A review of estimating animal abundance III

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Abstract

The literature describing methods of estimating animal abundance and related parameters continues to grow. This paper reviews recent developments in the subject over the past six years and updates two previous reviews.

Keywords: Adaptive sampling; age composition; animal abundance; animal movements; aerial censusing; band-recovery; bootstrap; breeding proportions; capture-recapture; catch-effort; change-in-ratio; Cormack-Jolly-Seber; coverage; double tagging; estimating equations; Gibbs sampler; home range; index of abundance; Jolly-Seber; kernel density; line transects; martingales; mark-recapture; model selection; Petersen; population index; radio tags; radiotelemetry; relative density; removal methods; senescence; survival estimation; tag loss; tag-migration models; tag-recovery; two-stage sampling.

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1 Introduction

The literature relating to the estimation of animal population parameters such as population size or survival rate continues to grow rapidly. We shall review the literature from about 1991 to the time of writing. The type of method used depends on the nature of the population investigated, namely whether it is "closed" or "open". A closed population is one that remains effectively unchanged during the investigation, while an open population is one that can change through such processes as birth, death and migration. The methods can be categorized by the type of information provided by the sampling process used.

The simplest methods are based on counting individuals or their signs (e.g. bird calls or animal droppings) on a random sample of plots where the plots may be quadrats or strips. In the case of individuals, the resulting sample estimate of the number per unit area can then be converted into a population total by multiplying by the population area. Where just signs are counted, we get a relative measure or "index" of population density. This is a number bearing (hopefully) a constant ratio to the size of the population. If the index doubles we can then assume that the population has doubled, even if we don't know the actual size of the population. Sometimes such a measure can be converted to a population density if we have a reliable and stable "correction" factor of the average number of signs per animal. Clearly standard survey methods can be used, like stratified sampling, post-stratification, sized biased sampling and two-stage sampling, as well as the more recent methods of adaptive sampling suitable for sparse but highly clustered populations. In adaptive sampling the neighborhoods of those sampled plots yielding useful information are sampled as well.

Other sampling units that can be used are lines and points. In line transect sampling, the observer walks, flies by plane or helicopter, or travels by boat down a random line (path). The observer measures or, more usually, estimates the perpendicular distances of all animals seen from the line out to a certain predetermined distance (or out to any distance). By modeling the probability of detection as a function of distance from the line, these distances can then be converted to an estimate of population density. In point sampling, one first chooses a sample of points. The observer then spends some time at each point and estimates the distances of all animals seen in any direction out to a given distance (or out to any distance).

There is a group of methods based on the idea of knowing how much effort is put into catching and removing animals from the population. Perhaps the simplest of these is the removal method which uses the idea that the same amount of effort will always remove the same proportion of the population that is there. These methods are particularly useful in fisheries where they are usually described as catch-effort models. They are also used to get estimates of relative densities of birds.

Another general method, called the change-in-ratio method, is based on a simple idea. Suppose that a population consists of males and females. A large enough number of males is removed from the population to significantly change the sex ratio. By sampling the population before and after the selective removal to estimate the sex ratio in each case, various population parameters can be estimated.

A widely used method of obtaining information about the population is to use tagging or marking; the so-called capture-recapture method. Here one takes a series of samples. The first sample is used to provide animals for tagging and releasing. The second sample then has tagged and untagged animals. The untagged animals are then tagged and all the animals are released. This process is repeated using unique tags for each individual. At the end of the experiment, each animal that is caught during the experiment will have a capture history. For example, the history 01001 of an individual means that the individual is caught in the second and fifth samples only. Such methods have been be used for both closed and open populations. For open populations, a number of variations of the method have been developed. In the the case of an open bird population, one can release a group of banded birds on each of a number of occasions (e.g. annually) and the birds are then either sighted alive or recaptured dead in the intervening periods. The deaths may be due to either natural or hunting mortality. Similar models are used for fisheries. These models have been generalized to allow for different ages and sexes, and have been extended to incorporate different areas where movement (migration) between areas takes place. Some of the tagging models focus on just survival, while others incorporate both abundance and survival. When miniaturized radio transmitters are used as tags so that individuals can be tracked, we can use this extra information to tell us more about movements and survival. Since one is interested in the capture histories of various subsets of the animals, most models consist of products of multinomial distributions. Often the number of parameters is very large and some of the parameters are not always estimable.

An important feature of the above methods is that they depend on certain underlying assumptions which need careful examination. For example, in locating or counting individuals on plots, there may be an observer bias. An experienced observer may do better at spotting animals than an inexperienced observer. Further, some animals may not be detectable. Deer are notoriously difficult to see! In distance methods, there is the problem that individuals may be disturbed before they are seen or one may even see the individuals in groups. In tagging experiments animals may lose their tags. Also tags may be overlooked or not returned if one has to rely on the general public for their return. Frequently there is heterogeneity in capture, sighting and survival probabilities. A lot of research has therefore been directed at both examining the effects of departures from the assumptions on the estimates and modifying the models to allow for such departures.

This paper follows a book and two previous reviews (Seber, 1982, 1986 and 1992). To maintain continuity, we have used the same title as those reviews. However, our scope is much wider than just abundance and includes related parameters such as survival rates, as in the title of Seber (1982). In putting this review together we have extensively used the Current Index to Statistics Extended Database (American Statistical Association/Institute for Mathematical Statistics, 1997), the Science Citation Index (Institute for Scientific Information, 1997), and Biological Abstracts on Compact Disc (Biological Abstracts, Inc, 1998). As we found a wide variety of key words for the same topic, making such searches difficult, we recommend that certain standard key words be always included in research articles. For example, capture-recapture should cover mark-recapture, tag-recapture, and band-recovery while radio tags should cover radio telemetry and telemetry, and so on.

The subject continues to grow, not only because of new statistical technology, but also because of the increasing number of applications to populations. Our primary aim is to review new methodology and just select some of the many applications, particularly those which pay close attention to the underlying assumptions or have unusual features. Pollock (1991), Nichols (1992), Pollock (1995), Lebreton, Pradel and Clobert (1993), Manly and McDonald (1996, at a popular level), IWGDMF (1995a, 1995b) and the encyclopedia articles of Cormack and Buckland (1997) and Chao (1998) present short overviews of capture-recapture and related methods. Chao and the articles by IWGDMF focus on epidemiological applications. An ornithological focus which includes general statistical methods is provided by Nichols (1994) and Morgan, Freeman, and Lebreton (1997), while Lancia, Nichols, and Pollock (1994) give an extensive coverage which concentrates on wildlife management using illustrative examples. Skalski and Robson (1992), Buckland (1994) and Conroy and Smith (1994) present guidelines for the design of large-scale wildlife surveys. We did not extensively review the fisheries literature as many of the techniques there are specific to just fish populations. However, a number of good books are available which admirably review the available literature such as Hilborn and Walters (1992), Gunderson (1993), Gallucci et al. (1996), and Quinn and Deriso (1998).

2 Statistical developments

In this section we take a broad brush view of some useful statistical developments with finer detail later.

Some populations, such a fish or birds, may be sparse but highly aggregated. A simple random sample of plots could then yield mainly empty plots. Seber (1992) noted that adaptive sampling, which uses information from the part of the sample obtained thus far to determine the future direction of the sampling, is a promising method for handling such populations. It has begun to be used in a variety of ways and the book by Thompson and Seber (1996) surveys the methods. To this we add the papers by Salehi and Seber (1997a, b) and Pollard and Buckland (1997), the brief summaries by Seber (1997, 1998) and the Ph.D. thesis of Salehi (1997). However, the question of when to use adaptive sampling instead of simple random sampling still needs further research. Incomplete detectability can also be a problem in sampling a population, and this is discussed by Thompson and Seber (1996, Chapter 9) for both conventional and adaptive sampling.

Sized-biased sampling, in which bigger objects have a greater chance of being selected, continues to be a useful tool. However, it can also be used in a time framework. Some animal abundance methods use surveys at a point in time so that events which last longer are more likely to be selected. This must be accounted for in the analysis. Hoenig et al. (1997) show when the mean-of-ratios or the ratio-of-means should be used in computing the CPUE (Catch Per Unit Effort) in angler surveys depending on whether the survey is a roving survey or an access survey - the former being size-biased. Total catch is estimated by multiplying the total effort by the catch rate per unit effort. Two ratio methods for estimating the catch rate for a sports fishery using various types of survey are available (Hoenig et al., 1997; Pollock et al., 1997); related papers are Hoenig et al. (1993) and Jones et al. (1995).

Logistic regression is assuming a greater role in abundance problems. Here a probability can be estimated by modeling it in terms of various covariates. It can also be combined with the so-called Horvitz-Thompson estimator (e.g. Skalski, 1994). For example N, the population size, can be estimated if the probability p_i that the ith individual or group is caught or sighted in the sample can be estimated. This follows from the fact that, for a sample of size n, $E(\sum_{i=1}^{n}(1/p_i) = N$. Such an approach has considerable potential and can be used in a variety ways. Buckland et al. (1993) combine it with a logistic model, using appropriate covariates, to obtain a correction for undetected whale pods in line transect sampling, while Huggins and Yip (1997) use a similar approach for a removal model. Manly, McDonald and Garner (1996), Borchers, Zucchini and Fewster (1999), and Borchers et al. (1999) apply logistic regression to line transect data from double counts (simultaneous counts from two observers). Logistic regression can also be used for modeling spatial distributions (Walker, 1990; Osborne and Tigar, 1992; Buckland and Elston, 1993; Augustin, Mugglestone and Buckland, 1996). Here the dependent variable, representing presence/absence or a measure of abundance of the species under consideration might be recorded for all, or a random selection of, sites. The rapid growth of geographic information systems (GIS) allows access to a wide variety of possible covariates. A similar type of model is the log-linear model, which is used particularly in capture-recapture applications.

Quasilikehood has also entered the abundance arena. We shall see later that it is being successfully used for capture-recapture models instead of a full likelihood approach, which is not always appropriate. As noted by Seber (1992), quasilikelihood is an important tool for modeling over- or under-dispersed data. An application to capture-recapture data in fisheries is given by Bayley (1993).

In the past, Bayesian methods have been hampered by the need to evaluate complex integrals for finding posterior distributions and their related parameters such as the posterior mean. However, with the advent of special Monte Carlo methods, it is now possible to sample from the posterior distribution without having to actually find it. For a univariate prior, if just the shape of the univariate posterior distribution (and not the normalizing constant) is known e.g. likelihood multiplied by the prior, then special sampling-resampling methods are available (see Smith and Gelfand, 1992, for an excellent introduction). For a multivariate prior, we can use the so-called Gibbs sampler whereby we can sample from the multivariate posterior and its marginals by simply sampling from a sequence of univariate conditional distributions. The theory behind this approach is referred to as the Markov Chain Monte Carlo (MCMC) method. For a very readable introduction and some earlier references see Casella and George (1992). Further details are given by Gelman et al. (1995), Besag et al. (1995), Gilks, Richardson and Speigalhalter (1996), and Tanner (1994). Manly (1997, Chapter 15) provides a helpful discussion using simple capture-recapture examples. We can now expect Bayesian methods to be used more extensively in modeling abundance problems. For example, a Bayesian method for handling an unknown mixture of completely and incompletely detected individuals is given by Solow and Palka (1996). Bayesian methods are also becoming very popular in fisheries modeling (Punt and Hilborn, 1997). Other examples will be given throughout the paper. Log-linear models are also used here, e.g. Quang and Becker (1996).

Bootstrapping is now extensively used for simulating samples from a real data set, evaluating bias, estimating variances, constructing confidence limits and so on (e.g. Manly, 1997). Two of the many examples are the evaluation of trawl survey abundance estimates and confidence intervals (Smith and Gavaris, 1993b; Smith, 1997), and finding the standard errors for a modified Kaplan-Meier survival estimate (Flint et al. 1995a, b). As mentioned later, bootstrapping is also used for incorporating model uncertainty.

Many of the models developed are based on a product multinomial likelihood with all parameters appearing directly in the likelihood. In some cases, the population process can be separated into two parts, namely the population dynamics and the observation process. This would lead to a natural formulation using state-space models which in turn lend themselves quite readily to Bayesian methods. Schnute (1994) develops a general modeling framework for fisheries models and a few authors, as noted below, have started similar frameworks for mark-recapture data. This methodology needs to be more widely explored in non-fisheries contexts.

Demographic methods also have a role. Although, in many cases, experiments only estimate a single demographic quantity at a time, e.g. survival rates. However, population management will require additional information usually in the form of a Leslie matrix. This matrix relates the age sructure at time $t+1$ with the age structure at time t for a stationary population (Seber, 1982 p. 550). For example, Franklin et al. (1996) discuss some standard demographic methods including the Leslie matrix method for the Northern Spotted Owl; Buckland et al. (1996) use a Leslie matrix model for the management of deer culling; and Raftery, Givens, and Zeh (1995) try and include variability of inputs into a Leslie matrix when studying bowhead whales.

There has been considerable development of powerful software to estimate population parameters, particularly in the analysis of capture-recapture experiments. In Appendix 1 we have listed some WWW pages with an annotated set of links to the most often-used software for analyzing population data. They will be discussed later as they arise. What is still lacking is a generalized software package for analyzing various kinds of survey data.

2.1 Quadrat and strip transects

As in Seber (1986, 1992), the negative binomial distribution continues to be used in plot studies for clustered populations. White and Bennetts (1996) and White (1996a) summarize some of the methodology. A two-way model is considered by Ramakrishnan and Meeter (1993), and Taylor's power law is revisited by Routledge and Swartz (1991).

Two-stage sampling (cf. Särndal et al., 1992) is a useful sampling technique. Here a sample of primary units (study plots) is taken and then some form of abundance estimation is applied within each primary unit such as estimation from animal signs, line transects, catch-effort sampling, change-in-ratio methods, two-sample capture-recapture and so on (Seber, 1982, pp.114-115; Jensen, 1994; Skalski, 1994). Salehi and Seber (1997b) give a method for designing an adaptive cluster sample using this approach. Three stage sampling is used by Szarzi et al. (1995) to estimate clam density.

Stratified sampling is also used extensively in abundance estimation. For example it is used for bottom trawl surveys in fisheries using depth as the major stratifying variable (Smith, 1990; Smith and Gavaris, 1993a; Smith and Page, 1996; and the readable summary by Smith, 1996). Irvine et al. (1992) estimate coho salmon spawning escapements by conducting visual surveys in areas selected using stratified random and stratified index sampling designs. Post stratification, along with bootstrapping, can be used as a bias reduction technique (Anganuzzi and Buckland, 1993; Buckland, Cattanach and Anganuzzi, 1992). With sparse but highly clustered populations, one can use the method of adaptive allocation within strata or primary units to achieve a greater precision of estimation (Thompson, Ramsey and Seber, 1992; Thompson and Seber, 1996 Chapter 5). Sequential sampling is a form of adaptive sampling and Stewart-Oaten (1996) gives a sequential method based on the proportion of nonempty units.

Unless observers are perfect, visibility bias may negatively bias estimates of abundance. One way of overcoming this problem is the so-called double count method in which two independent observers do the counting. Their counts, together with the numbers seen by both, can be used to calculate Petersen type estimators to correct for visibility. For example, Pojar, Bowden and Gill (1995) describe an experiment where random quadrat, strip transect, and double count methods are compared to estimate the density of pronghorn and note that some of the differences observed may be due to visibility bias. Heterogeneity in the sighting probabilities (cf. Seber, 1992 p. 133) can cause problems. Rivest et al. (1995) use a form of stratification while Manly, McDonald and Gardner (1996), Borchers, Zucchini and Fewster (1999), and Borchers et al (1999) use a logistic regression model incorporating the covariates affecting sightability to deal with this problem. Evans and Bonett (1993) also presented a method to account for differential visibility bias as a function of group size - presumably larger groups of animals are less likely to be overlooked.

An interesting method is presented by Skalski (1991) who developed a standard survey sample procedure (ratio estimation) to estimate animal abundance if an initial capture of animals can be marked so that their subsequent signs can be distinguished from unmarked animals. Becker (1991) used standard line-intercept methods combined with the Horvitz-Thompson estimator to estimate the number of furbearing animals by finding their tracks in the snow after a storm.

In Skalski's (1994) review of using standard survey methods to estimate animal abundance, he points out that such analyses must distinguish two levels of sampling variability, the natural variability in the parameters and the sampling variability in the estimates. This distinction was also considered by Barker and Sauer (1992) and Link and Nichols (1994) when investigating temporal trends, and in Link and Sauer (1996) when ranking populations by an appropriate parameter. Skalski and Robson (1992) discuss the importance of this distinction when planning wildlife studies using capture-recapture experiments.

2.2 Distance methods: line and point transects (variable circular plots)

Line transect methods provide a relatively cheap method of estimating animal abundance. As mentioned earlier, an observer travels along a transect line and records the perpendicular distances of all animals visible from the line. The use of such models hinges on being able to satisfactorily model the probability of detecting the animal as a function of perpendicular distance y, the so-called “detection function” $g(y)$. A wide range of methods for doing this are available and the standard reference is Buckland et al. (1993a). These authors have developed a software package called DISTANCE which is documented by Laake et al. (1993) and is available from the last site given in Appendix 1. There have been numerous papers using line transect methodology, for example, Pelletier and Krebs (1997) who estimate ptarmigan populations; Casagrande and Beissinger (1997) who compared four methods of estimating parrot populations and recommended line-transect methods; Trenkel et al. (1997) who evaluated line-transect methods for estimating red deer populations; Southwell (1994) who conducted field trials to estimate the number of kangaroos and wallabies and concluded that animals showed reactive movement in response to the observer walking the transect line; Ensign, Angermeier and Dolloff (1995) who compared line and strip transect methods for estimating fish population and concluded that line transect methods performed well; and Barlow (1995) who compared strip and line transects to estimate the abundance of cetaceans and found both methods worked well. Using a half-normal detection function, Karunamuni and Quinn (1995) seem to have developed the first Bayesian methods of estimation and showed that their estimators had good properties compared to the maximum likelihood and Fourier series estimators. Finally, Pollard and Buckland (1997) give a novel adaptive approach to line transects using zigzags.

Recent methodological advances have concentrated on methods which are robust to violations of the assumptions. Two key assumptions are that the detection probability $g(y)$ is the same for all animals, and that 100% of the animals are detected along the transect line, i.e., $g(0) = 1$. Buckland (1992a) examined the effects of heterogeneity in the sighting probabilities on the estimates and found that the bias could be severe. Buckland (1992b) also developed a new, robust methodolgy and mentioned the use of kernel estimates. This work, and the advantages and disadvantages of kernel estimates, are spelt out in greater detail in Buckland et al. (1993a). For example, covariates cannot be incorporated in the modeling with kernel methods. Another related assumption is that $g(y)$ is constant during the survey. Assuming $g(0) = 1$, Chen (1996a) uses a kernel estimator for $g(y)$ and showed that it is robust against changes in $g(y)$. However he only compares the method with the Fourier series method which is known to have poor coverage. The assumption that $g(0) = 1$ is often false and new methods have been developed to avoid this assumption. For example, Quang and Becker (1997) combine the line transect with double count sampling techniques in aerial surveys and use the double count to estimate the maximum of $g(y)$, which will generally not occur at $y = 0$, by fitting a Weibull curve to $g(y)$. Laake et al. (1997), using a team of observers and appropriate models, actually estimated $g(0)$ and found it to be considerably less than one. In an interesting experiment, Anderson and Southwell (1995) had seven experts in line-transect methodology and three novices independently analyze a data set from a population with a known density and found that their performance was similar but both groups underestimated density by about 10%. There have been several papers where line transect methods are combined with other methods. For example, Manly, McDonald and Gardner (1996), Alpizar-Jara and Pollock (1996, see also their references to researchers of the International Whaling Commission), Borchers, Zucchini and Fewster (1999), Borchers et al. (1999) and Skaug and Schweder (1999) combine line transect methods with multiple observer information to allow $g(0) < 1$. Other information can also be incorporated such as the size s of the object. For example the detection function can now take the bivariate form $g(y, s)$ and some theory is described by Buckland et al. (1993a, p. 81). Quang and Becker (1996) use a parametric logistic model involving other covariates as well, while Chen (1996b) uses a kernel approach.

Instead of just having multiple observers, another approach is to use observers on different "platforms", which may be on different ships or different planes. Some history of double platform methods is given by Buckland et al. (1993a, p. 202 ff.). Buckland and Turnock (1992) use dual observers on different platforms to combat problems such as those of animals moving and $g(0) \neq 0$, while Raftery and Schweder (1993) propose a Bayesian approach. Double platform methods have also been used by Hiby and Lovell (1998) and Borchers et al. (1999).

In concluding this section we briefly consider distance methods based on the so-called point transect, otherwise known as the circular plot survey. Here the line becomes a point and one measures the distance y of any animal seen from the point. Again, one models the detection probability $g(y)$ so that much of the line transect theory applies here. The standard reference is, again, Buckland et al. (1993a). Most applications seem to be to bird populations as animals may be disturbed or flushed by an observer approaching the point. Quang (1993) developed a non-parametric kernel estimator of $g(y)$. The trapping web design, in which detection occurs by live trapping, (cf. Buckland et al., 1993a p. 275) can also be analyzed using similar methods. Link and Barker (1994) modified the analysis to allow for the fact that the outermost traps are further apart.

2.3 Removal methods

Removal methods for estimating population size are special cases of catch-effort methods where the effort is assumed constant over sampling occasions and there is a constant probability of removal on all occasions (cf. Seber

(1982, 1992). They are also related to the behavioral model M_b in the closed-population mark-recapture methods (discussed in Section 3). Two interesting case studies of the use of the removal method are Helminen et al. (1993) who estimated stocks of fish in Finnish lakes and noted the problems with violations of assumptions, and Trpis, Hausermann, and Craig (1995) who estimated the number of female mosquitoes. Bedrick (1994) and Hirst (1994) both derived confidence intervals based on the likelihood ratio (commonly called profile likelihood intervals) and showed that they performed better in terms of coverage than the usual normal theory large sample intervals. Wang and Loneragan (1996) assume the catchability to be a random variable around the mean catchability, thus allowing for overdispersion in the observed catch.

Huggins and Yip (1997) derive a model where the probability of capture for each animal is a log-linear function of individual and sampling time covariates. A conditional likelihood function is then used to obtain estimates of the probability of capture for each observed animal over the course of the experiment and the population size can be estimated using the Horvitz-Thompson estimator mentioned in Section 2. Their method does not assume that the probability of capture is constant over the experiment, and so is applicable in the more general catch-effort case as well. Yip and Fong (1993) modify the removal model by releasing a known number of marked individuals prior to the experiment: they assume equicatchability of marked and unmarked. Their model is more general than that of Skalski and Robson (1982) in that they use a multi-hypergeometric model, and a constant probability of capture is not assumed.

In conclusion, there does not appear to be a specialized computer package available to compute estimates for the removal model, except for Program CAPTURE which estimates abundance under model M_b.

2.4 Change-in-ratio (CIR) Methods

As noted in Section 2, change-in-ratio methods can be used when removals from a closed population significantly change the proportions of animals in two or more attribute classes. A review of the change-in-ratio approach for estimating closed populations and future research directions is presented by Udevitz and Pollock (1992). Udevitz and Pollock (1991) develop likelihood theory for the general case of three or more classes with unequal probability of sightings in the classes, but where the ratio among the classes is constant over time. This is further generalized by Udevitz and Pollock (1995) to incorporate effort information and they show that earlier papers by a number of authors are special cases of this general model. They also show that estimation in change-of-ratio models can be done using a non-linear least squares routine available in many statistical packages such as PROC NLIN in SAS. Some code is available from them. Dawe, Hoenig, and Xu (1993) combine estimators from both a change-in-ratio method and an index-removal method to estimate the number of snow crabs in a fishery. Chen, Pollock and Hoenig (1998) extend this approach to include catch-effort information as well, and study the gains in efficiency in combining the various methods. White et al. (1996) use a slight modification of the usual CIR method, based on three age composition surveys, to estimate the overwintering survival rates of fawn and adult deer.

Finally, Udevitz and Pollock (1998) combine all three methods— CIR, catch-effort and index-removal— into one model. Using simulation they show that using all three methods is more efficient statistically than using any two.

2.5 Radio-tagging

Radio tags studies are commonly used to estimate movement of animals, home ranges, habitat analysis, survival, and abundance. They have also been used for detecting groups of animals (e.g. caribou, by Couturier et al. (1996); Rivest, Couturier and Crepeau, 1998). The standard reference is White and Garrott (1990). There are many papers demonstrating the use of radio-tagging to estimate various quantities as any literature search will quickly reveal - only the methodological advances will be reviewed below.

Surprisingly, most papers in the radio-tagging literature simply plot the locations of animals and do not try and quantify the movement among strata using methods, say, similar to the Cormack-Jolly-Seber methods discussed in Section 3. This is an area requiring further research. However, Worton (1995c) had good success in modeling movements using an Ornstein-Uhlenbeck diffusion process.

Related to movement is home range estimation. Worton (1995a, 1995b) comments that a majority of papers surveyed used a minimal convex polygon or modified polygon estimator but notes that these measures are sensitive to outliers, irrespective of the distribution of the inner points. He recommends a convex hull peeling method. Another approach is to fit a bivariate distribution to the animal's relative frequency of using each point in the area - the so-called utilization distribution. The home range can then be defined as the smallest area containing 95% of this distribution. Seaman and Powell (1996) investigate kernel methods for estimating the home ranges using simulated and real data sets and conclude that these methods seem to give the most accurate estimates of the simulated home ranges. Saltz (1994) noted that a key assumption of radio-tagging studies is that locations are accurately determined, say by triangulation, and commented that only a few studies quantified the degree of error in their location measurements. Most of the location error tends to come from reflections of the radio signal rather than from instrument imperfection. Anderson-Sprecher (1994) used a state-space time-series method to estimate locations when the signal is noisy. A review of software for estimating animal home ranges is given by Larkin and Halkin (1994).

Some of the problems associated with using radio-tracking to analyze habitat use were reviewed by Aebischer, Robertson and Kenward (1993). They recommended using a method based on the $\log(x_i)$, where x_i is the proportion of time an individual spends in the ith habitat ($i = 1, 2 \ldots, D$). The method is called compositional analysis as the proportions add to one. Schooley (1994) cautioned that some of the analyses based on pooling habitat-use data on animals over long periods of time may be misleading. The effects of triangulation error upon habitat analyses was considered by Samuel and Kenow (1992). Discriminant analysis is a technique often used for studying differences in vegetation structures or environmental conditions between sites classified by an animal's presence or absence. However, North and Reynolds (1996) suggested using logistic regression instead because it is based on fewer assumptions.

Estimating the survival rate of young birds from hatch to fledging is important for population management. The standard method involves observing the offspring identified by marks or radio-tags (cf. Seber, 1992 p. 150). A general method for estimating nest survival is given by Heisey and Nordheim (1995). By treating broods as clusters, Flint et al. (1995) and Flint, Sedinger and Pollock (1995) extend the Kaplan-Meier and Mayfield methods of estimating survival rates to allow for possible survival dependence among brood members and for brood mixing when individuals from one brood become part of another brood.Finally, Craig et al. (1997) estimated the number of manatees over several years by conducting aerial surveys of a number of sites and using hidden Markov models to account for the unobserved movement of animals between surveys. They did not measure the survival and recruitment rates directly, but rather fitted a simple trend line to assess if the population size was declining.

An overview of methods for estimating survival rates using the above methodology is given by Bunck and Pollock (1993) who suggest that further research is needed in finding methods that are intermediate between the Kaplan-Meier non-parametric methods and the fully parametric methods in their smoothing of the survival function. Usually, one assumes that all radios are functioning and all tagged alive animals can be located. Bunck, Chen, and Pollock (1995) show that slight modifications to the survival estimates are robust to uncertain relocation and Pollock et al. (1995) show how to combine the Cormack-Jolly-Seber and Kaplan-Meier methods of survival estimation to allow for uncertain detection of radio-tagged animals. This combined model appears as a specific multistrata capture-recapture model in Lebreton, Almeras and Pradel (1998). Radio-tagging can be combined with other methods. A common problem when birds are ringed as nestlings is that not all the survival parameters can be estimated: the so-called non-identifiability problem. However, Freeman, Morgan, and Catchpole (1992) showed how to incorporate radio tagging information with ring recovery information to overcome this problem. Underlying all this theory is the key assumption that survival is unaffected by the presence of a radio. However, Johannesen, Andreassen and Steen (1997) show that it is fairly straightforward to design a study to compare the survival rates of radio collared to non-radio collared animals.

Most methods using radio-tagging to estimate population size use simple Petersen estimates or a combination of Petersen estimates (mark-resight methods) as outlined by White and Garrott (1990), Neal et al. (1993), and White (1993). The key difference from mark-recapture methods is that unmarked animals are usually not captured. Bowden and Kufeld (1995) construct some new confidence intervals with a better coverage. Neal et al. (1993) and Miller et al. (1997) accommodate immigration and emigration by using the known subset of radio collared animals present in the study population as an indication of movement in or out of the study area. The program NOREMARK (White, 1996b) can be used in these circumstances.

Strong, Sawicki, and Bancroft (1994) use radio-tagged pigeons to estimate a regression relationship between number of nests and the number of incoming birds, and then use this relationship to estimate the number of nests on various keys in Florida.

2.6 Relative population density

As discussed in Seber (1982), it is not always possible to estimate the population density directly and that one sometimes has to make do with just a relative measure or index of density based, say, on animal signs. For example, one can use the number of calls per unit area for birds, or droppings and tracks in the snow for large animals. Roadside counts are also used extensively. These indices are based on the idea that a fixed amount of searching effort will always locate a fixed proportion of the population. This implies that the index is proportional to the density with the constant of proportionality always being (hopefully) the same. As noted in Section 1, if the index doubles we would like to infer that the population has doubled. Bird examples are the Common Birds Census, the Waterways Birds Survey and the Constant Effort Sites (CES) Ringing Scheme in the United Kingdom and the North American Breeding Bird Survey and Christmas Bird Count in North America. A collection of papers from a recent symposium on this index method, commonly referred to as the Point Count method, is found in Ralph, Sauer, and Droege (1995). The optimal allocation of effort among sites and count duration is discussed by Barker, Sauer, and Link (1993). Peach et al. (1996) discuss some statistical methods associated with the Constant Effort

Sites scheme with regard to mist-netting. Similar indices are used in fisheries where catch-per-unit-effort (CPUE) is used as a measure of relative abundance. We have not tried to review the extensive literature associated with this method but simply refer the reader to the fisheries literature and the books mentioned at the beginning of this review.

There have been several recent articles discussing the formal analysis of relative density studies using quasi-likelihood methods and accounting for changes in the ability of observers to see animals (Sauer, Peterjohn, and Link, 1994; James, McCulloch, and Wiedenfeld, 1996; Kendall, Peterjohn, and Sauer, 1996; Link and Sauer, 1997). White and Bennett (1996) use likelihood ratio methods based on the negative binomial model to make comparisons of the mean counts per sampling unit for different populations. They compare the efficiency of their method with the usual ANOVA or Poisson regression methods.

As noted in Section 1, it is sometimes possible to convert the index to an estimate of absolute abundance, for example, if one has a stable estimate of the number of calls per bird. In certain instances, sign counts can be calibrated by using sign-marking techniques. Skalski (1991) developed some theory for this situation in which there is an initial capture of animals and these are then marked so that their subsequent signs can be distinguished from the signs left by unmarked animals.

3 Mark-recapture methods for closed population models

3.1 Single Recaptures - the Petersen estimator

The Petersen estimator (cf. Seber 1982, 1992) is the simplest mark-recapture method. It has been used extensively this century for animal and human populations ; in the latter case it is also known as a dual-list method. Feinberg (1992), Pollock, Turner and Brown (1994), and Chao and Tsay (1998) present reviews of its use for census undercounts. Rockwood and Whiting (1992) present an example of using a Petersen method to estimate the number of hunter-trips where the first sample is a self-completed questionnaire and the second sample is obtained from a telephone survey of license holders. Laska and Meisner (1993) present a modified Petersen-type estimator where the first sample is replaced by a set of planted individuals who are added to the initial population. The second sample records the total number of individuals and the number of planted individuals observed. Further methods using planted individuals are mentioned in the next section. Sometimes a series of Petersen estimates is generated and it is of interest to regress the estimates against environmental covariates. Skalski (1996) compared weighted least squares and direct modeling approaches, and recommended the latter. A Petersen-like estimator for area sampling was presented by Jensen (1992) who used a sampling method similar to the two-stage sampling method mentioned above. In this method, fish are marked and released in an enclosed sub-area of the population, and then the second sample is obtained by killing the fish on a sub-subsample of the area where the fish were released using toxicants or explosives.

The assumptions and properties of the Petersen estimator are now well known. Recent work has concentrated on variants of the Petersen estimator to account for violation of its assumptions. Rajwani and Schwarz (1997) showed how to modify this estimator to account for tags that were overlooked during the initial recovery sample by using a second recovery sample to estimate the number of tags missed. Anderson (1995) showed how to modify the estimator to account for size selectivity in the probability of capture. Lloyd (personal communication) has developed a method suitable when a size attribute (say length) can be measured in both samples and the size selectivity doesn't change between samples. A smoothed histogram is first constructed for the length data and this will reflect the product of actual abundance at each length and sampling effort. Then a smoothed histogram is constructed for both the recaptures and the newly captured animals at the second sample. From the three curves, a Petersen estimate can be obtained for each length and the resulting estimates are then "integrated"over length to get an estimate of total abundance.

These studies, where different sizes have different probabilities of capture, are an example of where the captures and recaptures should be stratified. Darroch (1961) first considered the case of stratification in time or space to remove the effects of heterogeneity but was only able to obtain the maximum likelihood estimates for the case when the number of release and recovery strata were equal. Plante (1990) and Plante, Rivest and Tremblay (1998), however, obtained a general likelihood for cases where the number of strata were unequal. Banneheka, Routledge, and Schwarz (1997) developed a least-squares estimator that is easy to compute. Dorazio and Rago (1991) investigated under what conditions the stratified-Petersen method would tend to give inadmissible estimates of the nuisance parameters such as the recovery probabilities, that is give estimates out of the $[0, 1]$ range. Schwarz and Taylor (1998) present a survey of the use of the stratified-Petersen estimator in fisheries management and discuss many of the practical problems that can occur with real data. Most of the methods presented have been implemented in a computer package SPAS (Arnason et al., 1996), except that estimates may be out of their admissible ranges (but see Plante, Rivest and Tremblay, 1998, who have a method of scoring to prevent this). Ironically, the stratified-Petersen method is often too general in that it allows arbitrary patterns of movement among strata. If the movement can be modeled, better estimates can be obtained. For example, Dempson and Stansbury (1991) used partial-counting fences and the stratified-Petersen estimator to estimate the number of Atlantic smolt going to ocean. Here a “fence” is a type of trap from which one can regularly sample the fish moving downstream or make releases of tagged fish. Schwarz and Dempson (1994) developed a model for the actual travel times between the release and recovery fences that avoided many of the problems found when using the ordinary stratified-Petersen estimator.

New methods of “tagging” continue to be sought. For example photographs can play an important role not only for whales and dolphins (cf. Seber, 1992) but also for other animals e.g. tigers (Karanth, 1995) and grizzly bears (Mace et al., 1994). A very promising technique is genetic tagging, applied to humpback whales by Palsbøll et al. (1997).

3.2 Multiple Recaptures

Capture-recapture methods have a variety of uses. For example, with open populations, they has been used to check whether an index of population size is always a constant multiple of the actual population size (Van Horne et al.,1997, burrow entrances), to make ecological risk assessments for vertebrate populations (Anderson, White and Burnham, 1995), to obtain a global picture of survival rates for the Northern spotted owl using a "meta-analysis" approach in which one fits a global model with a large number of parameters (Burnham, Anderson and White, 1996), and to study the effect of group size on the survival of relocated prairie dogs (Robinette, Andelt and Burnham, 1995). For closed populations, they have been used to estimate the number of errors in a computer system (Chao, Ma and Yang, 1993; Yip, 1995; Goudie, Pollock and Ashbridge, 1998), and to estimate the amount of undercount in surveys and censuses (cf. Chao and Tsay, 1998 and their reference list). Capture-recapture is now used extensively in epidemiology to estimate the size of a population of people with a particular disease or characteristic from a number of incomplete lists, the so-called multi-list problem (see IWGDMF, 1995a, 1995b; Chao, 1998). Here "being caught in sample i" is now replaced by "being on list i". A novel application to plant populations is described by Alexander, Slade and Kettle (1997). Below we discuss several families of methods. What is needed now is a comparative study of these methods with respect to robustness and efficiency of estimation.

Seber (1992) described 8 models for a closed population, commonly referred as M_0, M_t, M_b, M_{bt}, M_h, M_{ht}, M_{bh}, and M_{bht} which could be used for estimating the population size N. Here the subscripts refer to the effects of *t*ime, *b*ehavior and *h*eterogeneity. These subscripts are now used rather loosely: for example, heterogeneity can be expressed in a number of different ways. When it comes to constructing confidence intervals, we reemphasize Seber's comment that profile likelihood methods are generally recommended for constructing confidence intervals (see Cormack, 1992) instead of using intervals based on the asymptotically normal properties of maximum likelihood estimators. Bolfarine, Leite and Rodrigues (1992) raise some of the problems that can occur with this approach. As is well known, likelihood methods are available for the first four models with removal type models for M_h and M_{bh}. Lloyd (1994a) provides a helpful overview of the first three. He reiterates a fact, noted by Darroch (see Seber, 1982 p. 164), that nothing is gained by using M_0, which assumes that probability of capture is constant for all samples, instead of M_t, which allows the probability to vary with time. He (Lloyd, 1995b) also compares several confidence-interval methods for M_0. Various ad hoc nonparametric methods such as the jackknife technique have been used in the past for models M_h and M_{bh}. Care is needed in choosing the order of the jackknife estimator for the model M_h when the capture probabilities are low (Rosenberg et al. 1995). Boulanger and Krebs (1996) compared various models for estimating the size of a snowshoe hare population to see how robust they were with respect to various biases such as trap saturation. They found that the jackknife estimator for model M_h was the most robust. Following a different approach, Norris and Pollock (1995, 1996a) use the theory of mixture models combined with the EM algorithm to develop nonparametric maximum likelihood estimators and associated goodness of fit statistics for M_h and M_{bh}. This method is very promising as it provides, among other things, an estimate of the discrete probability-of-capture distribution for the population, thus giving some idea as to the degree of heterogeneity. Using a logistic framework, Pledger (1998) extends this method of mixtures to provide estimation procedures for all of the 8 models. An important aspect of capture-recapture studies is the effect of movement and trap layout on population estimates (Crist and Wiens, 1995). Norris and Pollock (1996b) discuss a bootstrap approach in closed populations which takes into account the fact that the model is unknown. They also include some recommendations for open populations.

A fruitful concept in capture-recapture applications is that of sample coverage. This is defined as sum of the probabilities of capture of all the individuals ultimately caught in the experiment, divided by the sum of these probabilities for the whole population. Using this idea, Anne Chao and colleagues (Chao, Lee and Jeng, 1992; Lee and Chao, 1994) have developed estimators of N for all 8 models, as discussed in Seber (1992). Lee and Chao (1994) assumed that the relative efforts used for taking the different samples are known in models M_{bt} and M_{bht}. This assumption is relaxed by Lee (1996) who uses a conditional version of sample coverage to provide estimates for these two models. Chao and Lee (1993) develop a coverage estimator for M_{ht} for continuous-time models which uses only the frequencies of capture. From simulation studies they concluded that their estimator is most reliable when there is a reasonable amount of heterogeneity.

The martingale method, which springs from the theory of optimal estimating equations for stochastic processes (Godambe, 1985; Lloyd, 1987), was initially applied to capture-recapture models by Becker (1984) and Yip (1989), as referred to briefly in Seber (1992) (see also Lloyd and Yip, 1991). The method is based on using martingale theory to set up weighted estimating equations and then choosing the weights to minimize a certain information expression related to the asymptotic variance. Yip (1989) used unweighted estimating equations for the binomial formulation of M_t associated with random sample sizes and obtained the so-called Schnabel estimator of N, which is known to be inefficient. Yip (1991a) then used optimal weights to get an asymptotically efficient estimator and extended the theory (Yip, 1991b) to allow for known removals such as accidental losses on capture. He then developed the same theory but for the hypergeometric formulation associated with fixed sample sizes (Yip, 1993). Lloyd (1994) presented an estimate of N for the model M_b and a regression estimate for a special case of M_{bt}. He showed that the estimates of N for the models M_t and M_b are asymptotically fully efficient even though they are very different from the usual maximum likelihood estimators. Yip (1991c) applied the martingale theory to the model M_h using a beta distribution to model individual capture probabilities.

Chao et al. (1998) present a more general estimating equation (cf. Liang and Zeger, 1995) which incorporates sample coverage for the model M_{bht} under a constrained multiplicative structure for the capture probabilities. They derive estimators for all 8 models including those already mentioned above for models M_b, M_t and M_{bt} which used martingale estimating equations: the other estimators are new. However, the estimators for M_h and M_{ht} depend on the order of the samples, in contrast to the estimators of Lee and Chao (1994) which do not.

The martingale approach also lends itself to the development of continuous-time models where individuals are captured one at a time. Yip (1989, Table 2) gives a nice example of the method under a model M_t formulation, but he used unit rather than optimal weights so that the estimator is less efficient than the maximum likelihood estimator (Wilson, 1992: see also Wilson and Anderson, 1995). However, Becker and Heyde (1990) derived the maximum likelihood estimator and showed that the previous estimator has at least a 95% asymptotic efficiency when not more than half the population proportion is captured (see also Yip, Fong and Wilson, 1993). When optimal weights are used, Yip, Fong and Wilson (1993) arrive at the same maximum likelihood estimator obtained by Darroch and Ratcliff (1980) but using a different model. The latter estimator and several others are considered by Wilson and Collins (1992) for models M_0 and M_t. Becker (1984) provided an estimator for the model M_{ht} assuming a gamma distribution for individuals' capture intensities. He did not use optimal weights so that the estimator was not fully efficient: it also had some undesirable features (Wilson and Anderson, 1995). Incorporating the concept of sample coverage into the martingale-based estimating equations with optimal weights, Yip and Chao (1996) develop an alternative estimator for M_{ht} which does not require the gamma distribution assumption. Covariates can also be used, and Yip, Huggins and Lin (1996) develop a continuous time version of Huggins (1989) discrete model for M$_h$ which incorporates covariates for estimating capture probabilities. They use a Horvitz-Thompson estimator as described in Section 2 for estimating N.

An interesting application of the martingale method to the M$_t$ model is that of detecting the number of errors in a system such as a software package. This can be done by randomly inserting a known number of errors (marked individuals) into the system and then sampling one at a time. When an error is encountered, it is either removed as in the removal method (Yip, 1995) or retained for further "recapture" (Yip, 1996). This method of planting "tagged" individuals, mentioned briefly in the preceding section, has also been studied by Goudie and colleagues (e.g., Goudie, 1995; Goudie, Pollock and Ashbridge, 1998).

Bayesian models continue to be developed (Underhill, 1990; Bolfarine, Leite and Rodrigues, 1992; and Garthwaite, Yu and Hope, 1995, who discuss model M$_t$). With the advent of the Gibbs sampler, mentioned earlier in Section 2, there will be an upsurge of interest in Bayesian methods as more realistic priors can be used and compared (George and Robert, 1992; Lee and Chen, 1998). Madigan and York (1997) apply Bayesian methods to the multi-list problem mentioned previously in the context of epidemiology and use the methods to incorporate model uncertainty into the variance of the population estimates. Ananda (1997) uses a Bayesian method to analyze a mark-resighting survey in which an initial number of individuals are marked and in subsequent samples the tagged individuals are just resighted rather than recaptured.

Log-linear models are particularly useful for modeling both capture dependencies between samples and heterogeneity. They were initially introduced by Fienberg (1972) for capture-recapture models and further developed by Cormack (1989) who related the parameters from the model to functions of the biological parameters for the models M_0, M_t and specific M_b and M_{bt}. Cormack (1993a) discusses the use of generalized linear models in the analysis of recapture data and he (Cormack, 1993b) provides estimates of the variance of mark-recapture estimates using such models. The variance estimates had previously been difficult to obtain. Evans et al. (1994) give a very general method for analyzing such models which uses simpler functions of the biological parameters. This is achieved by building restrictions into the estimation process. For example, the log-linear version of the model M_t in which p_i is the probability of being caught in sample i (or at time i), can only incorporate both $\log(p_i)$ and $\log(q_i)$ by imposing the constraint $p_i + q_i = 1$. They develop a new general model for M_{bt} which includes the previous three models as special cases. They handle the remaining heterogeneity models by using stratification based on covariate information: this leads to a whole range of other submodels and follows the current trend of expanding generalized linear models. They also introduce the first log-linear model for removal data. This alternative approach to modeling capture-recapture models looks very promising. In a companion paper, Evans and Bonett (1994) show that the biases of the estimates for a k-sample capture-recapture experiment can be reduced by adding $(.5)^{k-1}$ to each cell in the multiway contingency table for the recaptures. In another paper, Evans and Bonett (1992) consider a modification to the theory in which sampling is performed without replacement on the last trapping occasion: the other samples can be dependent. By modeling heterogeneity differently, two further kinds of model are developed by Agresti (1994) for M_{ht}. These are special cases of the Rasch additive model of psychology and have the property of "quasi symmetry". One is a log-linear model and the other is a latent class model.

When applying capture-recapture methods to epidemiology, heterogeneity and list dependence (the behavior component) are the norm. Also, in contrast to capture-recapture applied to animal populations, there is no time order for the lists so that the "time effect" is now a list effect. Thus all three factors are generally present and the general model M_{bht} is the most appropriate one to fit. An alternative method of estimation using the idea of average sample coverage described above is given by Chao et al. (1996) and Chao and Tsay (1998). Because this area has been reviewed extensively by Chao (1998) and IWGDMF (1995a,b), we will not expand on new developments in this topic here except to note that the uncertainty introduced by model selection is now being incorporated into the estimates (Hook and Regal, 1997; Madigan and York, 1997).

Manning, Edge and Wolff (1995) provide one of those all too rare studies in which various methods are compared for populations of known size; in this case 9 closed populations of voles were available. The populations were small (30, 60 or 90 animals), four trapping occasions were used, and 11 estimators compared. Heterogeneity of catchability seemed to be the main factor in the choice of models and the jackknife estimators did surprisingly well. Crist and Wiens (1995) examine if movements of individually marked beetles can be modeled as coming from a correlated random walk and showed that estimates of population size based upon capture-recapture studies may be biased because of failing to account for the movement patterns of the individuals.

Program CAPTURE (Rexstad and Burnham, 1992) is a comprehensive package for fitting many of the models described above that have a formal likelihood associated with them as well as some of the Chao coverage models. The program can provide estimates of both density and abundance. Any standard statistical package that can fit log-linear models can be used for these models. Some special purpose software (e.g. the non-parametric heterogeneous likelihood) are available directly from Rexstad and Burnham. However it should be noted that model selection is not easy with some data sets and that corresponding hypothesis tests can have low power.

3.3 When not all animals can be distinguished

In some cases, a known number of marked animals is released into a population, but in subsequent captures, unmarked animals are not marked. For example, radio-collared animals could be released, and subsequent sightings are of collared and uncollared animals, but no further animals are collared. These methods in which animals are simply resighted rather than recaptured after their initial marking and releasing are often known as mark-resight methods. A Petersen estimator can be constructed at each sample time, and White and Garrott (1990) discuss how to combine these estimates. Neal et al. (1993) extend this to accommodate immigration and emigration. Minta and Mangel (1989) propose a bootstrap estimator based upon the frequency of resightings of marked individuals and the total sightings of unmarked individuals (some of which may be spotted more than once). Arnason, Schwarz, and Gerrard (1991) modified the Minta and Mangel estimator to cases where the number of marks is not known when the sample is taken. White (1993a) showed that confidence interval coverage for the Minta and Mangel procedure was not satisfactory and proposed a revised estimator, while Bowden and Kufeld (1995) proposed an improved method for computing confidence intervals that had good coverage. Gardner and Mangel (1996) updated the earlier estimators to allow for the incomplete detectability of the animals and they estimate the probability of detection using observations from two observers. Wileyto, Ewens, and Mullen (1994) discuss an interesting experiment where animals are self-marked, and the changes in the marked fraction over time can be used to estimate the population size using Markov-chain models. In a follow-up article, Wileyto (1995) examines the robustness of this method to violations of assumptions and found that large biases could occur if the population is open, or if the behavior changes after self-marking. Finally, we note that many of the estimators for mark-resight studies can be computed using NOREMARK (White, 1996b).

4 Capture-Recapture methods for open-populations

Research in this area has been very intense in the last few years. In general, it can be classified in the following areas: band-recovery models where typically only a single resighting is possible, e.g. from the recovery of the dead animal, and emphasis is on estimating survival and not abundance; Cormack-Jolly-Seber type models where multiple recaptures are possible for any animal, but there is no information on unmarked animals so that the emphasis is again on just estimating survival; Jolly-Seber models where both abundance and survival are of interest; and finally miscellaneous methods that combine features from the previous three types of models. There has also been a consolidation and unification of many previously separate types of models. For example, recoveries from both dead and live animals have been integrated into a single modeling framework. Many of the recent advances are found in the various EURING proceedings (Lebreton and North, 1993; North and Nichols, 1995; North and Baillie, in press). Lebreton (1995) provides a helpful summary of possible future development and gives useful links to survival models used in human health studies.

4.1 Single recoveries

4.1.1 General comments

This is a special case of general capture-recapture models where animals are recaptured only once, typically from the return of dead animals. There are a number of terms for these types of studies, the most common being tag-recovery, band-recovery, and ring-recovery. Many of the recent developments and applications in bird populations have been first presented in the EURING conference proceedings. The emphasis in these studies has been in estimating survival rates.

The basic modeling framework was summarized by Brownie et al. (1985) which is now the standard reference for these types of models. Dorazio (1993) developed models similar to those of Lebreton et al. (1992) which allow the modeling of survival and band recovery rates among groups. Cormack and Skalski (1992) use a log-linear analysis of the returns from coded-wire tagged fish that also could be used for the analysis of band-recoveries. A planning tool for studies with two-banding periods per year was developed by Otis (1994). Pollock, Hoenig and Jones (1991) generalize the formulation of the models in Brownie et al. (1985), but in a fisheries context, to incorporate further information about tag reporting from a creel survey or port sampling. This allows for the separate estimation of the natural and fishing mortalities.

In some applications to game management, estimates of harvest are needed. Check stations or telephone surveys are common methods of estimation. Some of the biases associated with these methods and the common problem of incomplete responses are discussed by White (1993b) and Steinert, Riffel and White (1994); further references are cited by these authors.

The programs ESTIMATE, BROWNIE, and MULT (Brownie et al., 1985; reviewed by Conroy, 1995) are the standard tools for the analysis of simple band-recovery experiments. More complex models can be fitted by SUR-

VIV (White, 1983). Because band-recovery models are a special case of the Cormack-Jolly-Seber model, programs developed for the latter can also be used, e.g. SURGE (Pradel and Lebreton, 1991), MARK (White and Burnham, in press) or EAGLE (Catchpole, 1995), the latter a package written in MATLAB. Most models can also be fitted as log-linear models with GLIM or S+.

4.1.2 Animals banded when young

It was noted in previous reviews (e.g. Seber, 1992 p. 148) that when animals are banded as young, that there are problems in maximizing the likelihood of Seber's (1971) model for this experiment. It was recommended that the method not be used unless an independent estimate of one of the parameters was available–such as information on survival of nestlings from radio-telemetry. However, Freeman, Morgan, and Catchpole (1992) demonstrated some problems in Seber's approach and do not recommend it as any error in estimating the first year survival rate permeates the other estimates. As well, Catchpole and Morgan (1994) obtained an explicit solution as to when estimates lying on the boundary of the parameter space will occur. Earlier, Morgan and Freeman (1989) showed that a more general formulation by allowing calendar-year dependence of survival rates for first year birds resolved this problem and illustrated it with a number of examples (Freeman and Morgan, 1990). Freeman and Morgan (1992) extended this model by also allowing calendar year dependence of the report rates and by allowing age-dependence of survival rates for older birds. However Catchpole, Freeman, and Morgan (1995) showed that some models with age dependence still had problems of non-identifiability, but were able to identify which models were parameter redundant using the approach of Catchpole, Freeman, and Morgan (1996) and Catchpole and Morgan (1997). Catchpole and Morgan (1996) noted that likelihood ratio tests are especially problematical in these models because of the problems of model fitting and parameters falling on the boundaries of parameter spaces. They investigated the use of score tests and found that these performed very well. Catchpole, Freeman, and Morgan (1993) demonstrated that additional information from recaptures at the end of the study greatly increased the precision of other estimates and reduced the boundary problems.

Two case studies of these methods are presented by Francis (1995), and Freeman and North (1990). Model fitting can be done for these studies using SURVIV (White, 1983) or EAGLE (Catchpole, 1995). Finally, Vounatsou and Smith (1995) present a Bayesian analysis using Markov Chain Monte Carlo methods and reanalyzed some of the data sets of Freeman and Morgan (1992).

4.1.3 Estimating movement

In most studies, recoveries are simply plotted on a map and a discussion of the general movement patterns takes place without trying to quantify the amount or direction of movement. This is because the movement pattern is confounded with the distribution of recovery effort. In recent years, there has been some work in estimating movement rates using capture-recapture rates, but most of this has taken place in the context of multiple-capture models of which single recovery data is a special case. The simplest types of studies have only a single release time and single recovery period. The stratified-Petersen method can be used to estimate movement rates among the strata and was discussed earlier.

Much of the development of methodology for estimating movement with multiple release times and multiple recovery times has taken place in a fisheries context. Schwarz and Arnason (1990), Schwarz, Schweigert, and Arnason (1993), and Schweigert and Schwarz (1993) demonstrate how to estimate migration among geographic strata based upon releases and recoveries from all strata. Schwarz (1993) used a similar methodology to study the movement of ducks among flyways in North America. However, a different approach was taken by Hilborn (1990) and Heifetz and Fujioka (1991) who directly modeled the population dynamics of fish movements and captures using catchability coefficients and known efforts. Anganuzzi, Hilborn, and Skalski (1994) extended the model to account for size selectivity. Xiao (1996a) developed a planning aid to assist in designing experiments using this model to determine necessary sample sizes and efforts to achieve a specified precision. Finally, using a random walk approach, Manly and Chatterjee (1993) develop a model where the probability of recapture is modeled as a function of the distance of the recapture site from the release site, the probability of survival, and possibly environmental variables.

4.1.4 Assumptions of the single-recoveries model

The assumptions and the effects of their violations upon model estimates have been extensively reported (Brownie et al., 1985, and appendices). Barker (1992) examined the effects of heterogeneity upon confidence interval coverage for survival rates and found that, except in extreme cases, coverage was close to nominal levels. Burnham and Rexstad (1993), and Rexstad and Anderson (1992) developed models that explicitly account for heterogeneity in survival rates among animals. Lebreton (1995 p. 1021) suggested using frailty models from epidemiology combined with radio-tracking to explore heterogeneity. Powell, Clark, and Klaas (1995) used the post-release stratification models of Schwarz, Burnham, and Arnason (1988) to detect heterogeneity in survival rates among recovery areas. Heterogeneity is also likely to exist in recovery rates and band-reporting rates. For example, Piper (1995) modeled the ring recovery process and showed that the rates varied with color, type of band, and area of recovery. Nichols et al. (1995) showed through a reward banding study, in which people are rewarded for returning bands, that geographic location had a large effect upon the reporting rate. Nichols et al. (1991) developed a logistic regression equation to predict the reporting rate as a function of the reward value. An interesting experiment using postcards as surrogates for tags to estimate tag return rates was done by Zale and Bain (1994).

The effects of tag-loss are well known. There have been many papers estimating actual tag-loss rates (through double tagging experiments) and comparing them among groups such as sex or age (e.g. neck bands in geese by Johnson, Shieck, and Searing, 1995; anchor tags in sturgeons by Clusgston, 1996; different tag location and type in seals by Stobo and Horne, 1994). Treble, Day, and Quinn (1993) examine the effects of changes in the tag-loss rate upon estimates of survival. Barrowman and Myers (1996) extend existing double-tagging methods to include a general formulation for multiple-tag types. They show how the inclusion of single-tagged subjects released simultaneously with the double-tagged subjects provides more precise estimates and enables one to test hypotheses previously thought untestable. Xiao (1996b) develops a model to estimate tag loss rates based on exact or pooled time at liberty from double tagging experiments and shows that these are a generalization of several earlier models developed for tag loss. A double tagging experiment can also be used to test if one of the tags has an effect upon subsequent survival, as illustrated by Castelli and Trost (1996) who examined the effect of neck bands upon the survival of Canadian geese.

When studying survival (or mortality) rates, a number of questions and hypotheses arise. For example, with harvested wildlife we would like to split total mortality into its various components. Pollock, Conroy and Hearn (1995) provide a review of separating hunting and natural mortality using various modifications to the study design (e.g. reward band, planted bands, surveys, pre- and post-season bandings), thus summarizing the work by Pollock and Hearn (1994) and by Pollock, Tsai, and Hoenig (1994). Conroy, Williams, and Hines (1995) point out that earlier work (Conroy, 1985) included many of the features of this later work. Myers, Barrowman, and Hutchings (1997) use a single release to apportion mortality among different fishing regions for the Atlantic cod, but needed to make strong assumptions in order to fit their model. Survival can also be affected by other factors. For example Krementz, Barker, and Nichols (1997) used a logistic model with covariates to examine the effects of geographic location, body mass, and phylogeny in the variations in annual survival of waterfowl from around the world. Hestbeck, Nichols, and Hines (1992) examined the relationship between survival rates and migration distances. There can also be age and sex differences in survival, and these differences can tell us something about the timing, magnitude, and causes of mortality. Reynolds et al. (1995) studied such questions for mallards by using spring and summer banding of young and older birds. Is the effect of hunting on annual survival compensatory or additive? This long-standing question (cf. Seber, 1992 p. 149) was examined by Barker, Hines and Nichols (1991) and Rexstad (1992).

In conclusion it is stressed that the sample of animals tagged should be a representative sample of the population, although in practice most recaptures tend to be convenience samples. Dufour, Ankney, and Weatherhead (1993b) examined convenience samples when selecting birds to be banded and showed they were far from representative of the population. Similarly, it is often assumed that recoveries are a representative sample, which again may not be true. Dufour, Ankney, and Weatherhead (1993a) showed that body condition was related to recovery for waterfowl.

4.2 Cormack-Jolly-Seber models – estimating survival

A key paper in the analysis of Cormack-Jolly-Seber (CJS) models for tagged individuals only was that of Lebreton et al. (1992) who described a unified general methodology for the estimation of survival and catchability from several groups of animals using an ANOVA type framework for model specification and the Akaike Information Criterion (AIC) for model selection. Their paper expanded and integrated the theoretical work of Burnham (1991) and some of the GLM philosophy followed by several authors. Using their methodology, one is able to test, for example, if survival rates are the same among different groups of animals, or equal over time. Individual animal covariates can also be handled (Skalski, Hoffman, and Smith 1993; Kingsolver and Smith, 1995). These developments have given rise to literally hundreds of papers exploiting this very powerful methodology as exemplified by the proceedings of the EURING conferences. The papers by Baillie (1995) and Clobert (1995) give a good overview of these applications. Some predictions about future research in this area were given by Anderson, Wotawa and Rexstad (1993) and Lebreton (1995), and many of these predictions have been presented at subsequent EURING meetings. There are, of course, always special variations on the general model. For example to get round a problem of sparse fish data, Modde, Burnham and Wick (1996) propose using an annual sequence of Petersen estimates based on pairs of consecutive years to give some idea of population trend. Survival rates are calculated by the usual methods for CJS models. Again, one of the models often considered in the CJS framework is equal survival over all time periods. However this may be too restrictive, and Burnham (in press) presents a model where the survival effects vary randomly among years around a common mean - similar to random effects in ANOVA.

The software package SURGE was the first package that could be used to fit these CJS models for just the tagged individuals and has gone through several generations (Pradel and Lebreton, 1991; Pradel, Reboulet and Viallefont, 1995; Reboulet, et al. in press). Cooch, Pradel and Nur (1997) have a very detailed monograph with many biological examples illustrating the use of SURGE. A newer program called MARK (White and Burnham, in press; White, 1998) has the capabilities of SURGE but also includes band-recovery, the robust design, the mixture of information models of Barker (1997), and the models of Pradel (1996) involving recruitment. Catchpole (1995) has also developed a series of MATLAB routines to fit capture-recapture and band-recovery data. The program POPAN (Arnason and Schwarz, 1995, and in press) can also be used to fit models in the CJS framework, but its emphasis is more on abundance estimation. Skalski, Hoffman and Smith (1993) developed SURPH for estimating the effect of individual animal covariates. Lebreton, Reboulet and Banco (1993) presented a comparative review of software, but given the speed at which software changes, it is now dated.

This general framework for CJS models can lead to models with well over 1000 parameters. The first problem with such large complex models is that of finding out how many parameters are identifiable, particularly when there are inherent limitations of the model or a sparcity of data. Catchpole and Morgan (1997) and Viallefont et al. (in press) develop necessary and sufficient conditions to identify parameter redundancy in recapture and recovery data and Catchpole, Morgan and Freeman (in press) and Morgan, Freeman, and Catchpole (1995) demonstrate how to estimate the identifiable parameters. The second problem with complex models is that of selecting a suitable model. Lebreton et al. (1992) recommend the use of Akaike's Information Criterion. The use of AIC has been investigated in more detail by Anderson, Burnham and White (1994), Burnham, White, and Anderson (1995), and Burnham, Anderson and White (1994, 1995) who recommend a quasi-likelihood adjusted AIC statistic and overdispersion estimator. In most cases, researchers report parameter estimates and precisions based upon the final selected model; this fails to account for uncertainty in the model selection procedure. Buckland, Burnham, and Augustin (1997) recommend a weighted estimator based upon estimates from various models and using AIC to determine the weights. Norris and Pollock (1996b) discuss a bootstrap approach in closed populations but also include some recommendation for use with open populations.

4.2.1 Violations of assumptions

The widespread availability of the programs JOLLY and RELEASE through web sites has enabled researchers to test the adequacy of the assumptions underlying their CJS model using appropriate goodness of fit procedures, as well as obtaining parameter estimates. One of the assumptions usually made in capture-recapture studies is that if animals leave a study area, they do so permanently. However, Burnham (1993) has shown how to redefine the parameters of the CJS model so that random emigration can be incorporated in the model. When emigration is permanent, mortality is not distinguishable from permanent emigration. However, there may be sub-populations with different emigration behavior which leads to heterogeneity in the apparent survival rates. For example, there may be transients which enter and leave the study population while a resident population remains. Pradel et al. (1997a) show how to modify the CJS models to account for transient animals by removing animals with only a single capture occasion. In Pradel et al. (1997c), the joint effects of both transients and trap-dependence (see below) are modeled. In some species, tagging is done on young animals but these then leave the colony for several years before returning to breed on a regular basis. This form of predictable temporary emigration was modeled by Nichols, Spendelow, and Hines (1990) for a colony of terns. Conroy et al. (in press) develop a model that includes both transient effects and an uncertain gender classification of a bird at the time of banding. Initial classification was done by wing length (based upon the results from a discriminant analysis). Some birds were recaptured later and could be sexed (and the gender 'corrected'; other birds were never recaptured and the proper gender could not be determined). They used a multi-state approach (see later) that allowed for the transitions from predicted gender to actual gender (with possible errors).

A crucial assumption of the CJS model is that all animals in a cohort have the same probability of capture and of survival. Heterogeneity can be caused, for example, by trap dependence. Pradel (1993) showed how to modify the CJS model to account for trap-dependence by splitting the complete capture history into a series of sub-histories and modeling the first occasion after release differently than subsequent survival periods. This was extended in Pugesek et al. (1995) to account for both age and trap-dependence effects. Heterogeneity may also be caused by transient animals, local emigration to other sites, handling effects, or permanent emigration of subpopulations (which is confounded with survival). In some cases these can be disentangled (see also Section 4.2.4 on Combining Sources of Information). Pradel, Cooch, and Cooke (1995) stratified a population of snow geese into birds first banded as goslings, birds banded as adults but previously webtagged as goslings, and birds first banded as adults and not previously marked. By comparing the estimated parameters among these groups, they were able to conclude that the latter group of animals had a higher permanent emigration rate and lower apparent survival rates. The effect of heterogeneity in the capture probabilities upon the estimates of survival is well known, and this information can be used to investigate if apparent differences in survival among groups may be related to heterogeneity in capture probabilities (cf. Prévot-Julliard, Lebreton, and Pradel (1998)).

Another key assumption is that all tags are reported and reported correctly. Nichols and Hines (1993) and Nichols et al. (1992a) considered the problem of tag loss and showed how to account for it in estimating survival rates when both recaptures and resighting data are available. An example of investigating the influences of color, type of application, colony site, cohort, calendar year etc. upon the neck bank loss rate using the above methodologies is given by Spendelow et al. (1994).

4.2.2 Breeding proportions and senescence

Lebreton et al. (1990) proposed models for estimating breeding proportions from data collected at several points in time, but without information on individual fates. Clobert et al. (1994) estimated age-specific breeding probabilities from recaptures or resightings of individual animals marked as young and using multiple cohort models. Both approaches assumed that survival rates were identical for breeders and non-breeders. In contrast, Pradel (1996a) developed a more general procedure based on analyzing the capture histories by reading them backward through time. Examples of this approach are presented in Pradel et al. (1997b) and in Viallefont, Cooke, and Lebreton (1995). Pradel and Lebreton (in press) contrast these two approaches and also consider a third approach based on a two-state model (with one of the states unobservable) developed by Nichols et al. (1994). They compare the interpretations of the estimates from the three approaches (see also the following section). If the breeding status and number of surviving offspring of each animal can also be recorded when it is resighted (e.g. a whale calf is seen along with its mother), then both the survival rates and age-specific fecundities can also be estimated (Barlow and Clapham, 1997) which allows a Leslie matrix (cf. Seber, 1982 p. 550) to be constructed directly and the population growth rate to be estimated. Tradeoffs between breeding and survival on snow geese were investigated by Viallefont, Cooch, and Cooke (1995), and between clutch-size and survival by Blondel, Pradel, and Lebreton (1992). The multi-strata approach, discussed later, can also be used. The proportion of animals returning to breed can also be estimated using the Robust Design as discussed later in Section 4.4.

Senescence, the long term decline in survival with age, has been theorized to occur for many species, but previous investigations have used life table methods requiring very restrictive assumptions or have used other methods requiring capture probabilities of one. The CJS modeling framework can be used to investigate this question, as was done indirectly by Pugesek et al. (1995), and directly by Nichols, Hines, and Blums (1997) who modeled a linear-logistic decline in survival as a function of age.

4.2.3 Movement and multi-strata models

Models for movement among distinct geographic areas measured using multiple recapture experiments were developed by Arnason (1972) and Arnason (1973) and were summarized and extended in Seber (1982). A review of the history of movement modeling is presented by Nichols et al. (1993) and Nichols (1996), who also indicate a number of biological research problems that could be investigated using the recently-developed methodology.

Schwarz, Schweigert, and Arnason (1993, Appendix B) provided the likelihood for the Arnason-Schwarz model, but concentrated upon a band-recovery context (see previous sections). Hestbeck, Nichols and Malecki (1991) used the multi-stratum models to estimate movement and site-fidelity using mark-resight data of wintering Canada geese and allowed the probability of movement to depend upon the location in the previous period. Brownie et al. (1993) extended these models to include cases when movements are non-

Markovian. Spendelow et al. (1995) used covariates to further model the movement probabilities in a tern colony as functions of intercolony distance and size of breeding colony. Lindberg, Sedinger and Rexstad (1995) used these models to investigate fidelity of black brant to nesting sites and Hestbeck (1995b) used movement models to investigate changes in survival of Canada geese in North America. The effects of violations of the assumptions and of heterogeneity in movement probabilities among individuals were investigated by Hestbeck (1995a) who found that the bias in survival/movement rates is likely to be small. Schwarz and Ganter (1995) used movement models to investigate interchange among staging areas of geese when there are problems of missing data, e.g. not all areas having effort at all times. It is necessary to make strong assumptions about closure and the equality of movements over time in order to have much success in fitting a model.

All of the above studies model movement among discrete strata. Mason, Nichols, and Hewitt (1995) used an approach similar to that of Manly and Chatterjee (1993) by using a random walk approach to investigate dispersal of grasshoppers using multiple resightings.

It should be stressed that movement models also include general multi-strata models where "movements" correspond to changes in strata membership, e.g. strata are age classes and "movement" represents the survival and aging process. For example, Nichols et al. (1992b) showed how to use this method to estimate transitions among weight or length strata, and also developed methods using the Pollock robust design (Section 4.4). Furthermore, Nichols et al. (1994) use a multi-state model to estimate breeding proportions and show how to investigate the costs of reproduction upon subsequent survival or breeding. Nichols and Kendall (1995) and Lebreton, Almeras and Pradel (in press) show how the multi-strata approach can also be used to investigate more general questions in ecology. Recapture and recovery data can be incorporated as well. In some cases, data may be too sparse or may require models too complex to be fitted using multi-strata models. Viallefont, Cooch, and Cooke (1995) demonstrate how some of the same questions about the effects of reproduction on survival and future reproduction can be answered using ordinary CJS models. Rather than classifying animals into coarse strata, other selection coefficients for continuous variables such as weight can be examined by using the CJS models with individual covariates (Skalski, Hoffman, and Smith; 1993; Kingsolver and Smith, 1995). A special version of SURVIV, MSSURVIV (Hines, 1994), is commonly used to analyze data from the movement studies described thus far.

Dupuis (1995) developed a Bayesian approach to these movement models and showed that if it is cast into a 'missing data' formulation - the missing data being the unknown locations of the animals between observations - Gibbs sampling can be used to obtain posterior distributions of the estimators. General non-specific movement (e.g. dispersal) could also be investigated using capture-recapture methods as outlined by Pradel (1996b) who detailed the data requirements and outlined how to analyze such experiments. Van Noordwijk (1995) shows that unless the distribution of recovery effort is taken into account, simple estimates of dispersal based upon subsequent sightings or recoveries can be misleading.

4.2.4 Combining sources of information

As noted by Seber (1992), multiple recapture and resighting models, and models based upon recoveries from dead animals are all part of the same basic model. Peach (1993) demonstrated how to combine several recapture data sets subject to a common effort of capture while Catchpole, Freeman and Morgan (1993) showed how to supplement recovery data from birds marked with young and recovery data from birds marked as adults. Radio-tagging data can be used in conjunction with tag-recovery studies and the consequences were studied by Catchpole and Morgan (1994) and Freeman, Morgan and Catchpole (1992). Burnham (1993) developed a complete theory for the joint analysis of live recapture and dead recovery data for the time dependent case and showed that it enabled the researcher to separate the effects of mortality from those of emigration. Lebreton et al. (1995) considered the problem of combining information from two related but independent sets of recovery and recapture data for birds marked as young. The combined analysis of live-recapture, resightings, and dead-recoveries was developed by Barker (1997). More general results including age effects and short term handling effects are given by Barker (1995) and Catchpole et al. (in press) who extended the work by Catchpole et al. (1993) on animals tagged as young. Blums et al. (1996) used separate band-recovery (based on large geographic areas) and capture-recapture analyses (based on site of banding) of the same data set to estimate philopatry in ducks based on the different interpretation of 'survival' from the two studies. This data can now be analyzed using the single model of Barker (1997).

Nichols et al. (1992a) and Nichols and Hines (1993) considered the problem of tag loss and showed how to account for it in estimating survival rates when both recaptures and resighting data are available. The latter paper also has a nice review of the effects of tag loss and they note that recapture data is the most appropriate source of data from double tagging experiments to estimate tag retention.

4.3 Jolly-Seber models - estimating survival and abundance.

The Jolly-Seber (JS) model is a more general case of the Cormack-Jolly-Seber (CJS) model considered above in that abundance is of interest in addition to survival. This often requires that the number of unmarked animals is also recorded at each sampling occasion and that these are marked and returned to the population. Because estimation of survival relies mainly upon the capture histories of marked animals, many of the results from the CJS model are also applicable here.

The current standard reference for the analysis of JS experiments is Pollock et al. (1990). An outstanding problem with the Jolly-Seber model is related to how the contribution from unmarked animals is integrated into the likelihood. Schwarz and Arnason (1996) used the methodology of Crosbie and Manly (1985) to develop a fully multinomial likelihood that keeps all parameter estimates within admissible ranges and allows simple testing and modeling of the recruitment parameters. Burnham (1997) extended

Burnham (1991) to derive another version of a likelihood and also found distributions of the sufficient statistics in the special cases of no death or no recruitment. Pradel (1996a) also developed methodology to estimate the recruitment and population growth rate by reading capture histories 'backwards' (cf. Nichols et al., 1986) which treats 'survival' and 'recruitment' in a symmetric fashion. Pradel (in press) has developed a general likelihood function which combines his previous approach to recruitment with the usual JS approach. Schwarz and Arnason (1996) extended the methodology given in Lebreton et al. (1992) to also apply to the abundance and "birth" parameters in a JS model, i.e. having parameters in common across groups. Derocher and Stirling (1995) describe a careful study to estimate and compare the polar bear population size, survival, and other parameters in western Hudson Bay for both males and females. Software available for the JS model includes the Jolly suite of programs described by Pollock et al. (1990), and a software package called POPAN (Arnason and Schwarz, 1995; Arnason and Schwarz, in press). The POPAN programs implement the models described by Schwarz and Arnason (1996) and is a comprehensive, integrated program to analyze mark-recapture data.

The JS estimator provides estimates of abundance but not of density as it is difficult to determine the appropriate population area for an open population. Matlock, Welch, and Parker (1996) converted the estimates of abundance of screwworms into density estimates by also estimating the area of dispersal based on the observed distances of movements of marked animals. In some cases, interest lies in the total number of entries into a population - including those animals that enter but die before having a chance of being sampled (which are ignored by the regular Jolly-Seber model). Schwarz et al. (1993) developed the methodology for this situation in the context of estimating the number of salmon returning to spawn.

The crucial assumption for estimating abundance under simpler models is that all animals are equally catchable at each sample occasion. Using the coverage methods that have worked so well with closed populations, Hwang and Chao (1995) examined the effects of unequal catchability upon the estimates of abundance and proposed new estimators that have much less bias if the coefficient of variation in the catchabilities is greater than 0.4. In some cases, capture histories are pooled (e.g. individual daily capture histories are pooled into a single weekly capture occasion) to reduce the effects of heterogeneity. An alternative approach, based on a simulation method of Carothers ((1979), is given by Pledger and Efford (1998) who show how to estimate the biases caused by the heterogeneity.

A variety of hypotheses can be tested for the JS model and these are documented in Seber (1986, 1992). Brawn, Karr, and Nichols (1995) examined a 9 year record of 25 species of neotropical birds and examined the relationship between body size, phylogenetic affiliation, foraging guild and social behavior and the population parameters of survival rate, population size, and recruitment between sampling occasions by performing simple regression upon the estimates obtained from a JS model. With the methods developed by Schwarz and Arnason (1996) and now available in POPAN (Arnason and Schwarz, in press), it should be possible to model covariate effects directly for the JS model, as was done by Nichols, Hines and Blums (1997) for the CJS model when they modeled the survival parameter using a logistic model. Covariates have been used routinely with SURGE for the CJS model (Lebreton, personal communication).

4.3.1 Combined methods

JS estimators of abundance can also be combined with other estimators. Sheaffer and Jarvis (1995) outline a method where a JS estimate is used on marked animals only by treating the first sighting of a marked animal as if it were unmarked and subsequent resighting as "recaptures". This gives an estimate of the number of marked animals alive at each time point. Simple surveys are used to estimate the marked to unmarked ratio at each time point. These can be combined together to get estimates of abundance at each time point. Sheaffer and Jarvis (1995) also investigate the size of the bias in the population estimates that can arise when neck bands are not 'verified' when read. This has the effect of increasing the estimates of the size of the marked population and hence the final estimates of the population size.

In some cases, the overall goodness-of-fit statistic indicates that the JS model does not fit. However, estimates of abundance can still be obtained by fitting a complex CJS model to just the resighting or recapture data only and then using simple moment estimators of population size based on the observed numbers of unmarked animals. For example, Loery, Nichols, and Hines (1997) fitted a CJS model incorporating transients and then used the resulting estimates of capture probabilities to estimate the population size of chickadees. These were then regressed against time to look for time trends.

4.4 Robust design

The robust design was first proposed by Pollock (1982) to alleviate bias in estimates of abundance caused by heterogeneity in the capture-probabilities on a particular sampling occasion. This design consists of a sequence of capture-recapture experiments spaced in time. Each individual capture-recapture experiment is carried out over a short enough time span so that closed-population methods can be used to obtain an estimate of population size. We refer to the short time periods between each sample in an individual capture-recapture experiment as secondary time periods, and the time periods between experiments as primary periods. Kendall and Pollock (1992) give a recent review and evaluation of this design and conclude that the robust design should be used whenever possible in place of the usual JS open population model. Until recently, estimators under the robust design were *ad hoc*, but Kendall, Pollock, and Brownie (1995) developed a formal likelihood approach for this design. Program RDSURVIV is available from the Patuxent Wildlife Research Centre Software WWW page to analyze data from the robust design.

The robust design can also be used to estimate temporary emigration or breeding proportions. Nichols and Pollock (1990) and Pollock, Kendall and Nichols (1993) used the robust design to separate recruitment from immigration using *ad hoc* estimators. Kendall and Nichols (1995) and Kendall, Nichols, and Hines (1997) develop likelihood theory for the case where the population during the secondary periods is closed, while Schwarz and Stobo (1997) develop likelihood theory for the case when the population during the secondary periods is open. In the robust design, primary period parameters are usually estimated by collapsing secondary periods (where the population is closed) to a single instance of captured or not captured. Hargrove and Borland (1994) showed that estimates derived using these reduced capture histories are relatively unbiased unless the population has a very high turnover during the secondary sampling periods. Gould and Pollock (1997a) replaced the capture-recapture protocol during the secondary samples with catch-effort protocols. We suspect that in the near future, more study designs will be developed using a variety of methods for the secondary periods.

5 Catch-Effort Models

In catch-effort experiments, the decline in the catch over time when known amounts of catching effort are applied to catch members of a population is used to predict the initial population size. Such models are most often used in fisheries management (over 100 citations from 1992 to 1997), but Novak et al. (1991) and Lancia et al. (1996) give examples involving large mammals. In fisheries, effort might be measured, for example, in terms of time spent fishing and the number of long lines used, or in terms of the size of the net and the length of the tow. We note that the emphasis is sometimes on estimating "sustainable catch" rather than on estimating the initial (virgin) population size. In pre-computer days "equilibrium" catch-effort models were used: these models still occasionally surface. Rather than try to survey fisheries literature, we will concentrate here on methodological improvements in the last few years. We note that the removal methods in Section 2.3, where the amount of effort is kept constant from sample to sample, are a special case of catch-effort models.

Traditionally, regression methods have been used with this protocol because of the difficulties in computing the estimates. These regression methods will only work if the population is being reduced enough to produce a visible decline in the catch per unit effort (CPUE) over time. However, Bishir and Lancia (1996) show how catch-effort models can be used in more general situations where animals are added, sightings are treated as "catches", and both removals and sightings may be present. They further showed that non-linear least squares could be used to estimate the parameters of the model. Gould and Pollock (1997b) show that the maximum likelihood estimates could be easily computed with modern software and were consistently less biased and more precise than estimates from ordinary regression methods. Reed and Simons (1996b) used the Kalman filter to estimate the parameters of the catch-effort model but recommended that their methodology primarily be used to estimate the CPUE.

Various assumptions underlying catch-effort models can be violated. For example, catchability can vary. Yamakawa, Matsumiya, and Kitada (1994) used covariates to 'explain' some of the variability in catchability, while Reed and Simons (1996a) investigated the effect of contagion in the catch upon the estimates. A simulation to investigate the effects of other violations of assumptions upon the estimators in crab and lobster fisheries was conducted by Miller and Mohnn (1993). They showed that some of the biases could be corrected if certain supplemental information was also collected. Gear saturation can also occur, in which the gear (e.g. nets or pots) used to catch the fish becomes completely full of fish so that no more can be caught irrespective of the size of the population. Somerton and Kikkawa (1995) examined this problem and proposed a method where the time between individual catches could be used to determine a population index of relative abundance. Another major problem in using catch-effort data in fisheries management is that measurement errors are present in both the catch and effort variables. Gould, Stefanski, and Pollock (1997) showed that this could introduce considerable bias into the estimates, but that the maximum likelihood estimates were the most robust to measurement error.

Several other approaches to studying population changes are possible. Rather than estimating abundance directly, Richards and Schnute (1992) showed how to estimate the CPUE under various models that incorporate management effects on the effort variable. Gould and Pollock (1997b) combine catch-effort protocols into a robust design and show by simulations that the maximum likelihood estimators were superior and more flexible than the usual regression estimators.

There is no specialized general purpose software available for catch-effort models, but standard linear and non-linear regression routines could be used.

Gould and Pollock (1997b) showed that SURVIV could be used to estimate model parameters.

6 Summary

The explosion of papers on estimating animal population parameters in the last 20 years reflects the importance of the subject, the increased computing power available, and the increased statistical sophistication of the practitioners. As already noted, the concepts of overdispersion, covariates, quasilikelihood, profile likelihood intervals, random effects models, estimating equations, Horvitz-Thompson estimators, state-space models, generalized linear models, model selection criteria, Bayesian methods, EM algorithm, Monte Carlo Markov Chain methods, and so on, were all bound to eventually invade the subject, though some invasions were unexpected. For example, who would have foreseen the application of martingale and coverage methods to capture-recapture models? One lesson from this is that the training of future scientists in the subject area should not only concentrate on population methodology, but the training also needs to be broadly based with regard to statistics and computing. Bootstrapping and Monte Carlo methods are now essential tools.

One area that has developed substantially is the estimation of survival and related parameters for open populations using capture-recapture. In the past, different models have been used for different types of data depending on whether there are live -recaptures, live resightings or dead recoveries. It may not be appreciated that these distinctions between the models are no longer important. We now have more general models which can combine all types of data thus leading to a greater flexibility of research programs and an increased efficiency of estimation. Such complex models usually have a large number of parameters, so that one is faced with the twin problems of parameter identifiability and model selection, both of which are receiving considerable attention. There has also been substantial progress in the development of goodness of fit tests. As models become more complex, there is a greater need for good model diagnostics combined with good model selection techniques. Residuals, for example, have received little attention in the literature. Instead of using a single "best" model, a more appropriate method of getting a final estimate is to combine estimates from "good" models. However, how to combine them still needs further investigation. Unfortunately the literature describing all this new methodology is getting complex and is not easily accessible at times. If it is going to be more widely used, it needs to be better packaged. The availability of web sites with access to software has been an important development. However, for some applications mentioned in this review, there is still a need for user-friendly software.

In an editorial, North and Nichols (1995, p. 553) note that bird bands (rings) were originally introduced to provide information about birds' movements. However, having swung away from this idea to that of estimating survival parameters, there needs to be a swing back again to methods of spatial analysis. As seen from this review, there has been an upsurge of interest in stratified capture-recapture models. Firstly, there has been the stratified-Petersen method with a single release time and a single recovery time for closed populations, mainly in a fisheries context. Secondly, multiple recaptures with multiple recovery times have been used for studying movement patterns in open populations, particularly with birds. This work needs to be extended using various movement models and different strata based on variables such as age or length rather than just place (Nichols and Kendall, 1995).

An ongoing area of research activity is the investigation of model robustness for each new model developed. Heterogeneity always seems to be present. Clearly other types of model such as random effects models are appearing on the scene and need to be developed. Coupled with new model development there is the need for guidelines with respect to experimental design. For example, adaptive sampling will eventually be used more widely given that information from a pilot study using two-stage sampling can now be used. Such guidelines need to be readily available for capture-recapture studies.

The whole subject area is now becoming too big for one person to keep up with. We recommend that more reviews and expositional articles be written. Perhaps someone might start a journal on the subject!

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APPENDIX

WWW sites where software may be downloaded

http://www.biol.sfu.ca/cmr/index.html : Maintained by E. G. Cooch. Has links to many of the software packages to analyze capture-recapture data.

http://www.mbr.nbs.gov/software.html : Maintained by the Patuxent Wildlife Research Centre and has packages for the analysis of transect data, capture-recapture data, and band-recovery data.

http://www.cs.umanitoba.ca/∼popan/ : Maintained by the Population Analysis Research Group and has packages for the analysis of capture-recapture data and stratified-Petersen experiment.

http://www.im.nbs.gov/tws/cse.html : Maintained by the Wildlife Society and has links to software presented in the Wildlife Bulletin.

http://nhsbig.inhs.uiuc.edu/ : Maintained by the Illinois Natural History Survey and has links to software for a wide range of ecological applications.

http://www.cnr.colostate.edu/∼gwhite/software.html : Maintained by the Department of Fishery and Wildlife Biology and the Colorado Cooperative Fish and Wildlife Unit at Colorado State University. Has links to programs for the analysis of capture-recapture data, transect data, and radio-telemetry data.

http://nmml01.afsc.noaa.gov: Maintained by the National Mammal Laboratory. The distance sampling software package DISTANCE (for line and point transect surveys) may be downloaded from here.

http://www.cnr.colostate.edu/ gwhite/mark/mark.htm : Maintained by Gary White. The package MARK has the capabilities of SURGE but also includes band-recovery, the robust design, the mixture of information models of Barker (1997), and the models of Pradel (1996) involving recruitment.