S model), B (constant survival probability), C (constant probability of capture), and D (constant survival and probability of capture). These are a useful addition to the spectrum of models. Finally, Manly (1985) considers the important problem of separating death and emigration, and discusses a method due to Jackson (1939).

In spite of the above developments we still have some way to go in the development of flexible capture–recapture models for open populations (Jolly, 1981). The problem of heterogeneity of capture is still a major obstacle. In conclusion, we mention an interesting new application of capture–recapture models to fossil data by Nichols and Pollock (1983b), and Brownie and Pollock (1985).

4.2 Recoveries from Dead Animals

An important special case of the J–S model, which I have called the multisample single-recapture census, utilises recoveries from dead animals (Sb, pp. 511–530; Seber, 1985). A cohort of tagged individuals is released each year and the tags are recovered from animals that are found dead or are exploited (e.g., hunting, sports, and commercial fishing). Survival and band recovery rates may be age- and year-dependent, and Brownie et al. (1978) give an extensive package of models, with associated hypothesis tests, which is particularly useful for bird-banding studies. Applications of these models are given by Rakestraw (1981), Munro and Kimball (1982), Nichols, Pospahala, and Hines (1982a), Conroy and Eberhardt (1983), and Sauer and Boyce (1983). More flexible models, including those based on radiotelemetry data, can be handled numerically; out-of-range estimates can also be avoided by numerical maximisation subject to parameter constraints (White, 1983; Conroy and Williams, 1984).

Since the paper by Anderson and Burnham (1976) there has been considerable interest in studying the effect of hunting pressure on natural mortality (Cowardin and Johnson, 1979; Anderson and Burnham, 1981; Nichols and Hines, 1983; Burnham and Anderson, 1984). In the hunting situation there are problems with recovering bands from hunters. Not all solicited bands get reported and even some reward bands may not get reported (Conroy and Williams, 1981). The design and application of a reward band model is discussed by Conroy and Blandin (1984) and Conroy (1985). Radio transmitter tags will be useful in this situation.

One model, introduced by Seber (1970) and Robson and Youngs (1971) for banded adult birds (called Model 1 by Brownie et al., 1978), has received considerable attention. This model assumes that all birds have the same survival and band recovery rates in a particular year. It has even been applied to fossil data by Nichols and Pollock (1983b) and its robustness has been studied by several people. Pollock and Raveling (1982), for example, investigated the effect of heterogeneous survival and/or recovery rates on the estimates. They found that if the survival rate is constant during a particular year but the recovery rate is stratified (due, for example, to band reporting rates varying with recovery region), then the survival-rate estimates are approximately unbiased and the recovery-rate estimates are approximately unbiased estimates of the average regional recovery rates. This supports the contention of Conroy and Williams (1981) that recovery data should not be adjusted for variable reporting rates when estimating survival rates. The model is also insensitive to recovery rates varying as a function of years after banding (Munro and Kimball, 1982, p. 82). If survival rates are stratified, but recovery rates are similar (or stratified and independent of survival), then survival estimates have positive bias. However, if both rates vary with the individual and are negatively related, then survival estimates will usually be negatively biased. Nichols et al. (1982b) showed that with a positive relationship, survival

estimates are positively biased, often with greater biases; recovery rates have small negative biases. Band loss can result in negative biases for survival rates, but the biases can generally be ignored unless loss rates are high (Nelson, Anderson, and Burnham, 1980; Seguin and Cook, 1983). Small positive biases in the survival rates can result if there is any delayed reporting of band recoveries, though the biases can generally be ignored (Anderson and Burnham, 1980). Finally, we note that Model 1 can be modified to incorporate live recaptures (Buckland, 1980). Mardekian and McDonald (1981) suggested a crude but simple method using final recaptures only. However, this method for analysing multiple capture–recapture data can be very inefficient compared with the J–S method (Brownie and Pollock, 1985).

Another model that has attracted considerable attention is the model with age-specific survival probabilities (rates) ϕ_i ($i = 1, \dots, t$) and constant reporting probability (rate) λ ; the birds are banded as nestlings (see Sb, p. 528 for references). This model was investigated by Seber (1971), who showed that the parameters are not identifiable and one constraint is needed such as $\phi_{t-1} = \phi_t$. He also proposed a conditional model that eliminated λ and provided explicit maximum likelihood estimates of the ϕ_i . However, North and Cormack (1981) studied the latter method in detail and showed convincingly that it was inappropriate. The estimates can be extremely unreliable even when the internal goodness of fit to the model is satisfactory. Unfortunately, the unconditional model does not escape criticism either. The lack of identifiability makes the model unstable, and a wide variety of parameter values with $\phi_i \approx \phi_{i-1}$, or even $\phi_i \approx \phi_{i+1} \approx \dots \approx \phi_t$, can lead to the same expected recoveries (Lakhani and Newton, 1983; Lakhani, 1985). Clearly the model should not be used unless an independent estimate of one of the parameters is available, say from radiotelemetry. In another approach, North and Morgan (1979) and North (1979) proposed making the survival probability for birds in their first year time-dependent, and then related the probability to weather variables. Apart from the statistical difficulties underlying the age-specific model, the biological assumptions seem to be false in many situations (Burnham and Anderson, 1979; Anderson, Wywiałowski, and Burnham, 1981). Reporting rates appear to be generally both time- and age-specific (at least for the first or second age classes). I wish to strongly reaffirm, with Anderson, Burnham, and White (1985) that life-table methods of analysis, the so-called composite dynamic method, should not be used. Another age-dependent model is considered by Piper, Mundy, and Ledger (1981) but it has the same identifiability problems.

As cheap, light, robust radio transmitters, with negligible failure rate, become readily available, many of the above problems of identifiability, incomplete reporting, and so forth, will be largely avoided as $\lambda = 1$. Survival estimates will then be much more reliable and more general models will be possible (White, 1983).

In concluding our discussion on survival estimation for birds, we consider the problem of estimating the average daily probability of survival when animals are visited periodically at possibly irregular intervals. For regular intervals, Mayfield (1961, 1975) proposed an estimate that was shown by Hensler and Nichols (1981) to be the maximum likelihood solution. It was applied to estimating duckling survival among broods by Ringelman and Longcore (1982). Unfortunately, the sampling distribution of the estimate is skewed, causing problems for interval estimation. If visits are irregular, then there is also the problem of determining when an animal died, and the estimate may be biased. The irregular case is considered by Bart and Robson (1982), who provide a maximum likelihood solution, along with a normalising transformation. They also discuss questions of design, robustness, and visitation frequency. Further extensions are considered by Hensler (1985).

The multisample single-recapture census has also been applied to fisheries. The question of tag loss and the role of double tagging have received some attention (Sb, p. 524; Russell, 1980; Kirkwood, 1981) and a useful review, together with some new methods, is given by Wetherall (1982).

5. Catch–Effort Methods

For the usual catch–effort model for a closed population, Pollock et al. (1984) proposed a potentially useful logistic framework for the probability of capture that allows for the possible incorporation of auxiliary variables as well as effort. Butler and McDonald (1979) carried out a simulation study of the catch–effort model of Chapman (1961) and Paloheimo (1961) for open populations. The former claimed that the estimates of the instantaneous natural mortality rate and the Poisson coefficient of catchability did not simultaneously have acceptable properties in the ranges anticipated in practice. However, their analysis was criticised by Paloheimo (1982), who suggested that, in some cases, the nonlinear model is preferred to the linear version. We also note that, for their simulation procedure, the expected value of the cumulative effort was a constant times the cumulative time. This will lead to ill-conditioning in the regression model. Paloheimo (1980) and Fournier and Archibald (1982) [see also Deriso, Quinn, and Neal, 1985; Schnute, 1985] proposed modifications of this model to handle catch–effort data from a number of cohorts followed through for several years. The usual model, based on the ratio of catch per unit effort for pairs of consecutive years, was found to be unreliable for parameter estimation (especially with freshwater fish) as sampling fluctuations in the data tended to obscure the effect of natural mortality (Robson and Spangler, 1978). The new methods have some similarity with that proposed by Doubleday (1976). Algorithms for solving the catch equations (Sb, p. 329) are given by Sims (1982). Sometimes catch per unit effort can be converted to a density estimate (Eggers et al., 1982).

In fisheries there are difficulties in combining catch–effort data from different gear and locations, especially if some of the information is missing. Methods for adjusting the data are given by Gavaris (1980) and Quinn and Hoag (1982). Fowler (1980) suggested that effort should sometimes be modified by the size of the catch and gives such a modifier for sperm whale of the North Pacific. The problem of allocating effort to different species in a mixed-species trawl fishery is considered by Westerheim (1983). In some fisheries, the coefficient of catchability may be density-dependent (Peterman and Steer, 1981). Methods of estimating the number of angler trips in a marine recreational fishery are considered by Fraidenburg and Bargmann (1982).

Several fishery models for mortality and recruitment are available (Sb, pp. 336, 542). Further models are given by Collie and Sissenwine (1983); they use $n(t)$ and $r(t)$ to denote, respectively, catch and recruitment per unit effort.

All the above models have strong assumptions about the natural mortality and exploitation rates. However, the first attempt at a comprehensive model that allows for variable rates and the inclusion of auxiliary variables is made by Dupont (1983).

Finally, we mention a nonlinear least-squares procedure given by Paloheimo and Fraser (1981) for estimating harvest rates and differential vulnerability from age and effort data.

6. Demographic and Other Methods

A wide variety of fishing models based on tag returns from one or more releases made before the fishing season have been developed (Sb, p. 238, Chap. 6, pp. 518–524). Tag returns have also been used to provide length or age–length data for estimating parameters in various growth models such as the von Bertalanffy model (Laurs and Wetherall, 1981), Richards' model (Ebert, 1980), and a two-parameter power function (McCaughran, 1981). For further aspects of growth models see Cloern and Nichols (1978), Gallucci and Quinn (1979), Cohen and Fishman (1980), Kimura (1980), Misra (1980), Sainsbury (1980), Schnute and Fournier (1980), Schnute (1981), Foucher and Fournier (1982), and Bartoo and Parker (1983). New methods of estimating age composition from length data are given by Clark (1981) and Smith and Sedransk (1982). Further references on age-composition

methods and their assessment by sensitivity analysis are given by Majkowski and Hampton (1983). Some practical guidelines are listed by Dapson (1980).

Extensions of models for estimating stage-specific survival rates and related parameters are given by Birley (1979), Chubachi (1979), Derr and Ord (1979), Bellows and Birley (1981), Bellows et al. (1982), Van Straalen (1982), and Sawyer and Haynes (1984); further references are given in these papers. The problem of estimating mortality factors in insect life-table analysis is discussed by Royama (1981).

Several papers on applications of the Leslie matrix (Sb, p. 550) have appeared. General methods of estimating the parameters of the matrix and associated quantities are given by Aalto and Newsome (1980), Michod and Anderson (1980), Reed (1980, optimum age-specific harvesting), and Flipse and Veling (1984); extensions to competing species are considered by Travis et al. (1980). A related problem, that of estimating the rate of increase, is considered by Tait and Bunnell (1980) and corrects a misconception of Caughley and Birch (1971). For further discussion and an application see Rago and Dorazio (1984) and Van Ballenberghe (1983), respectively.

One topic which has received some attention is that of estimating sex and age ratios such as buck/doe and fawn/(doe + fawn) ratios (Otis and Bowden, 1979; Czaplewski, Crowe, and McDonald, 1983; Bowden et al., 1984). Change in ratio (CIR) methods (Sb, p. 353) have also been used for estimating population parameters. Otis (1980) has extended the method from two to three categories. A new CIR method which is robust to the unequal catchability of types of animal is given by Pollock et al. (1985).

Finally, a time series analysis is applied to a series of fish abundance indices based on trawl surveys by Pennington (1985).

RÉSUMÉ

Il y a eu, au cours de ces cinq dernières années, des développements importants dans l'estimation des populations animales et des paramètres qui leur sont attachés, comme les taux de survie. Un grand nombre de techniques nouvelles qui supplantent des méthodes plus anciennes méritent d'être largement diffusées. C'est l'objet de ce papier que de revoir ces travaux et de suggérer de nouveaux thèmes de recherche.

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