Estimating animal abundance: review III

Carl J. Schwarz and George A. F. Seber[*]

Abstract

The literature describing methods for estimating animal abundance and related parameters continues to grow. This paper reviews recent developments in the subject over the past seven 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;

[*]Carl J. Schwarz is an Associate Professor, Department of Mathematics and Statistics, Simon Fraser University, Burnaby, BC V5A 1S6, Canada (e-mail: cschwarz@cs.sfu.ca). George A. F. Seber is a Professor, Department of Statistics, Auckland University, Private Bag 92019, Auckland, New Zealand (e-mail: seber@stat.auckland.ac.nz).

Petersen; population index; radio tags; radiotelemetry; relative density; removal methods; senescence; survival estimation; tag loss; tag-migration models; tag-recovery; two-stage sampling.

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 for estimation 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. Standard survey methods such as stratified sampling, post-stratification, size-biased sampling and two-stage sampling can be used. The more recent methods of

adaptive sampling are 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

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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 for obtaining information about the population is to use tagging or marking; this approach is known as the capture-recapture method. In capture-recapture, one collects a series of samples. Animals in the first sample are tagged and are then released back into the population. The second sample then has tagged (i.e. recaptured) and untagged animals. If the process stops there so that we have just two samples of respective sizes n_1 and n_2, and m_2 recaptures, a very simple but famous estimator of the population size N for a closed population called the Petersen estimator (Seber, 1982 and 1992) is available. This estimator, which is referred to several times in this paper, is obtained by equating the population proportion of tagged (n_1/N) in the population with the proportion of tagged in the second sample (m_2/n_2) to get $\hat{N} = n_1 n_2 / m_2$. If we collect more than two samples we can tag the untagged animals in the second sample and then release all the animals again. This process is repeated using unique tags for each individual. At the end of the experiment, each animal that was caught during the experiment will have a capture history. For example, the history 01001 corresponds to an individual that was caught in the second and fifth samples only. Such methods have been 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. A related problem that is receiving increasing attention is that of choosing an appropriate model from a range of possible models.

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, observer bias may occur. 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, individuals may be disturbed before they are seen or one may even see the individuals in groups. In tagging experiments animals may lose theirtags. Tags may be overlooked or may not be return ed when found by the general public. 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 at modifying the models to allow for such departures.

This paper follows a book and two previous reviews (Seber, 1982, 1986 and 1992). In this third review our scope is once again wider than just abundance and includes related parameters such as survival rates. In putting this review together we have extensively used the Current Index to Statistics Extended Database (American Statistical Association/Institute of Mathematical Statistics, 1997), the Science Citation Index (Institute for Scientific Information, 1997), and Biological Abstracts on Compact Disc (Biological Abstracts, Inc, 1998). Such searches may be difficult due to the wide variety of key words used for the same topic. We therefore 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 that has become available, but also because of the increasing number of applications of the abundance methodology to different animal populations. Our primary aim is to review new methodology and select some of the many applications for illustration, particularly those which pay close attention to 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 (1999).

2   Statistical developments

In this section we take a broad brush view of some useful statistical developments. More detail is given later in this work.

Some populations, such as those of 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 direc-

tion of the sampling, is a promising method for handling such populations. This method is essentially a cluster sampling technique and it has begun to be used in a variety of ways. The reader is referred to Seber (1997, 1998) for a brief introduction, or to Thompson and Seber (1996) for a detailed exposition. Salehi and Seber (1997a) provide a without-replacement adaptive scheme for reducing the amount of sampling effort. 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.

Size-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 of individual catches and effort 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 then estimated by multiplying the total effort by the CPUE. Hoenig et al. (1997) and Pollock et al. (1997) discuss the properties of the two estimators of the CPUE while Hoenig et al. (1993) give methods for estimating the sportsfishing effort. These papers should be consulted for further references.

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 nonzero 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 from any design, $E(\sum_{i=1}^{n}(1/p_i)) = N$. 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 (1998), and Borchers et al. (1998) also estimate the p_i by applying logistic regression to line transect data from double counts (simultaneous counts from two observers). These three papers, that are referred to again later, incorporate an extensive array of very general models that represent a major breakthrough in line transect methodology.

Logistic regression can also be used for modeling spatial distributions. For example, Osborne and Tigar (1992) and Buckland and Elston(1993) use a generalized linear model with a logistic link function to model a dependent variable which represents presence/absence or a measure of abundance of the species under consideration. This variable is recorded for all, or just for a random selection of, sites. They also incorporate habitat and other spatial covariates to allow for a hetergeneous environment. Augustin, Mugglestone

and Buckland (1996) go one step further and model the spatial autocorrelation as well. 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.

Likelihood methods are a major tool in population studies and, unless otherwise stated, the likelihoods referred to in this paper are invariably a product of multinomial distributions. However, quasi-likelihood has now entered the abundance arena as well. 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), quasi-likelihood 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 novel Monte Carlo methods, it is now possible to sample from the posterior distribution without having to actually obtain 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 problem, we can sometimes use the Gibbs sampler whereby we can sample from the multivariate posterior

and its marginals by simply drawing values from a sequence of univariate conditional distributions. When the Gibbs sampler is impractical, more flexible sampling methods such the Metropolis-Hastings algorithm are also available. The theory behind these approaches is referred to as Markov chain Monte Carlo (MCMC). 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 Spiegalhalter (1996), and Tanner (1994). Manly (1997, Chapter 15) provides a helpful discussion using simple capture-recapture examples, and Brooks, Catchpole and Morgan (in press) provide an excellent background for analyzing recapture data from open populations. 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 in this area (e.g. Quang and Becker, 1996).

Bootstrapping (Efron and Tibshirani, 1993) 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 using the bootstrap 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 into estimation.

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 in providing estimates of population parameters even though in many cases experiments only address a single demographic quantity at a time, e.g. survival rate. However, population management requires additional information usually in the form of a Leslie matrix. This matrix relates the age structure 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) 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 was earlier pointed out by Seber (1986, 1992), the negative binomial distribution is a popular model 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 and Gavaris, 1993a; Smith and Page, 1996;

and the readable summary by Smith, 1996). Covariates and model based estimates can also be used (Smith, 1990). 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 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 covari-

ates affecting the probability of sighting an animal 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 for 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 "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 and others have developed a software package called Distance which is documented by Thomas et al. (1998) and Thomas (1999) and is available from the last site given in Appendix 1. This package was shown by Cassey and McArdle (in press) to perform well under an extensive range of simulated conditions. 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 for 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; Barlow (1995) who compared strip and line transects to estimate the abundance of cetaceans and found that both methods worked well; and Cassey et al. (in press) who showed that distance sampling based on random transects performed well compared with several common alternatives in estimating the size of a known banded population of wild birds in regenerating bush. Using a half-normal detection function, Karunamuni and Quinn (1995) seem to have developed the first Bayesian methods for 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., $g(0) = 1$. We note that the first assumption is not critical if the second assumption is true because of the role of pooling robustness. 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 methodology and mentioned the use of kernel estimates for estimating the density function associated with $g(y)$. 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 $g(y)$ remains 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 such as the size s of the object can also be incorporated. For example the detection function can now take on the bivariate form $g(y, s)$ and some supporting theory is described by Buckland et al. (1993a, p. 81). Quang and Becker (1996) use a parametric logistic model involving other covariates as

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well, while Chen (1996b) uses a kernel method for estimating the bivariate density associated with $g(y, s)$. Mack and Quang (1998) also adopt a kernel approach.

Instead of just having multiple observers, another approach is to use observers on different "platforms" such as on different ships or different planes. Some history related to 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 animals moving and $g(0) \neq 1$, 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). An important problem in all these applications is that of measurement error (Chen, 1998).

In concluding this section we briefly consider distance methods based on the point transect, otherwise known as the variable circular plot survey. Here the line becomes a point and one measures the distance y of any animal seen from the point. 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 in a Kenyan village. Bedrick (1994) and Hirst (1994) both derived confidence intervals for the population size 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 equal probability of capture of marked and unmarked animals. 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.

There does not appear to be a specialized computer package available to compute estimates for the removal model, except for Program CAPTURE described at the end of Section 3.2 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 nonlinear least squares routine available in many statistical packages such as PROC NLIN in SAS. 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.

2.5   Radio-tagging

Radio tag 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 Rivest, Couturier and Crépeau, 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 4.2. Another approach is to try and model the radio-tracking

data using some sort of spatial process, for example Worton (1995c) used an Ornstein-Uhlenbeck diffusion process. This whole area requires further research.

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 of home range but notes that these measures are sensitive to outliers, irrespective of the distribution of the inner points. He recommends a convex hull peeling method for indicating the general shape of the home range. An alternative approach is to fit a bivariate distribution to the animal's relative frequency of using each point in the area, which is known as the 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 in 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 errors tend 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 similar to the compositional analysis approach proposed by Aitchison (1986), 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. Samuel and Kenow (1992) showed how triangulation error can lead to habitat misclassification and developed a subsampling technique to overcome some of the problems. 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 estimation 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). They use a general bivariate contingency table approach based on the EM algorithm that allows for both censored and truncated data. By treating broods as clusters, Flint et al. (1995) and Flint, Sedinger and Pollock (1995) extend the Kaplan-Meier and Mayfield methods for 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 whether 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 an alternative to the nonparametric Kaplan-Meier methods and the fully parametric methods used for smoothing the survival function. A typical assumption is that all radios are functioning and that all tagged alive animals can be located. Bunck, Chen and Pollock (1995) show how to modify some of the previously mentioned estimators to allow for uncertain relocation, and Pollock et al. (1995) show how to combine the Cormack-Jolly-Seber and Kaplan-Meier methods for 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; this is known as the 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 of the methods that use radio-tagging to estimate population size use simple Petersen estimators (see Section 1) or a combination of Petersen estimators (mark-resight methods) as outlined, for example, by White and Garrott (1990) and Neal et al. (1993). White (1993) compares several such estimators using simulation. The key difference between radio tagging and mark-recapture methods is that in radio tagging studies unmarked animals are usually not captured. Bowden and Kufeld (1995) construct some new confidence intervals of population size with better coverage than the usual one based on the asymptotic normality of the Petersen estimate. 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 to estimate population size. 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. Sometimes researchers have 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 as a measure of population density. 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 and that the rate of proportionality is (hopefully) constant. As noted in Section 1, if the index doubles we would like to be able to infer that the population has doubled. Examples of surveys that use some of the above indices to estimate population densities 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 whereby birds are captured in an almost invisible hanging net. 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 Bennetts (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 their method with the usual ANOVA or Poisson regression methods. Although the ANOVA method is fairly robust against departures from the usual assumptions such as normality, it is limited in the parameter comparisons that can be made. The Poisson regression method performed poorly even when corrected for overdispersion.

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 theory for the 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 Capture-recapture methods for closed population models

3.1 Single Recaptures - the Petersen estimator

The Petersen estimator mentioned in Section 1 is the simplest estimator used in mark-recapture. It has been used extensively this century to estimate population size for animal and human populations ; in the latter case it is also known as a dual-list method. Fienberg (1992), Pollock, Turner and Brown (1994), and Chao and Tsay (1998) present reviews of its use to estimate census undercounts. Rockwood and Whiting (1992) present an example where the Petersen method is used 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) illustrate the use of 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 pre-

viously in Section 2.1. 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 developing 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 (1998, 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 to 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

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space to remove the effects of heterogeneity but was only able to obtain the maximum likelihood estimates for the case when the numbers 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 out-of-range estimates of nuisance parameters such as 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 the computer package SPAS (Arnason et al., 1996), except that users must exercise caution as estimates may be out of the parameter space (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, more efficient 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 such as 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 defined earlier in Section 1 and developed in the previous section have a variety of uses. For example, with open populations, they have 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). In 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. This is known as the 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 to departures from underlying assumptions and the efficiency of estimation.

Seber (1992) described eight 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 for N, 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 a likelihood approach and suggest a Bayesian alternative. 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} (Seber, 1992). 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 sources of bias 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 eight 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 for estimating N 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. It was originally used to provide a method of estimating the number of species (i.e. groups) in a population (cf. Bunge and Fitzpatrick, 1993, for a brief review). Using this idea, Anne Chao and colleagues (Chao, Lee and Jeng, 1992; Lee and Chao, 1994) have developed estimators of N for all eight models, as discussed in Seber (1992). Lee and Chao (1994) assumed that the relative efforts used for collecting 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 in the population.

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 derived the "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 (1994a) 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. (1999) 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 eight 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 N in 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 for N is less efficient than the maximum likelihood estimator (Wilson, 1992: see also Wilson and Anderson, 1995). However, Becker and Heyde (1990) derived the max-

imum 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 and therefore the estimator was not fully efficient: it also had some other undesirable features such as being affected by behavioral effects in the capture probabilities (cf. 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. 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 using the M_t model is to detect 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). The 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 is 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 (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. Evans et al. also introduce the first log-linear model to fit 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 statistically 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. Carriquiry and Fienberg (1998a,b) discuss recent developments in log-linear and Rasch models and illustrate their application to capture-recapture models.

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When applying capture-recapture methods in 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 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 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, nine 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 whether 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 failure to account for the movement patterns of the individuals.

The program CAPTURE (Rexstad and Burnham, 1992) is a comprehensive package for fitting many of the models described above that have an associated likelihood and 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 to estimate the parameters in these models. Some special purpose software (e.g. for 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 may be released, in which case subsequent sightings include both collared and uncollared animals, but no further animals are collared. The 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 approach 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

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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 have 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) examined the robustness of this method to violations of assumptions and found that large biases could occur if the population is open, or if 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 particular, investigators have concentrated 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 have been published 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.

We now discuss each of the research areas mentioned above.

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 were 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 to vary among groups. Cormack and Skalski (1992) use a log-linear analysis of the returns from coded-wire tagged fish that could also 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 additional information about tag reporting from a creel survey or port sampling. This allows for the separate estimation of the natural and fishing mortalities. A Bayesian approach for handling band-recovery models is given by Brooks, Catchpole and Morgan (in press).

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, there are problems in maximizing the likelihood function associated with 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. Also, Catchpole and Morgan (1994) obtained explicit conditions that determine when estimates on the boundary of the parameter space will occur. Earlier, Morgan and Freeman (1989) showed how to solve this problem using a more general formulation, namely by allowing calendar-year dependence of survival rates for first year birds. They illustrated the approach with a number of examples (Freeman and Morgan, 1990). Freeman and Morgan (1992) extended this model by also allowing calendar year dependence of the reporting 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 non-identifiability problems, and were able to identify which were the models with parameter redundancies 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 problematic in these models because of the problems in model fitting and because of parameter estimates 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). However, The unique estimates from the Bayesian analysis are, however, heavily dependent on the priors in the parameter-redundant cases (Brooks et al. , in press).

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 patterns are often confounded with the distribution of recovery efforts. In recent years, there has been some work that addresses the development of estimation methods for movement rates using capture-recapture rates, but most of this has taken place in the context of multiple-capture models of which the single recovery modle is a special case. The simplest types of studies have a single release time and a single recovery period. The stratified-Petersen method, discussed earlier, can be used to estimate movement rates among the strata.

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. A different approach, however, 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. Through a reward banding study in which people are rewarded for returning bands, Nichols et al. (1995) showed that geographic location had a large effect on reporting rates. 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 methods for 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, 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) used a single release to apportion mortality among different fishing regions for the Atlantic cod, but had to make several strong assumptions about the model and parameters 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 that 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 generalized linear model 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 if they are 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 have been realized and presented at subsequent EURING meetings. There are, of course, always special variations on the general model. For example to get around the 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 an ANOVA model. A Bayesian approach to CJS models is given by Brooks, Catchpole and Morgan (in press).

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. ,to appear). 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 (1996a) 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, 1999) 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 on parameter estimates. Lebreton, Reboulet and Banco (1993) presented a comparative review of software but, given the speed at which software changes, the review is now dated.

The 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. (1998) develop necessary and sufficient conditions to identify parameter redundancy in recapture and recovery data and Catchpole, Morgan and Freeman (1998) demonstrate how to estimate the identifiable parameters. Morgan, Freeman and Catchpole (1995) list several common models, together with a statement of whether of whether or not they are parameter-redundant and,if so, their rank deficiency. This latter quantity tells us how many contraints are needed to get unique maximum likelihood estimates. 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. Brooks, Catchpole and Morgan (in press) recommend a Bayesian model-averaging approach. Norris and Pollock (1996b) discuss a bootstrap approach in closed populations but also include some recommendations for use with open populations. For some related developments in model selection the reader is referred to Raftery, Madigan and

Hoeting (1997) and Hoeting et al. (1999).

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 to obtain 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 into the model. When emigration is permanent, mortality is not distinguishable from permanent emigration. However, there may be subpopulations 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 in the area. 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 capture probabilities

on the estimates of survival is well known (cf. Seber, 1986 p. 277), 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 that is sometimes violated 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. on the neck band loss rate using the above methodologies is given by Spendelow et al. (1994).

4.2.2 Breeding proportions and senescence

Not only is population size an important parameter to estimate in the study of a population, but we may also wish to estimate the proportion of the population that breeds. Another aspect of a population's dynamics is the decline of survival with age, or senescence. We put these two somewhat unrelated topics together here as they are short and can be studied using capture-recapture.

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

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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 the animal 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 for parameter estimation. The proportion of animals returning to breed can also be estimated using the Robust Design as discussed later in Section 4.4.

Senescence has been theorized to occur for many species, but previous investigations have used life table methods requiring very restrictive assump-

tions or have used other methods requiring capture probabilities equal to 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 in 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 on the location of the animal 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 have 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 any movement 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 considering a random walk approach to investigate dispersal of grasshoppers using multiple resightings.

It should be stressed that movement models also include general multistrata 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 on 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 about, for example, population genetics and evolutionary ecology. The probabilities of transitions between individual states, such as reproductive status, weight classes and so on, can be estimated and compared. Recapture and recovery data can also be incorporated into the multi-strata model 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 collected in movement studies such as those described thus far.

Dupuis (1995) developed a Bayesian approach to estimate the population parameters in these movement models and showed that if the problem 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 parameters. 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 while 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. (1998) who extended the work by Catchpole, Freeman, and Morgan (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. These 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; the authors note that recapture data are the most appropriate source of information 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, in addition to survival, abundance is also of interest. This often requires that the number of unmarked animals be recorded at each sampling occasion and that unmarked animals be 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 Pol-

lock et al. (1990). An outstanding problem with the Jolly-Seber model is related to the way in which 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 the parameter space and allows simple testing and modeling of the recruitment parameters. Burnham (1997) extended Burnham (1991) to derive another version of a likelihood associated with the JS model and also derived distributions of the sufficient statistics in the special cases of no death or no recruitment. Pradel (1996a) developed methodology to estimate the recruitment and population growth rate by reading capture histories "backwards" (cf. Nichols et al., 1986) which treats "survival" (including emigration) and "recruitment" (including birth and immigration) in a symmetric fashion. Pradel (in press) has developed a general likelihood function for the parameters in his model 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 estimation of the abundance and "birth" parameters in a JS model. 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 (see Section 3.2), Hwang and Chao (1995) examined the effects of unequal catchability on the estimates of abundance and proposed new estimators that are less biased 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 heterogeneity in the capture probabilities.

A variety of hypotheses can be tested for the JS model and these are documented in Seber (1986, 1992). Brawn, Karr and Nichols (1995) exam-

ined a nine year record of 25 species of neotropical birds and investigated the relationship between body size, phylogenetic affiliation, foraging guild and social behavior and estimates from a JS model of survival rate, population size, and recruitment using linearised regressions. 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

The 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 treating 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, 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 on time to look for time trends in the population size.

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) developed likelihood theory for the case where the population during the secondary periods is closed, while Schwarz and Stobo (1997) extended the likelihood theory to the case where 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 appeared 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 which assume that the population is in equilibrium with respect to the various processes such as recruitment and removal still occasionally surface. Rather than try to survey the fisheries literature, we will concentrate here on methodological improvements achieved 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, least squares regression methods have been used with this protocol because of the difficulties in computing the estimates. These 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 gen-

eral 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 maximum likelihood estimates from the underlying multinomial model could be easily computed with modern software and were consistently less biased and more precise than least squares estimates from the linear regression model. Reed and Simons (1996b) used the Kalman filter to estimate the parameters of the catch-effort model but recommended that their methodology be primarily used to estimate the CPUE.

Various assumptions underlying catch-effort models can be violated. For example, catchability can vary in many ways (cf. Seber, 1982, p. 81). 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 on the estimates. A simulation study to investigate the effects of other violations of assumptions on the estimators of population size in crab and lobster fisheries was conducted by Miller and Mohnn (1993). They showed that some of the biases in these estimates 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 regardless 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. An-

other 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 of abundance and catchability, 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) combined catch-effort protocols into a robust design and showed by simulations that the maximum likelihood estimators of abundance and catchability were superior and more flexible than the ordinary least squares estimators.

There is no specialized general purpose software available for catch-effort models, but standard linear and nonlinear regression routines can be used to analyze data from catch-effort experiments. 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 that have appeared in the last 20 years reflects the importance of the subject, the increased computing power available, and the increased statistical sophisti-

cation of practitioners. As already noted, the concepts of overdispersion, covariates, quasi-likelihood, 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 rather needs to be broadly based regarding to statistics and computing. Bootstrapping and Monte Carlo methods are now essential tools for practitioners in animal ecology.

One area that has developed substantially is the estimation of survival and related parameters for open populations using capture-recapture approaches. In the past, different models were used for different types of data depending on whether there were live recaptures, live resightings or dead recoveries. However, the distinctions between the models are no longer important. We now have more general models which can be fitted to a combined set of all types of data thus leading to 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 in the literature. There also has been substantial progress in the development of goodness of fit tests for the various models

used. As models become more complex, there is a greater need for good model diagnostics combined with good model selection techniques. Residual analyses, for example, have received little attention in the literature. Instead of using a single "best" model, an appropriate alternative method for getting a final estimate is to combine estimates from several "good" models known as "model averaging". However, how to combine models still needs further investigation. 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. First, the stratified-Petersen method with a single release time and a single recovery time for closed populations was mainly presented in a fisheries context. Second, 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 in the model parameters

always seems to be present. Other types of model such as random effects models are now being used in ecological studies and need to be expanded and adopted to better suite the problems that practitioners encounter. In addition, 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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REFERENCES

AEBISCHER, N. J., ROBERTSON, P. A. and KENWARD, R. E. (1993). Compositional analysis of habitat use from radio-tracking data. *Ecology* **74** 1313–1325.

AGRESTI, A. (1994). Simple capture-recapture models permitting unequal catchability and variable sampling effort. *Biometrics* **50** 494–500.

AITCHISON, J. (1986). *The Statistical Analysis of Compositional Data*. Chapman and Hall: London.

ALEXANDER, H. M., SLADE, N. A. and KETTLE, W. D. (1997). Application of mark-recapture models to estimation of the population size of plants. *Ecology* **78** 1230–1237.

ALPIZAR-JARA, R. and POLLOCK, K. H. (1996). A combination of line transect and capture-recapture sampling model for multiple observers in aerial survey. *Journal of Ecological and Environmental Statistics* **3** 311–327.

AMERICAN STATISTICAL ASSOCIATION/INSTITUTE OF MATHEMATICAL STATISTICS (ASA/IMS) (1997). Current Index to Statistics Extended Database [computer file]. Author: Hayward, CA.

ANANDA, M.M.A. (1997). Bayesian method for mark-resighting surveys. *Communications in Statistics - Theory and Methods* **26** 685–697.

ANDERSON, C. S. (1995). Measuring and correcting for size selection in

electrofishing mark-recapture experiments. *Transactions of the American Fisheries Society* **124** 663–676.

ANDERSON, D. R. and SOUTHWELL, C. (1995). Estimates of macropod density from line transect surveys relative to analyst expertise. *Journal of Wildlife Management* **59** 852–857.

ANDERSON, D. R., BURNHAM, K. P. and WHITE, G. C. (1994). AIC model selection in overdispersed capture-recapture data. *Ecology* **75** 1780–1793.

ANDERSON, D. R., WHITE, G. C. and BURNHAM, K. P. (1995). Some specialized risk assessment methodologies for vertebrate populations. *Environmental and Ecological Statistics* **2** 95–115.

ANDERSON, D. R., WOTOWA, M. A. and REXSTAD, E. A. (1993). Trends in the analysis of recovery and recapture data. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 373–386. Birkhäuser Verlag: Basel, Switzerland.

ANDERSON-SPRECHER, R. (1994). Robust estimates of wildlife location using telemetry data. *Biometrics* **50** 406–416.

ANGANUZZI, A. A. and BUCKLAND, S. T. (1993). Post-stratification as a bias reduction technique. *Journal of Wildlife Management* **57** 827–834.

ANGANUZZI, A. A., HILBORN, R. and SKALSKI, J. R. (1994). Estimation of size selectivity and movement rates from mark-recovery data. *Canadian Journal of Fisheries and Aquatic Sciences* **51** 734–742.

ARNASON, A. N. (1972). Parameter estimation from mark-recapture experiments on two populations subject to migration and death. *Researches in Population Ecology* **13** 97–113.

ARNASON, A. N. (1973). The estimation of population size, migration rates, and survival in a stratified population. *Researches in Population Ecology* **15** 1–8.

ARNASON, A. N. and SCHWARZ, C. J. (1995). POPAN-4: enhancements to a system for the analysis of mark-recapture data from open populations. *Journal of Applied Statistics* **22** 785–799.

ARNASON, A. N. and SCHWARZ, C. J. (in press). Using POPAN-5 to analyze banding data. *Bird Study*, to appear.

ARNASON, A. N., SCHWARZ, C. J. and GERRARD J. M. (1991). Estimating closed population size and number of marked animals from sighting data. *Journal of Wildlife Management* **55** 716–730.

ARNASON, A. N., KIRBY, C. W., SCHWARZ, C. J. and IRVINE, J. R. (1996). Computer analysis of marking data from stratified populations for estimation of salmonid escapements and the size of other populations. *Canadian Technical Report in Fisheries and Aquatic Sciences* No. 2106. National Research Council. Canada.

AUGUSTIN, N. H., MUGGLESTONE, M. A. and BUCKLAND, S. T. (1996). An autologistic model for the spatial distribution of wildlife. *Journal of Applied*

Ecology **33** 339–347.

BAILLIE, S. R. (1995). Uses of ringing data for the conservation and management of bird population: a ringing perspective. *Journal of Applied Statistics* **22** 967–987.

BANNEHEKA, S. G., ROUTLEDGE, R. D. and SCHWARZ, C. J. (1997). Stratified two-sample tag-recovery census of closed populations. *Biometrics* **53** 1212–1224.

BARKER, R. J. (1992). Effect of heterogeneous survival on bird-banding model confidence interval coverage rates. *Journal of Wildlife Management* **56** 111–116.

BARKER, R. J. (1995). Open population mark-recapture models including ancillary sightings. Ph.D. Thesis, Massey University, Palmerston North, New Zealand.

BARKER, R. J. (1997). Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics* **53** 657–668.

BARKER, R. J. and SAUER, J. R. (1992). Modeling population change from time series data. In *Wildlife 2001: Populations*, D. R. McCullough and R. H. Barrett, (eds), 182–194. Elsevier Applied Science: New York.

BARKER, R. J., HINES, J. E. and NICHOLS, J. D. (1991). Effect of hunting on annual survival of gray ducks in New Zealand. *Journal of Wildlife Management* **55** 260–265.

BARKER, R. J., SAUER, J. R. and LINK, W. (1993). Optimal allocation of point-count sampling effort. *Auk* **110** 752–758.

BARLOW, J. (1995). The abundance of cetaceans in California waters. 1. Ship surveys in summer and fall of 1991. *Fishery Bulletin* **93** 1–14.

BARLOW, J. and CLAPHAM, P. J. (1997). A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecology* **78** 535–546.

BARROWMAN, N. J. and MYERS, R. A. (1996). Estimating tag-shedding rates for experiments with multiple-tag types. *Biometrics* **52** 1410–1416.

BAYLEY, P. B. (1993). Quasi-likelihood estimation of marked fish recapture. *Canadian Journal of Fisheries and Aquatic Sciences* **50** 2077–2085.

BECKER, E. F. (1991). A terrestrial furbearer estimator based on probability sampling. *Journal of Wildlife Management* **55** 730–737.

BECKER, N. G. (1984). Estimating population size from capture-recapture experiments in continuous time. *Australian Journal of Statistics* **26** 1–7.

BECKER, N. G. and HEYDE, C. C. (1990). Estimating population size from multiple recaptures experiments. *Stochastic Processes and their Applications* **36** 77–83.

BEDRICK, E. J. (1994). Maximum-likelihood estimation for the removal method. *Canadian Journal of Statistics* **22** 285–293.

BESAG, J., GREEN, P., HIGDON, D. and MENGERSEN, K. (1995). Bayesian computation and stochastic systems (with discussion). *Statistical Science* **10** 3–66.

BIOLOGICAL ABSTRACTS, Inc. (1998). Biological Abstracts on Compact Disc [computer file]/BIOSIS. Author: Philadelphia.

BISHIR, J. and Lancia, R. A. (1996) On catch-effort methods of estimating animal abundance. *Biometrics* **52** 1457–1466.

BLONDEL, J., PRADEL, R. and LEBRETON, J.-D. (1992). Low fecundity insular blue tits do not survive better as adults than high fecundity mainland ones. *Journal of Animal Ecology* **61** 205–213.

BLUMS, P., MEDNIS, A., BAUGA, I., NICHOLS, J. D. and HINES, J. E. (1996). Age-specific survival and philopatry in three species of European ducks: a long-term study. *Condor* **98** 61–74.

BOLFARINE, H., LEITE, J. G. and RODRIGUES, J. (1992). On the estimation of the size of a finite and closed population. *Biometrical Journal* **34** 577–593.

BORCHERS, D. L., ZUCCHINI, W. and FEWSTER, R. M. (1998). Mark-recapture models for line transect surveys. *Biometrics* **54** 1207–1220.

BORCHERS, D. L., BUCKLAND, S. T., GOEDHART, P. W., CLARKE, E. D. and CUMBERWORTH, S. L. (1998). Horvitz-Thompson estimators for double-platform line transect surveys. *Biometrics* **54** 1221–1237.

BOULANGER, J. G. and KREBS, C. J. (1996). Robustness of capture-recapture estimators to sample biases in a cyclic snowshoe hare population. *Journal of Applied Ecology* **33** 530–542.

BOWDEN, D. C. and KUFELD, R. C. (1995). Generalized mark-sight population-size estimation applied to Colorado moose. *Journal of Wildlife Management* **59** 840–851.

BRAWN, J. D., KARR, J. R. and NICHOLS, J. D. (1995). Demography of birds in a neotropical forest: effects of allometry, taxonomy, and ecology. *Ecology* **76** 41–51.

BROOKS, S. P., CATCHPOLE, E. A. and MORGAN, B. J. T. (in press). Bayesian animal survival estimation. *Statistical Science*, to appear.

BROOKS, S. P., CATCHPLOLE, E. A., MORGAN, B. J. T. and B ARRY, S.C. (in press). On the Bayesian analysis of ring-recovery data. *Biometrics*, to appear.

BROWNIE, C., ANDERSON, D. R., BURNHAM, K. P. and ROBSON, D. S. (1985). *Statistical Inference from band-recovery data - a handbook,* 2nd edition. U.S. Fish and Wildlife Service, Resource Publication No. 156. U.S. Department of the Interior: Washington, D.C.

BROWNIE, C., HINES, J. E., NICHOLS, J. D., POLLOCK, K. H. and HESTBECK, J. B. (1993). Capture-recapture studies for multiple strata including non-Markovian transition probabilities. *Biometrics* **49** 1173–1187.

BUCKLAND, S. T. (1992a). Effects of heterogeneity on estimation of probability of detection on the trackline. *Report of the International Whaling Commission* **42** 569–573.

BUCKLAND, S. T. (1992b). Fitting density functions with polynomials. *Applied Statistics* **41** 63–76.

BUCKLAND, S. T. (1994). The principles and practice of large-scale wildlife surveys. *Transactions of the North American Wildlife and Natural Resource Conference* **59** 149–158.

BUCKLAND, S. T. and ELSTON, D. A. (1993). Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* **30** 478–495.

BUCKLAND, S. T. and TURNOCK, B. J. (1992). A robust line transect method. *Biometrics* **48** 901–909.

BUCKLAND, S. T., BURNHAM, K. P. and AUGUSTIN, N. H. (1997). Model selection: an integral part of inference. *Biometrics* **53** 603–618.

BUCKLAND, S. T., CATTANACH, K. L. and ANGANUZZI, A. A. (1992). Estimating trends in abundance of dolphins associated with tuna in the eastern tropical Pacific. *Fishery Bulletin* **90** 1–12.

BUCKLAND, S. T., AHMADI, S., STAINES, B. W., GORDON, I. J. and YOUNGSON, R. W. (1996). Estimating the minimum population size that allows a given annual number of mature red deer stags to be culled sustainably. *Journal of Applied Ecology* **33** 118–130.

BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P. and LAAKE, J. L. (1993a). *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall: London.

BUCKLAND, S. T., BREIWICK, J. M., CATTANACH, K. L. and LAAKE, J. L. (1993b). Estimated population size of the California gray whale. *Marine Mammal Science* **9** 235–249.

BUNCK, C. M. and POLLOCK, K. H. (1993). Estimating survival of radio-tagged birds. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 51-63. Birkhäuser Verlag: Basel.

BUNCK, C. M., CHEN, C. L. and POLLOCK, K. H. (1995). Robustness of survival estimates from radiotelemetry studies with uncertain relocation of individuals. *Journal of Wildlife Management* **59** 790–794.

BUNGE, J. and FITZPATRICK, M. (1993). Estimating the number of species: a review. *Journal of the American Statistical Association* **88** 364–373.

BURNHAM, K. P. (1991). On a unified theory for release-resampling of animal populations. In *Proceedings of 1990 Taipai Symposium in Statistics*, M. T. Chao and P. E. Cheng (eds), 11-36. Institute of Statistical Science, Academia Sinica: Taipei, Taiwan.

BURNHAM, K. P. (1993). A theory for the combined analysis of ring recovery and recapture data. In *Marked Individuals in the Study of Bird Populations,* J.-D. Lebreton and P. M. North (eds), 199-213. Birkhäuser Verlag:

Basel.

BURNHAM, K .P. (1997). Distributional results for special cases of the Jolly-Seber model. *Communications in Statistics - Theory and Methods* **26** 1395–1409.

BURNHAM, K. P. (in press). Random effects models in ringing and capture-recapture studies. *Bird Study*, to appear.

BURNHAM, K. P. and REXSTAD, E. A. (1993). Modeling heterogeneity in survival rates of banded waterfowl. *Biometrics* **49** 1194–1208.

BURNHAM, K. P., ANDERSON, D. R. and WHITE, G. C. (1994). Evaluation of the Kullback-Leibler discrepancy for model selection in open population capture-recapture models. *Biometrical Journal* **36** 299–315.

BURNHAM, K. P., ANDERSON, D. R. and WHITE, G. C. (1995). Selection among open population capture-recapture models when capture probabilities are heterogeneous. *Journal of Applied Statistics* **22** 611–624.

BURNHAM, K. P., ANDERSON, D. R. and WHITE, G. C. (1996). Meta-analysis of vital rates of the Northern Spotted Owl. *Studies in Avian Biology* **17** 92–101.

BURNHAM, K. P., WHITE, G. C. and ANDERSON, D. R. (1995). Model selection strategy in the analysis of capture-recapture data. *Biometrics* **51** 888–898.

CARRIQUIRY, A. L. and FIENBERG, S. E. (1998a). Loglinear models. In *En-*

cyclopedia of Biostatistics, Volume 3, P. Armitage and T. Colton (eds), 2333–2349. Wiley: New York.

CAROTHERS, A. D. (1979). Quantifying unequal catchability and its effects on survival in an actual population. *Journal of Animal Ecology* **48** 863–869.

CARRIQUIRY, A. L. and FIENBERG, S. E. (1998b). Rasch model. In *Encyclopedia of Biostatistics, Volume 5*, P. Armitage and T. Colton (eds), 3724–3730. Wiley: New York.

CASAGRANDE, D. G. and BEISSINGER, S. R. (1997). Evaluation of four methods for estimating parrot population size. *Condor* **99** 445–457.

CASELLA, G. and GEORGE, E. I. (1992). Explaining the Gibbs sampler. *American Statistician* **46** 167–174.

CASSEY, P., CRAIG, J. L., MCARDLE, B. H., WALTER, B. (in press). Comparison of distance sampling techniques for estimating saddleback density. *Journal of Wildlife Management*, to appear.

CASSEY, P., MCARDLE, B. H. (1999). An assessment of distance sampling techniques for estimating animal abundance. *Environmetrics* **10** 261–278.

CASTELLI, P. M. and TROST, R. E. (1996). Neck bands reduce survival of Canada geese in New Jersey. *Journal of Wildlife Management* **60** 891–898.

CATCHPOLE, E. A. (1995). MATLAB: an environment for analyzing ring

recovery and recapture data. *Journal of Applied Statistics* **22** 801–816.

CATCHPOLE, E. A. and MORGAN, B. J. T. (1994). Boundary estimation in ring recovery models. *Journal of the Royal Statistical Society B* **56** 385–391.

CATCHPOLE, E. A. and MORGAN, B. J. T. (1996). Model selection ring-recovery models using score tests. *Biometrics* **52** 664–672.

CATCHPOLE, E. A. and MORGAN, B. J. T. (1997). Detecting parameter redundancy. *Biometrika* **84** 197–196.

CATCHPOLE, E. A., FREEMAN, S. N. and MORGAN, B. J. T. (1993). On boundary estimation in ring recovery models and the effect of adding recapture information. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 215–228. Birkhäuser Verlag: Basel.

CATCHPOLE, E. A., FREEMAN, S. N., and MORGAN, B. J. T. (1995). Modeling age variation in survival and reporting rates for recovery models. *Journal of Applied Statistics* **22** 597–609.

CATCHPOLE, E. A., FREEMAN, S. N. and MORGAN, B. J. T. (1996). Steps to parameter redundancy in age-dependent recovery models. *Journal of the Royal Statistical Society B* **58** 763-774.

CATCHPOLE, E. A., MORGAN, B. J. T. and FREEMAN, S. N. (1998). Estimation in parameter-redundant models. *Biometrika* **85** 462–468.

CATCHPOLE, E. A., FREEMAN, S. N., MORGAN, B. J. T. and HARRIS, M. P.

(1998). Integrated recovery/recapture data analysis. *Biometrics* **54** 33–46.

CHAO, A. (1998). Capture-recapture. In *Encyclopedia of Biostatistics, Volume 1*, P. Armitage and T. Colton (eds), 482–486. Wiley: New York.

CHAO, A. and LEE, S.-M. (1993). Estimating population size for continuous-time capture-recapture models via sample coverage. *Biometrical Journal* **35** 29–45.

CHAO, A. and TSAY, P. K. (1998). A sample coverage approach to multiple-system estimation with application to census undercount. *Journal of the American Statistical Association* **93** 283–293.

CHAO, A, LEE, S.-M., and JENG, S.-L. (1992) Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* **48** 201–216.

CHAO, A., MA, M.-C. and YANG, M. C. K. (1993). Stopping rules and estimation for recapture debugging with unequal failure rates. *Biometrika* **80** 193–201.

CHAO, A., TSAY, P. K., SHAU, W.-Y. and CHAO, D.-Y. (1996). Population size estimation for capture-recapture models with application to epidemiological data. *Proceedings of the American Statistical Association*, Biometrics Section 108–117.

CHAO, A., YIP, P., LEE, M.-L. and CHU, W. (1999). Population size estima-

tion based on estimating functions for closed capture-recapture models. *Journal of Statistical Planning and Inference*, under revision.

CHEN, C-L, POLLOCK, K. H. and HOENIG, J. M. (1998). Combining change-in-ratio, index-removal, and removal models for estimating population size. *Biometrics* **54** 815–827.

CHEN, S. X. (1996a). A kernel estimate for the density of a biological population by using line transect sampling. *Applied Statistics* **45** 135–150.

CHEN, S. X. (1996b). Studying school size effects in line transect sampling using the kernel method. *Biometrics* **52** 1283–1294.

CHEN, S. X. (1998). Measurement errors in line transect surveys. *Biometrics* **54** 899–908.

CLOBERT, J. (1995). Capture-recapture and evolutionary ecology: a difficult wedding! *Journal of Applied Statistics* **22** 989-1008.

CLOBERT, J., LEBRETON, J.-D., ALLAINE, D. and GAILLARD, J. M. (1994). The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. *Biometrics* **50** 375–387.

CLUGSTON, J. P. (1996). Retention of T-bar anchor tags and passive integrated transponders by gulf sturgeons. *North American Journal of Fisheries Management* **16** 682–685.

CONROY, M. J. (1985). Maximum likelihood methods for reporting rates of rings of hunter-shot birds. In *Statistics in Ornithology*, B. J. T. MORGAN and P. M. NORTH (eds), 215–241. Springer-Verlag: New York.

CONROY, M. J. (1995). Comparison of programs MULT, ESTIMATE, and BROWNIE. *Journal of Applied Statistics* **22** 763–773.

CONROY, M. J. and SMITH, D. R. (1994). Designing large-scale surveys of wildlife abundance and diversity using statistical sampling principles. *Transactions of the North American Wildlife and Natural Resources Conference* **59**, 159–169.

CONROY, M. J., WILLIAMS, B. K. and HINES, J. E. (1995). Use of solicited bands and separation of hunting and natural mortality: A comment. *Journal of Wildlife Management* **59** 619–621.

CONROY, M. J., SENAR, J. C., HINES, J. E. and DOMENECH, J. (in press). Development and application of a mark-recapture model incorporating predicted sex and transitory behavior. *Bird Study*, to appear.

COOCH, E. G., PRADEL, R. and NUR, N. (1997). *A Practical Guide to Mark-Recapture Analysis using SURGE - 2nd Edition.* Centre d'Ecologie Fonctionelle et Evolutive - CNRS, Montpellier, France. 134 pp.

CORMACK, R. M. (1992). Interval estimation for mark-recapture studies of closed populations. *Biometrics* **48** 567–576.

CORMACK, R. M. (1989). Log-linear models for capture-recapture. *Biometrics*

45 395–413.

CORMACK, R. M. (1993a). The flexibility of GLIM Analyses of Multiple-recapture or resighting data. In *Marked Individuals in the Study of Bird Populations,* J.-D. Lebreton and P. M. North (eds), 39–49. Birkhäuser Verlag: Basel.

CORMACK, R. M. (1993b). Variances of mark-recapture estimates. *Biometrics* **49** 1188–1193.

CORMACK, R. M. and BUCKLAND, S. T. (1997). Capture-recapture (update). In *Encyclopedia of Statistical Sciences Update Volume 1*, S. Kotz, C. B. Read and D. L. Banks (eds), 79–84. Wiley: New York.

CORMACK, R. M. and SKALSKI, J. R. (1992). Analysis of coded wire tag returns from commercial catches. *Canadian Journal of Fisheries and Aquatic Sciences* **49** 1816–1825.

CRAIG, B. A., NEWTON, M. A., GARROTT, R. A., REYNOLDS III, J. E. and WILCOX, J. R. (1997). Analysis of aerial survey data on Florida manatee using Markov chain Monte Carlo. *Biometrics* **53** 524–541.

CRIST, T. O. and WIENS, J. A. (1995). Individual movements and estimation of population size in darkling beetles (*Coleoptera: Tenebrionidae*). *Journal of Animal Ecology* **64** 733–746.

CROSBIE, S. F. and MANLY, B. F. J. (1985). Parsimonious modeling of capture-mark-recapture studies. *Biometrics* **41** 385–398.

DARROCH, J. N. (1961). The two-sample capture-recapture census when tagging and sampling are stratified. *Biometrika* **48** 241–260.

DARROCH, J. N. and RATCLIFF, D. (1980). A note on capture-recapture estimation. *Biometrics* **36** 149–153.

DAWE, E. G., HEONIG, J. M. and XU, X. (1993). Change-in-ratio and index-removal methods for population assessment and their application to snow crab (*Chionoecetes opilio*). *Canadian Journal of Fisheries and Aquatic Sciences* **50** 1461–1476.

DEMPSON, J. B. and STANSBURY, D. E. (1991). Using partial counting fences and a two-sample stratified design for mark-recapture estimation of an Atlantic salmon smolt population. *North American Journal of Fisheries Management* **11** 27–37.

DEROCHER, A. E. and STIRLING, I. (1995). Estimation of polar bear population size and survival in western Hudson Bay. *Journal of Wildlife Management* **59** 215–221.

DORAZIO, R. M. (1993). Prerelease stratification in tag-recovery with time dependence. *Canadian Journal of Fisheries and Aquatic Sciences* **50** 535–541.

DORAZIO, R. M. and RAGO, P. J. (1991). Evaluation of a mark-recapture method for estimating mortality and migration rates of stratified populations. *Canadian Journal of Fisheries and Aquatic Sciences* **48** 254–260.

DUFOUR, K. W., ANKNEY, C. D. and WEATHERHEAD, P. J. (1993a). Condition and vulnerability to hunting among mallards staging at Lake St. Clair, Ontario. *Journal of Wildlife Management* **57** 209–215.

DUFOUR, K. W., ANKNEY, C. D. and WEATHERHEAD, P. J. (1993b). Nonrepresentative sampling during waterfowl banding - emphasis on body condition. *Journal of Wildlife Management* **57** 741–751.

DUPUIS, J. A. (1995). Bayesian estimation of movement and survival probabilities from capture-recapture data. *Biometrika* **82** 761–772.

EFRON, B. and TIBSHIRANI, R. J. (1993). *An Introduction to the Bootstrap.* Chapman and Hall: London.

ENSIGN, W. E., ANGERMEIER, P. L. and DOLLOFF, C. A. (1995). Use of line-transect methods to estimate abundance of benthic stream fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **52** 213–222.

EVANS, M. A. and BONETT, D. G. (1992). Multiple recapture methods when sampling without replacement in the last occasion. *Communications in Statistics - Theory and Methods* **21** 2609–2624.

EVANS, M. A. and BONETT, D. G. (1993). A constrained Cook-Jacobson model of visibility bias. *Biometrics* **49** 853–859.

EVANS, M. A. and BONETT, D. G. (1994). Bias reduction for multiple-recapture estimators of closed population size. *Biometrics* **50** 388–395.

EVANS, M. A., BONETT, D. G. and MCDONALD, L. L. (1994). A general theory for modeling capture-recapture data from a closed population. *Biometrics* **50** 396–405.

FIENBERG, S. E. (1972). The multiple recapture census for closed populations and incomplete 2^k contingency tables. *Biometrika* **59** 591–603.

FIENBERG, S. E. (1992). Bibliography on capture-recapture modeling with application to census undercount adjustment. *Survey Methodology* **18**, 143–154.

FLINT, P. L., SEDINGER, J. S. and POLLOCK, K. H. (1995b). Survival of juvenile black brant during brood rearing. *Journal of Wildlife Management* **59** 455–463.

FLINT, P. L., POLLOCK, K. H., THOMAS D. and SEDINGER, J. S. (1995a). Estimating prefledging survival: allowing for brood mixing and dependence among brood mates. *Journal of Wildlife Management* **59** 448–455.

FRANCIS, C. M. (1995). Estimating survival rates from recoveries of birds ringed as young: a case study. *Journal of Applied Statistics* **22** 567–577.

FRANKLIN, A. B, ANDERSON, D. R., FORSMAN, E. D., BURNHAM, K. P. and WAGNER, F. W. (1996). Methods for collecting and analyzing demographic data on the Northern Spotted Owl. *Studies in Avian Biology* **17** 2–20.

FREEMAN, S. N. and MORGAN, B. J. T (1990). Studies in the analysis of ring-recovery data. *The Ring* **13** 271–288.

FREEMAN, S. N. and MORGAN, B. J. T. (1992). A modeling strategy for recovery data from birds ringed as nestlings. *Biometrics* **48** 217–235.

FREEMAN, S. N. and NORTH, P. M. (1990). Estimation of survival rates of British and French grey herons. *The Ring* **13** 139–166.

FREEMAN, S. N., MORGAN, B. J. T. and CATCHPOLE, E. (1992). On the augmentation of ring recovery data with field information. *Journal of Animal Ecology* **61** 649–657.

GALLUCCI, V. F., SAILA, S. B., GUSTAFSON, D. J. and ROTHSCHILD, B. J. (1996). *Stock Assessment: Quantitative Methods and Applications for Small-scale Fisheries*. CRC Press: Boca Raton, Florida.

GARDNER, S. N. and MANGEL, M. (1996). Mark-resight population estimation with imperfect observations. *Ecology* **77** 880–884.

GARTHWAITE, P. H., YU, K. and HOPE, P. B. (1995). Bayesian analysis of a multiple-recapture model. *Communications in Statistics - Theory and Methods* **24** 2229–2247.

GELMAN, A., CARLIN, J., STERN, H. and RUBIN, D. B. (1995). *Bayesian Data Analysis*. Chapman and Hall: New York.

GEORGE, E. I. and ROBERT, C. P. (1992). Capture-recapture estimation via Gibbs sampling. *Biometrika* **79** 677–683.

GILKS, W. R., RICHARDSON, S. and SPEIGALHALTER, D. J. (1996). *Markov*

Chain Monte Carlo in Practice. Chapman and Hall: New York.

GODAMBE, V. P. (1985). The foundations of finite sample estimation in a stochastic process. *Biometrika* **72** 419–428.

GOUDIE, I. B. J. (1995). A plant-capture method for achieving complete coverage of a population. *Communications in Statistics - Theory and Methods* **24** 1293–1305.

GOUDIE, I. B. J., POLLOCK, K. H. and ASHBRIDGE, J. (1998). A plant-recapture approach for population size estimation in continuous time. *Communications in Statistics - Theory and Methods* **27** 433–451.

GOULD, W. R. and POLLOCK, K. H. (1997a). Catch-effort estimation of population parameters under the robust design. *Biometrics* **53** 207–216.

GOULD, W. R. and POLLOCK, K. H. (1997b). Catch-effort maximum likelihood estimation of important population parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **54** 890–897.

GOULD, W. R., STEFANSKI, L. A. and POLLOCK, K. H. (1997). Effects of measurement error on catch-effort estimation. *Canadian Journal of Fisheries and Aquatic Sciences* **54** 898–906.

GUNDERSON, D. R. (1993). *Surveys of Fisheries Resources*. Wiley: New York.

HARGROVE, J. W. and BORLAND, C. H. (1994). Pooled population parameter estimates from mark-recapture data. *Biometrics* **50** 1129–1141.

HEIFETZ, J. and FUJIOKA, J. T. (1991). Movement dynamics of tagged sablefish in the northeastern pacific. *Fisheries Research* **11** 355–374.

HEISEY, D.M. and NORDHEIM, E.V.(1995). Modeling age-specific survival in nesting studies, using a general approach for doubly-censored and truncated data. *Biometrics* **51** 51–60.

HELMINEN, H., ENNOLA, K., HIRVONEN, A. and SARVALA, J. (1993). Fish stock assessment in lakes based on mass removal. *Journal of Fish Biology* **42** 255–263.

HESTBECK, J. B. (1995a). Bias in transition-specific survival and movement probabilities estimated using capture-recapture data. *Journal of Applied Statistics* **22** 737–750.

HESTBECK, J. B. (1995b). Population study and management of Atlantic Flyway Canada geese. *Journal of Applied Statistics* **22** 877–890.

HESTBECK, J. B., NICHOLS, J. D. and HINES, J. E. (1992). The relationship between annual survival rate and migration distance in mallards: An example of the time-allocation hypothesis for the evolution of migration. *Canadian Journal of Zoology* **70** 2021–2027.

HESTBECK, J. B., NICHOLS, J. D. and MALECKI, R. A. (1991). Estimates of movement and site-fidelity using mark-resight data of wintering Canada geese. *Ecology* **72** 523–533.

HIBY, A. R. and LOVELL, P. A. (1998). Using aircraft in tandem formation

to estimate abundance of harbor porpoise. *Biometrics* **54** 1280–1289.

HILBORN, R. (1990). Determination of fish movement patterns from tag-recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* **47** 635–643.

HILBORN, R. and WALTERS, C. J. (1992). *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty.* Chapman and Hall: New York.

HINES, J. E. (1994). *MSSURVIV User's Manual.* Patuxent Environmental Sciences Center: Laurel, MD.

HIRST, D. (1994). An improved removal method for estimating animal abundance. *Biometrics* **50** 501–505.

HOENIG, J. M., JONES, C. M., POLLOCK, K. H., ROBSON, D. S. and WADE, D. L. (1997). Calculation of catch rate and total catch in roving surveys of anglers. *Biometrics* **53** 306–317.

HOENIG, J. M., ROBSON, D. S., JONES, C. M. and POLLOCK, K. H. (1993). Scheduling counts in the instantaneous and progressive count methods for estimating sports fishing effort. *North American Journal of Fisheries Management* **13** 723–736.

HOETING, J. A., MADIGAN, D., RAFTERY, A. E. and VOLINSKY, C. T. (1999). Bayesian model averaging: a tutorial. Submitted to *Statistical Science.*

HOOK, E. B. and REGAL, R. R. (1997). Validity of methods for model selection, weighting for model uncertainty, and small sample adjustment in capture-recapture estimation. *American Journal of Epidemiology* **145** 1138–1144.

HUGGINS, R. M. (1989). On the statistical analysis of capture experiments. *Biometrika* **76** 133–140.

HUGGINS, R. M. and YIP, P. S. F. (1997). Statistical analysis of removal experiments with the use of auxiliary variables. *Statistica Sinica* **7** 705–712.

HWANG, W.-D. and CHAO, A. (1995). Quantifying the effects of unequal catchabilities on Jolly-Seber estimators via sample coverage. *Biometrics* **51** 128–141.

INSTITUTE FOR SCIENTIFIC INFORMATION (ISI) (1997). Science Citation Index [computer file]. Author: Philadelphia.

IWGDMF, International Working Group for Disease Monitoring and Forecasting. (1995a). Capture-recapture and multiple-record systems estimation: I. History and theoretical development. *American Journal of Epidemiology* **142** 1047–1058.

IWGDMF, International Working Group for Disease Monitoring and Forecasting. (1995b). Capture-recapture and multiple-record systems estimation: II. Applications in human diseases. *American Journal of Epidemiol-*

ogy **142** 1059–1068.

IRVINE, J. R., R. C. BOCKING, K. K. ENGLISH and LABELLE, M. (1992). Estimating coho salmon *(Oncorhynchus kistuch)* spawning escapements by conducting visual surveys in areas selected using stratified random and stratified index sampling designs. *Canadian Journal of Fisheries and Aquatic Sciences* **49** 1972–1981.

JAMES, F. C., MCCULLOCH, C. E. and WIENDENFELD, D. A. (1996). New approaches to the analysis of population trends in land birds. *Ecology* **77** 13–21.

JENSEN, A. L. (1992). Integrated area sampling and mark-recapture experiments for sampling fish populations. *Biometrics* **48** 1201–1205.

JENSEN, A. L. (1994). Subsampling with mark and recapture for estimation abundance of mobile populations. *Environmetrics* **5** 191–196

JOHANNESEN, E., ANDREASSEN, H. P. and STEEN, H. (1997). Effect of radiocollars on survival of root voles. *Journal of Mammalogy* **78** 638–642.

JOHNSON, S. R., SCHIEK, J. O. and SEARING, G. F. (1995). Neck band loss rates for lesser snow geese. *Journal of Wildlife Management* **59** 747–752.

KARANTH, K. U. (1995). Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture. *Biological Conservation* **71** 333–338.

KARUNAMUNI, R. J. and QUINN II, T. J. (1995). Bayesian estimation of animal abundance for line transect sampling. *Biometrics* **51** 1325–1337.

KENDALL, W. L. and NICHOLS, J. D. (1995). On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* **22** 751–762.

KENDALL, W. L. and POLLOCK, K. H. (1992). The robust design in capture-recapture studies: A review and evaluation by Monte Carlo simulation. In *Wildlife 2001 Populations*, D. R. McCullough and R. H. Barrett (eds), 31–43. Elsevier: London.

KENDALL, W. L., NICHOLS, J. D. and HINES, J. E. (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* **78** 563–578.

KENDALL, W. L., PETERJOHN, B. G. and SAUER, J. R. (1996). First-time observer effects in the North American Breeding Bird Survey. *Auk* **113** 823–829.

KENDALL, W. L., POLLOCK, K. H. and BROWNIE, C. (1995). A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* **51** 293–308.

KINGSOLVER, J. G. and SMITH, S. G. (1995). Estimation selection on quantitative traits using capture-recapture data. *Evolution* **49** 384–388.

KREMENTZ, D. G., BARKER, R. J. and NICHOLS, J. D. (1997). Sources of

variation in waterfowl survival rates. *Auk* **114** 93–102.

LAAKE, J. L., CALAMBOKIDIS, J., OSMEK, S. D. and RUGH, D. J. (1997). Probability of detecting harbor porpoise from aerial surveys: estimating g(0). *Journal of Wildlife Management* **61** 63–75.

LANCIA, R. A., NICHOLS, J. D. and POLLOCK, K. H. (1994). Estimating the number of animals in wildlife populations. In *Research and Management Techniques for Wildlife and Habitats. 5th edition*, T. A. Bookhout (ed), 215–253. The Wildlife Society: Bethesda, Md.

LANCIA, R. A., BISHIR, J. W., CONNER, M. C. and ROSENBERRY, C. S. (1996). Use of catch-effort to estimate population size. *Wildlife Society Bulletin* **24** 731–737.

LARKIN, R. P. and HALKIN, D. H. (1994). A review of software packages for estimation of animal home ranges. *Wildlife Society Bulletin* **22** 274–287.

LASKA, E. M. and MEISNER, N. (1993). A plant-capture method for estimating the size of a population from a single sample. *Biometrics* **49** 209–220.

LEBRETON, J.-D. (1995). The future of population dynamic studies using marked animals: A statistician's perspective. *Journal of Applied Statistics* **22** 1009–1030.

LEBRETON, J.-D. and NORTH, P. M. (eds). (1993). *Marked Individuals in the Study of Bird Populations.* Birkhäuser Verlag: Basel, Switzerland.

LEBRETON, J.-D., ALMERAS, T. and PRADEL, R. (in press). Competing events, mixture of information, and multi-strata recapture models. *Bird Study*, to appear.

LEBRETON, J.-D., PRADEL, R. and CLOBERT, J. (1993). The statistical analysis of survival in animal populations. *Tree* **8** 91–95.

LEBRETON, J.-D., REBOULET, A.-M. and BANCO, G. (1993). An overview of software for terrestrial vertebrate population dynamics. In *Marked Individuals in the Study of Bird Populations,* J.-D. Lebreton and P. M. North (eds), 357-371. Birkhäuser Verlag: Basel.

LEBRETON, J.-D., BURNHAM, K. P., CLOBERT, J. and ANDERSON, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals. A unified approach with case studies. *Ecological Monographs* **62** 67–118.

LEBRETON, J.-D., HEMERY, G., CLOBERT, J. and COQUILLART, H. (1990). The estimation of age-specific breeding probabilities from recapture or resightings in vertebrate populations. I. Transversal models. *Biometrics* **46** 609–622.

LEBRETON, J.-D., MORGAN, B.J. T, PRADEL, R. and FREEMAN, S. N. (1995). A simultaneous survival rate analysis of dead recovery and live recapture data. *Biometrics* **51** 1418–1428.

LEE, S.-M. (1996). Estimating population size for capture-recapture data when capture probabilities vary by time, behavior and individual animal.

Communications in Statistics-Simulation **25** 431–457.

LEE, S.-M. and CHAO, A. (1994). Estimating population size via sample coverage for closed capture-recapture models. *Biometrics* **50** 88–97.

LEE, S.-M. and CHEN, C. W. S. (1998). Bayesian inference of population size for behavioral response models. *Statistica Sinica* **8** 1233–1248.

LIANG, K.-Y. and ZEGER, S. L. (1995). Inference based on estimating equations in the presence of nuisance parameters (with discussion). *Statistical Science* **10** 158–199.

LINDBERG, M. A., SEDINGER, J. S. and REXSTAD, E. A. (1995). Estimating nest site fidelity of adult female black brant with multi-state modeling and geographic information systems. *Journal of Applied Statistics* **22** 725–735.

LINK, W. A. and BARKER, R. J. (1994). Density estimation using the trapping web design: a geometric approach. *Biometrics* **50** 733–745.

LINK, W. A. and NICHOLS, J. D. (1994). On the importance of sampling variance to investigations of temporal variations in animal population size. *Oikos* **69** 539–544.

LINK, W. A. and SAUER, J. R. (1996). Extremes in ecology: avoiding the misleading effects of sampling variation in summary analyses. *Ecology* **77** 1633–1640.

LINK, W. A. and SAUER, J. R. (1997). Estimation of population trajectories

from count data. *Biometrics* **53** 488–497.

LLOYD, C. J. (1987). Optimal martingale estimating equations in a stochastic process. *Statistics and Probability Letters* **5** 381–387.

LLOYD, C. J. (1994a). Efficiency of martingale methods in recapture studies. *Biometrika* **81** 88–97.

LLOYD, C. J. (1994b). Accurate confidence intervals from recapture experiments. *Communications in Statistics-Theory and Methods* **24** 1235–1253.

LLOYD, C. J. (1998). Personal communication.

LLOYD, C. J. and YIP, P. (1991). A unification of inference for capture-recapture studies through martingale estimating functions. In *Estimating Equations*, V. P. Godambe (ed.), 65–68. Clarendon Press: Oxford.

LOERY, G., NICHOLS, J. D. and HINES, J. E. (1997). Capture-recapture analysis of a wintering black-capped chickadee population in Connecticut, 1958-1993. *Auk* **114** 431–442.

MACE, R. D., MIONTA, S. C., MANLEY, T. L. and AUNE, K. E. (1994). Estimating grizzly bear population-size using camera sightings. *Wildlife Society Bulletin* **22** 64–83.

MACK, Y. P. and QUANG, P. X. (1998). Kernel methods in line and point transect sampling. *Biometrics* **54** 606–619.

MADIGAN, D. and YORK, J. C. (1997). Bayesian methods for estimation of

the size of a closed population. *Biometrika* **84** 19–31.

MANLY, B. F. J. (1997). *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edition. Chapman and Hall: London.

MANLY, B. F. J. and CHATTERJEE, C. (1993). A model for mark-recapture data allowing for animal movement. In *Marked Individuals in the Study of Bird Populations,* J.-D. Lebreton and P. M. North (eds), 309–322. Birkhäuser Verlag: Basel.

MANLY, B. F. J. and McDONALD, L. L. (1996). Sampling wildlife populations. *Chance* **9** 9–19.

MANLY, B. F. J., McDONALD, L. L. and GARDNER, G. W. (1996). Maximum likelihood estimation for the double count method with independent observers. *Journal of Agricultural, Biological, and Environmental Statistics* **1** 170–189.

MANNING, T. G., EDGE, W. D. and WOLFF, J. O. (1995). Evaluating population-size estimators: an empirical approach. *Journal of Mammalogy* **76** 1149–1158.

MASON, P. L., NICHOLS, R. A. and HEWITT, G. M. (1995). Philopatry in the alpine grasshopper, *Podisma pedestris*: a novel experimental and analytical method. *Ecological Entomology* **20** 137–145.

MATLOCK, R. B., WELCH, J. B. and PARKER, F. D. (1996) Estimating population density per unit area from mark, release, recapture data. *Ecological*

Applications **6** 1241–1253.

MILLER, R. J. and MOHN, R. K. (1993). Critique of the Leslie method for estimating sizes of crab and lobster populations. *North American Journal of Fisheries Management* **13** 676–685.

MILLER, S. D., WHITE, G. C., SELLERS, R. A., REYNOLDS, H. V., SCHOEN, J. W., TITUS, K., BARNES, V. G., SMITH, R. B., NELSIN, R. R., BALLARD, W. B. and SCHWARTZ, C. C. (1997). Brown and black bear density estimation in Alaska using radio telemetry and replicated mark-resight techniques. *Wildlife Monographs* **133** 1–55.

MINTA, S. and MANGEL, M. (1989). A simple population estimate based on simulation for capture-recapture and capture-resight data. *Ecology* **70** 1738–1751.

MODDE, T., BURNHAM, K. P. and WICK, E. J. (1996). Population status of the razorback sucker in the Middle Green River (U.S.A.) *Conservation Biology* **10** 110–119.

MORGAN, B. J. T. and FREEMAN, S. N (1989). A model with first-year variation for ring-recovery data. *Biometrics* **45** 1087–1101.

MORGAN, B. J. T., FREEMAN, S. N. and CATCHPOLE, E. A. (1995). Developments in modeling avian survival. *Bulletin of the International Statistical Institute* **50** 1335–1348.

MORGAN, B. J. T., FREEMAN, S. N. and LEBRETON, J.-D. (1997). Statistics in

Ornithology. In *Encyclopedia of Statistical Sciences Update Volume 1*, S. Kotz, C. B. Read, and D. L. Banks (eds), 438–447. Wiley: New York.

MYERS, R. A., BARROWMAN, N. J. and HUTCHINGS, J. A. (1997). Inshore exploitation of Newfound Atlantic cod (Gadus morhua) since 1948 as estimated by mark-recapture data *Canadian Journal of Fisheries and Aquatic Sciences* **54** (supplement 1) 224–235.

NEAL, A. K., WHITE, G. C., GILL, R. B., REED, D. F. and OLTERMAN, J. H. (1993). Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. *Journal of Wildlife Management* **57** 436–450.

NICHOLS, J. D. (1992). Capture-recapture models: Using marked animals to study population dynamics. *Bioscience* **42** 94–102.

NICHOLS, J. D. (1994). Capture-recapture methods for bird population studies. *Atti del 6 Convegno Italiano di Ornitologia, Torino, 8–11 Ottobre 1991*, 31–51. Museo regionale Scienze naturale, Torino.

NICHOLS, J. D. (1996). Source of variation in migratory movement of animal populations: statistical inference and a selective review of empirical results for birds. In *Population Dynamics in Ecological Space and Time*, O. E. Rhodes Jr., R. K. Chesser, M. H. Smith (eds), 147–197. University of Chicago Press: Chicago.

NICHOLS, J. D. and HINES, J. E. (1993). Survival rate estimation in the presence of tag loss using joint analysis of capture-recapture and resighting

data. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 229–243. Birkhäuser Verlag: Basel.

NICHOLS, J. D. and KENDALL, W. L. (1995). The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* **22** 835–846.

NICHOLS, J. D. and POLLOCK, K. H. (1990). Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. *Ecology* **71** 21–26.

NICHOLS, J. D., HINES, J. E. and BLUMS, P. (1997). Tests for senescent decline in annual survival probabilities of common pochards, *Aythya ferina*. *Ecology* **78** 1009–1018.

NICHOLS , J. D., SPENDELOW, J. A. and HINES, J. E. (1990). Capture-recapture estimation of prebreeding survival rate for birds exhibiting delayed maturation. *Journal of Field Ornithology* **61** 347–354.

NICHOLS, J. D., BART, J., LIMPERT, R. J., SLADEN, W. J. L. and HINES, J. E. (1992a). Annual survival rates of adult and immature eastern population tundra swans. *Journal of Wildlife Management* **56** 485–494.

NICHOLS, J. D., BLOHM, R. J., REYNOLDS, R. E., TROST, R. E., HINES, J. E. and BLANDEN, J. P. (1991). Band reporting rates for mallards with reward bands of different dollar values. *Journal of Wildlife Management* **55** 119–126.

NICHOLS, J. D., BROWNIE, C., HINES, J. E., POLLOCK, K. H. and HESTBECK, J. B. (1993). The estimation of exchanges among population or subpopulations. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 265–279. Birkhäuser Verlag: Basel.

NICHOLS, J. D., HINES, J. E., POLLOCK, K. H., HINZ, R. L. and LINK, W. A. (1994). Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology* **75** 2052–2065.

NICHOLS, J. D., MORRIS, R. W., BROWNIE, C. and POLLOCK, K. H. (1986). Sources of variation in extinction rates, turnover, and diversity of marine invertebrate families during the Paleozic. *Paleobiology* **12** 421–432.

NICHOLS, J. D., REYNOLDS, R. E., BLOHM, R. J., TROST, R. E, HINES, J. E. and BLADEN, J. P. (1995). Geographic variation in band reporting rates for mallards based on reward banding. *Journal of Wildlife Management* **59** 697–708.

NICHOLS, J. D., SAUER, J. R., POLLOCK, K. H. and HESTBECK, J. B. (1992b). Estimating transition probabilities for stage-based population matrices using capture-recapture data. *Ecology* **73** 306–312.

NORRIS, J. L. and POLLOCK, K. H. (1995). A capture-recapture model with heterogeneity and behavioral response. *Environmental and Ecological Statistics* **2** 305–313.

NORRIS, J. L. and POLLOCK, K. H. (1996a). Nonparametric MLE under two

closed capture-recapture models with heterogeneity. *Biometrics* **52** 639–649.

NORRIS, J. L. and POLLOCK, K. H. (1996b). Including model uncertainty in estimating variances in multiple capture studies. *Environmental and Ecological Statistics* **3** 233–244.

NORTH, P. M. and BAILLIE, S.R. (eds). (in press). *Proceedings of Euring'97 - Bird Study*, to appear.

NORTH, P. M. and NICHOLS, J. D. (1995). (eds). *Journal of Applied Statistics* **22**, Nos 5 & 6; special issue on statistics and ornithology.

NORTH, M. P. and REYNOLDS, J. H. (1996). Micro-habitat analysis using radio telemetry locations and polytomous logistic regression. *Journal of Wildlife Management* **60** 639–653.

NOVAK, J. M., SCRIBNER, K. T., DUPONT, W. D. and SMITH, M. H. (1991). Catch-effort estimation of white tailed deer population size. *Journal of Wildlife Management* **55** 31–38.

OSBORNE, P. E. and TIGAR, B. J. (1992). Interpreting bird atlas data using logistic models: an example from Lesotho, Southern Africa. *Journal of Applied Ecology* **29** 55–62.

OTIS, D. L. (1994). Optimum sample size allocation for wood duck banding studies. *Journal of Wildlife Management* **58** 114–123.

PALSBØLL, P. J., ALLEN, J., BÉRUBÉ, M., CLAPHAM, P. J., FEDDERSEN, T. P., HAMMOND, P. S., HUDSON, R. R., JØRGENSEN, H., KATANA, S., LARSEN, A. H., LARSEN, F., LIEN, J., MATTILA, D. K., SIGURJÓNSSON, J., SEARS, R., SMITH, J., SPONER, R., STEVICK, P. and ØIEN, N. (1997). Genetic tagging of humpback whales. *Nature* **388** 767–769.

PEACH, W. J. (1993). Combining mark-recapture data sets for small passerines. In *Marked Individuals in the Study of Bird Populations,* J.-D. Lebreton and P. M. North (eds), 107–122. Birkhäuser Verlag: Basel.

PEACH, W. J., BUCKLAND, S. T. and BAILLIE, S. R. (1996). The use of constant effort mist-netting to measure between-year changes in the abundance and productivity of common passerines. *Bird Study* **43** 142–156.

PELLETIER, L. and KREBS, C. J. (1997). Line-transect sampling for estimating ptarmigan (*Lagopus spp.*) density. *Canadian Journal of Zoology* **75** 1185–1192.

PIPER, S. E. (1995). A model for the ring-recovery reporting process for the Cape Griffon *Igyps coprotheres. Journal of Applied Statistics* **22** 641–659.

PLANTE, N. (1990). Estimation de la taille d'une population animale à l'aide d'un modèle de capture-recapture avec stratification. M.Sc Thesis, Université Laval, Canada.

PLANTE, N., RIVEST, L.P. and TREMBLAY, G. (1998). Stratified capture-recapture of the size of a closed population. *Biometrics* **54** 47–60.

PLEDGER, Shirley. (1998). Unified maximum likelihood estimates for closed capture-recapture models using mixtures. Research Report 98-15, School of Mathematical and Computing Sciences, Victoria University, New Zealand.

PLEDGER, Shirley and EFFORD, M. (1998). Correction of bias to heterogeneous capture probability in capture-recapture studies of open populations. *Biometrics* **54** 319–329.

POJAR, T. M., BOWDEN, D. C. and GILL, R. B. (1995). Aerial counting experiments to estimate pronghorn density and herd structure. *Journal of Wildlife Management* **59** 117–128.

POLLARD, J. H. and BUCKLAND, S. T. (1997). A strategy for adaptive sampling in shipboard line transect surveys. *Report of the International Whaling Commission* **47** 921–932.

POLLOCK, K. H. (1982). A capture-recapture design robust to unequal probabilities of capture. *Journal of Wildlife Management* **46** 757–760.

POLLOCK, K. H. (1991). Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. *Journal of the American Statistical Association* **86** 225–238.

POLLOCK, K. H. (1995). The challenges of measuring change in wildlife populations: A biometrician's perspective. In *Conservation Through Sustainable Uses of Wildlife*, G.C. Grigg, P. T. Hale, and D. Lunney (eds), 117–

121. Centre for Conservation Biology, The University of Queensland.

POLLOCK, K. H., CONROY, M. J. and HEARN, W. S. (1995). Separation of hunting and natural mortality using ring-return models: an overview. *Journal of Applied Statistics* **22** 557–566.

POLLOCK, K. H., HOENIG, J. M. and JONES, C. M. (1991). Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. *American Fisheries Society Symposium* **12** 423–434.

POLLOCK, K. H., KENDALL, W. L. and NICHOLS, J. D. (1993). The "robust" capture-recapture design allows components of recruitment to be estimated. In *Marked Individuals in the Study of Bird Populations,* J.-D. Lebreton and P. M. North (eds), 245–252. Birkhäuser Verlag: Basel.

POLLOCK, K. H., TSAI, K. and HOENIG, J. M. (1994). Band return models: use of solicited bands and separation of hunting and natural mortality. *Journal of Wildlife Management* **58** 193–198.

POLLOCK, K. H., TURNER, S. C. and BROWN, C. A. (1994). Use of capture-recapture techniques to estimate population size and population totals when a complete frame in unavailable. *Survey Methodology* **20** 117–124.

POLLOCK, K. H., BUNCK, C. M., WINTERSTEIN, S. R. and CHEN, C.-L. (1995). A capture-recapture survival analysis model for radio-tagged animals. *Journal of Applied Statistics* **22** 661–672.

POLLOCK, K. H., HOENIG, J. M., JONES, C. M., ROBSON, D. S. and GREENE, C. J. (1997). Catch rate estimation for roving and access point surveys. *North American Journal of Fisheries Management* **17** 11–19.

POLLOCK , K. H., NICHOLS, J. D., BROWNIE, C. and HINES, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**.

POWELL, L. A., CLARK, W. R. and KLAAS, E. E. (1995). Using post-release stratification to detect heterogeneity in mallard survival. *Journal of Wildlife Management* **59** 683–690.

PRADEL, R. (1993). Flexibility in survival analysis from recapture-data: handling trap-dependence. In *Marked Individuals in the Study of Bird Populations,* J.-D. Lebreton and P. M. North (eds), 29–38. Birkhäuser Verlag: Basel.

PRADEL, R. (1996a). Utilization of capture-mark-recapture for the study of recruitment and population growth rates. *Biometrics* **52** 703–709.

PRADEL, R. (1996b). Animal dispersal within subdivided populations: An approach based on monitoring individuals. *Acta Oecologica* **17** 475–483.

PRADEL, R. (in press). Capture-mark-recapture population dynamics analysis *Bird Study*, to appear.

PRADEL, R. and LEBRETON, J.-D. (1991). *User's manual for Program SURGE, Version 4.2.* Centre d'Ecologie Fonctionelle et Evolutive - CNRS, Mont-

pellier, France.

PRADEL, R. and LEBRETON, J.-D. (in press). Comparison of different approaches to study the local recruitment of breeders. *Bird Study*, to appear.

PRADEL, R., COOCH, E. G. and COOKE, F. (1995). Transient animals in a resident population of snow geese: local emigration or heterogeneity. *Journal of Applied Statistics* **22** 695–710.

PRADEL, R., REBOULET, A.-M. and VIALLEFONT, A. (1995). Testing hypotheses and estimating survival from capture histories with CR. *Journal of Applied Statistics* **22** 775–784.

PRADEL, R., HINES, J. E., LEBRETON, J.-D. and NICHOLS, J. D. (1997a). Capture-recapture survival models taking account of transients. *Biometrics* **53** 60–72.

PRADEL, R., JOHNSON, A. R., VIALLEFONT, A., NAGER, R. G. and CEZILLY, F. (1997b). Local recruitment in the greater flamingo: A new approach using capture-mark-recapture data. *Ecology* **78** 1431–1445.

PRADEL, R., RIOUX, N., TAMISIER, A. and LEBRETON, J.-D. (1997c). Individual turnover among wintering teal in Camargue: a mark-recapture study. *Journal of Wildlife Management* **61** 816–821.

PRÉVOT-JULLIARD, A.-C., LEBRETON, J.-D. and PRADEL, R. (1998). Re-evaluation of the adult survival of black-headed gull (*Larus ridibundus*) in the presence of recapture heterogeneity. *Auk* **115** 85–95.

115

PUGESEK, B. H., NATIONS, C., DIEM, K. L. and PRADEL, R. (1995). Mark-resighting analysis of a California gull population. *Journal of Applied Statistics* **22** 625–639.

PUNT, A. E. and HILBORN, R. (1997). Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews of Fisheries Biology and Fisheries* **7** 35–63.

QUANG, P. X. (1993). Non-parametric estimators for variable circular plot surveys. *Biometrics* **49** 837–852.

QUANG, P. X. and BECKER, E. F. (1996). Line transect sampling under varying conditions with applications to aerial surveys. *Ecology* **77** 1297–1302.

QUANG, P. X. and BECKER, E. R. (1997). Combining line transect and double count sampling techniques for aerial surveys. *Journal of Agricultural, Biological, and Environmental Statistics* **2** 230–242.

QUINN II, T. J. and DERISO, R. B. (1999). *Quantitative Fish Dynamics*. Oxford University Press: New York.

RAFTERY, A. E. and SCHWEDER, T. (1993). Inference about the ratio of two parameters, with applications to whale censusing. *American Statistician* **47** 259–264.

RAFTERY, A. E., GIVENS, G. H. and ZEH, J. E. (1995). Inference from a deterministic population dynamics model for bowhead whales. *Journal of the American Statistical Association* **90** 402–416.

RAFTERY, A. E., MADIGAN, D. and HOETING, J. A. (1997). Bayesian model averaging for linear regression models. *Journal of the American Statistical Association* **92** 179–191.

RAJWANI, K. and SCHWARZ, C. J. (1997). Adjusting for missing tags in salmon escapement surveys. *Canadian Journal of Fisheries and Aquatic Sciences* **54** 800–808.

RALPH, C. J., SAUER, J. R. and DROEGE, S., (eds). (1995). *Monitoring Bird Populations by Point Counts.* General Technical Report PWS-GTR-149. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. 187 pp.

RAMAKRISHNAN, V. and MEETER, D. (1993). Negative binomial cross-tabulations, with applications to abundance data. *Biometrics* **49** 195–207

REBOULET, A.-M., VIALLEFONT, A., PRADEL, R., and LEBRETON, J.-D. (in press). Selection of survival and recruitment models with SURGE 5.0. *Bird Study*, to appear.

REED, W. J. and SIMONS, C. M. (1996a). A contagion model of a fishery and its use in analyzing catch-effort data. *Ecological Modeling* **92** 179–191.

REED, W. J. and SIMONS, C. M. (1996b). Analyzing catch-effort data by means of the Kalman filter. *Canadian Journal of Fisheries and Aquatic Sciences* **53** 2157–2166.

REXSTAD, E. A. (1992). Effect of hunting on annual survival of Canada geese

in Utah. *Journal of Wildlife Management* **56** 297–305.

REXSTAD, E. A. and ANDERSON, D. R. (1992). Heterogeneous survival rates of mallards (*Anas platyrhynchos*). *Canadian Journal of Zoology* **70** 1878–1885.

REXSTAD, E. and BURNHAM, K. (1992). User's guide for interactive program CAPTURE. Fort Collins: Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University. 29 pp.

REYNOLDS, R. E., BLOHM, R. J., NICHOLS, J. D. and HINES, J. E.(1995). Spring-summer survival rates of yearling versus adult mallard females. *Journal of Wildlife Management* **59** 691–696.

RICHARDS, L.J. and SCHNUTE, J. T. (1992). Statistical models for estimating CPUE from catch and effort data. *Canadian Journal of Fisheries and Aquatic Sciences* **49** 1315–1327.

RIVEST, L.-P., POTVIN, F., CRÉPEAU, H. and DAIGLE, G. (1995). Statistical methods for aerial surveys using the double count technique to correct visibility bias. *Biometrics* **51** 461–470.

RIVEST, L.-P., COUTURIER, S., and CRÉPEAU, H. (1995). Statistical methods for estimating caribou abundance using postcalving aggregations detected by radio telemetry. *Biometrics* **54** 865–876.

ROBINETTE, K. W, ANDELT, W. F. and BURNHAM, K. P. (1995). Effect of group size on survival of relocated prairie dogs. *Journal of Wildlife Management*

59, 867–874.

Rockwood, S. V. and Whiting, R. M. (1992). Estimating waterfowl hunter-trips using a capture-recapture technique. *Wildlife Society Bulletin* **20** 15–20.

Rosenberg, D. K., Overton, W. S. and Anthony, R. G. (1995). Estimation of animal abundance when capture probabilities are low and heterogeneous. *Journal of Wildlife Management* **59** 252–261.

Routledge, R. D. and Swartz, T. B. (1991). Taylor's power law re-examined. *Oikos* **60** 107–112

Salehi, M. and Seber, G. A. F. (1997a). Adaptive cluster sampling with networks selected without replacement. *Biometrika* **84** 209–219.

Salehi, M. and Seber, G. A. F. (1997b). Two-stage adaptive sampling. *Biometrics* **53**, 959–970.

Saltz, D. (1994). Reporting error measures in radio location by triangulation: a review. *Journal of Wildlife Management* **58** 181–184.

Samuel, M. D. and Kenow, K. P. (1992). Evaluating habitat selection with radio-telemetry triangulation error. *Journal of Wildlife Management* **56** 725–734.

Särndal, C. E., Swensson, B. and Wretman, J. (1992). *Model Assisted Survey Sampling.* Springer-Verlag: New York.

SAUER, J. R., PETERJOHN, B. G. and LINK, W. A. (1994). Observer differences in the North American Breeding Bird Survey. *Auk* **111** 50–62.

SCHOOLEY, R. L. (1994). Annual variation in habitat selection: patterns concealed by pooled data. *Journal of Wildlife Management* **58** 367–374.

SCHNUTE, J. T. (1994). A general framework for developing sequential fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences* **51** 1676–1688.

SCHWARZ, C. J. (1993) Estimating migration rates using tag-recovery data. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 255–264. Birkhäuser Verlag: Basel.

SCHWARZ, C. J. and ARNARSON, A. N. (1990). Use of tag-recovery information in migration and movement studies. *American Fisheries Society Symposium* **7** 588–603.

SCHWARZ, C. J. and ARNASON, A. N. (1996). A general methodology for the analysis of open-model capture recapture experiments. *Biometrics* **52** 860–873.

SCHWARZ, C. J. and DEMPSON, J. B. (1994). Mark-recapture estimation of a salmon smolt population. *Biometrics* **50** 98–108.

SCHWARZ, C. J. and GANTER, B. (1995). Estimating the movement among staging areas of the barnacle goods (*Branta leucopsis*). *Journal of Applied Statistics* **22** 711–725.

SCHWARZ, C. J. and STOBO, W. T. (1997). Estimating temporary migration using the robust design. *Biometrics* **53** 178–194.

SCHWARZ, C. J. and TAYLOR, C. G. (1998). The use of the stratified-Petersen estimator in fisheries management: estimating the number of pink salmon (*Oncorhynchus gorbuscha*) spawners in the Fraser River. *Canadian Journal of Fisheries and Aquatic Sciences* **55** 281–297.

SCHWARZ, C. J., BURNHAM, K. P. and ARNASON, A. N. (1988). Post-release stratification in band-recovery models. *Biometrics* **44** 765–785.

SCHWARZ, C. J., SCHWEIGERT, J. and ARNASON, A. N. (1993). Estimating migration rates using tag recovery data. *Biometrics* **49** 177–194.

SCHWARZ, C. J., BAILEY, R. E, IRVINE, J. R. and DALZIEL, F. C. (1993). Estimating salmon spawning escapement using capture-recapture methods. *Canadian Journal of Fisheries and Aquatic Sciences* **50** 1181–1191.

SCHWEIGERT, J. F. and SCHWARZ, C. J. (1993). Estimating migration rates for Pacific herring (*Clupea pallasi)* using tag-recovery data. *Canadian Journal of Fisheries and Aquatic Sciences* **50** 1530–1540.

SEAMAN, D. E. and POWELL, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77** 2075–1085.

SEBER, G. A. F. (1965). A note on the multiple recapture census. *Biometrika* **52** 249–259.

SEBER, G. A. F. (1971). Estimating age-specific rates from bird-band returns when the reporting rate is constant. *Biometrika* **58** 491–497.

SEBER, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters,* 2nd edition. Edward Arnold: London.

SEBER, G. A. F. (1986). A review of estimating animal abundance. *Biometrics* **42** 267–292.

SEBER, G. A. F. (1992). A review of estimating animal abundance. II. *International Statistical Review* **60** 129–166.

SEBER, G. A. F. (1997). Adaptive sampling. In *Encyclopedia of Statistical Sciences, Update Volume 1*, S. Kotz, C. B. Read and D. L. Banks (eds), 6–11. Wiley: New York.

SEBER, G. A. F. (1998). Adaptive sampling. In *Encyclopedia of Biostatistics, Volume 1*, P. Armitage and T. Colton (eds), 52–58. Wiley: New York.

SHEAFFER, S. E. and JARVIS, R. L. (1995). Bias in Canada Goose population size estimates from sighting data. *Journal of Wildlife Management* **59** 464–473.

SKALSKI, J. R. (1991). Using sign counts to quantify animal abundance. *Journal of Wildlife Management* **55** 705–715.

SKALSKI, J. R. (1994). Estimating wildlife populations based on incomplete area surveys. *Wildlife Society Bulletin* **22** 192–203.

SKALSKI, J. R. (1996). Regression of abundance estimates from mark-recapture surveys against environmental covariates. *Canadian Journal of Fisheries and Aquatic Sciences* **53** 196–204.

SKALSKI, J. R. and ROBSON, D. S. (1982). A mark and removal field procedure for estimating population abundance. *Journal of Wildlife Management* **46** 741–751.

SKALSKI, J. R. and ROBSON, D. S. (1992). *Techniques for Wildlife Investigations. Design and Analysis of Capture Data.* Academic Press: New York.

SKALSKI, J. R., HOFFMAN, A. and SMITH, S. G. (1993). Testing the significance of individual and cohort-level covariates in animal survival studies. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 9–28. Birkhäuser Verlag: Basel.

SKAUG, H. J. and SCHWEDER, T. (1999). Hazard models for line transect surveys with independent observers. *Biometrics* **55**, 29–36.

SMITH, A. F. M. and GELFAND, A. E. (1992). Bayesian statistics without tears: a sampling-resampling perspective. *American Statistician* **46** 84–88.

SMITH, S. J. (1990). Use of statistical models for the estimation of abundance from ground fish trawl survey data. *Canadian Journal of Fisheries and Aquatic Sciences* **47** 894–903.

SMITH, S. J. (1996). Assessment of ground fish stocks based on bottom trawl

survey results. *NAFO Scientific Council Studies* **28** 25–53.

SMITH, S. J. (1997). Bootstrap confidence limits for ground fish trawl survey estimates of mean abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **54** 616–630.

SMITH, S. J. and GAVARIS, S. (1993a). Improving the precision of abundance estimates of Eastern Scotian Atlantic cod from bottom trawl surveys. *North American Journal of Fisheries Management* **13** 35–47.

SMITH, S. J. and GAVARIS, S. (1993b). Evaluating the accuracy of projected catch estimates from sequential population analysis and trawl survey abundance estimates. In *Risk Evaluation and Biological Reference Points for Fisheries Management*, S. J. Smith, J. J. Hunt, and D. Rivard (eds), *Canadian Special Publication of Fisheries and Aquatic Sciences* **120** 163–172.

SMITH, S. J. and PAGE, F. H. (1996). Associations between Atlantic cod (*Gadus morhua*) and hydrographic variables: implications for the management of the 4VsW cod stock. *ICES Journal of Marine Science* **53** 597–614.

SOLOW, A. R. and PALKA, D. (1996). On Bayesian estimation of group size. *Biometrics* **52** 335–340.

SOMERTON, D. A. and KIKKAWA, B. S. (1995). A stock survey technique using the time to capture individual fish on longlines. *Canadian Journal of Fisheries and Aquatic Sciences* **52** 260–267.

SOUTHWELL, C. (1994). Evaluation of walked line transect counts for estimating macropod density. *Journal of Wildlife Management* **58** 348–358.

SPENDELOW, J. A., BURGER, J., NISBET, I. C. T., NICHOLS, J. D., HINES, J. E., HAYES, H., CORMONS , G. D. and GOCHFELD, M. (1994). Sources of variation in loss rates of color bands applied to adult roseate terns (*Sterna dougallii*) in the western north Atlantic. *Auk* **111** 881–887.

SPENDELOW, J. A., NICHOLS, J. D., NISBET, I. C. T, HAYES, H., CORMONS, G. D, BURGE, J., SAFINA, C., HINES, J. E. and GOCHFELD, M. (1995). Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. *Ecology* **76** 2415–2428.

STEINERT, S. F., RIFFEL, H. D. and WHITE, G. C. (1994). Comparisons of big game harvest estimates from check station and telephone surveys. *Journal of Wildlife Management* **58** 335–340.

STEWART-OATEN, A. (1996). Sequential estimation of log(abundance). *Biometrics* **52** 38–49.

STOBO W. T. and HORNE, J. K. (1994). Tag loss in grey seals (Halichoerus grypus) and potential effects on population estimates. *Canadian Journal of Zoology* **72** 555–561.

STRONG, A. M., SAWICKI, R. J. and BANCROFT, G. T. (1994). Estimating white-crowned pigeon population size from flight-line counts. *Journal of Wildlife Management* **58** 156–162.

SZARZI, N. J., QUINN II, T. J. and McBRIDE, D. N. (1995). Assessment of shallow-water clam resources: case study of razor clams, eastern Cook Inlet, Alaska. *ICES Marine Science Symposium* **199** 274–286.

TANNER, M. (1994). *Tools for Statistical Inference: Methods for the Exploration of Posterior Distributions and Likelihood Functions.* Springer-Verlag: New York.

THOMAS, L. (1999). Distance 3.5. *Bulletin of the Ecological Society of America* **80** 114–115. THOMPSON, S. K. and SEBER, G. A. F. (1996). *Adaptive Sampling.* Wiley: New York.

THOMAS, L., LAAKE, J. L., DERRY, J. F., BUCKLAND, S. T., BORCHERS, D. L., ANDERSON, D. A., BURNHAM, K. P., STRINDBERG, S., HEDLEY, S. L., BURT, M. L., MARQUES, F., POLLARD, J. H. and FEWSTER, R. M. (1998). *Distnce 3.5.* Research Unit for Wildlife Population Assessment, Uni. of St. Andrews, UK.

THOMPSON, S. K., RAMSEY, F. L. and SEBER, G. A. F. (1992). An adaptive procedure for sampling animal populations. *Biometrics* **48** 1195–1199.

TREBLE, R. J., DAY, R. W. and QUINN II, T. J. (1993). Detection and effects on mortality estimates of changes in tag loss. *Canadian Journal of Fisheries and Aquatic Sciences* **50** 1435–1441.

TRENKEL, V. M., BUCKLAND, S. T., McLEAN, C. and ELSON, D. A. (1997). Evaluation of aerial line transect methodology for estimating red deer

(*Cervus elaphus*) abundance in Scotland. *Journal of Environmental Management* **50** 39–50.

TRPIS, M., HÄUSERMANN, W. and CRAIG, G. B. (1995). Estimates of population size, dispersal, and longevity of domestic *Aedes aegyptic aegypti (Diptera, Culicidae)* by mark-release-recapture in the village of Shauri-Moyo in Eastern Kenya. *Journal of Medical Entomology* **32** 27–33.

UDEVITZ, M. S. and POLLOCK, K. H. (1991). Change-in-ratio estimators for populations with more than two subclasses. *Biometrics* **47** 1531–1546.

UDEVITZ, M. S. and POLLOCK, K. H. (1992). Change-in-ratio methods for estimating population size. In *Wildlife 2001: Populations,* D. R. McCullough and R. H. Barrett (eds), 90–101. Elsevier Science Publishers: London.

UDEVITZ, M. S. and POLLOCK, K. H. (1995). Using effort information with change-in-ratio data for population estimation. *Biometrics* **51** 471–481.

UNDERHILL, L. G. (1990). Bayesian estimation of the size of a closed populations. *The Ring* **13** 235–254.

VAN HORNE, B., SCHOOLEY, R. L., KNICK, S. T., OLSON, G. S. and BURNHAM, K. P. (1997). Use of burrow entrances to indicate densities of Towsend's ground squirrels. *Journal of Wildlife Management* **61** 92–101.

VAN NOORDWIJK, A. J. (1995). On bias due to observer distribution in the analysis of data on natal dispersal in birds. *Journal of Applied Statistics* **22** 683–694.

VIALLEFONT, A., COOCH, E. G. and COOKE, F. (1995). Estimation of trade-offs with capture-recapture models: a case study on the lesser snow goose. *Journal of Applied Statistics* **22** 847–861.

VIALLEFONT, A., COOKE, F. and LEBRETON, J.-D. (1995). Age-specific costs of first time breeding. *Auk* **112** 67–76.

VIALLEFONT, A., LEBRETON, J.-D., REBOULET, A.-M. and GORY, G. (1998). Parameter identifiability and model selection in capture-recapture models: a numerical approach. *Biometrical Journal* **40** 313–325.

VOUNATSOU, P. and SMITH, A. F. M. (1995). Bayesian analysis of ring-recovery data via Markov chain Monte Carlo simulation. *Biometrics* **51** 687–708.

WANG, Y.-G. and LONERAGAN, N. R. (1996). An extravariation model for improving confidence intervals of population size estimates from removal data. *Canadian Journal of Fisheries and Aquatic Sciences* **53** 2533–2539.

WHITE, G. C. (1983). Numerical estimation of survival rates from band recovery and biotelemetry data. *Journal of Wildlife Management* **47** 716–728.

WHITE, G. C. (1993a). Evaluation of radio tagging marking and sighting estimators of population size using Monte Carlo simulations. In *Marked Individuals in the Study of Bird Populations*, J.-D. Lebreton and P. M. North (eds), 91–103. Birkhäuser Verlag: Basel.

WHITE, G. C. (1993b). Precision of harvest estimates obtained from incom-

plete responses. *Journal of Wildlife Management* **57** 129–134.

WHITE, G. C. (1996a). Analysis of frequency count data using the negative binomial distribution. *Ecology* **77** 2549–2557.

WHITE, G. C. (1996b). NOREMARK: Population estimation from mark-resight surveys. *Wildlife Society Bulletin* **24** 50–52.

WHITE, G. C. (1998). Program MARK.
http://www.cnr.colostate.edu/gwhite/mark/mark.htm (1 Sept 1998).

WHITE, G. C and BENNETTS, R. E. (1996). Analysis of frequency count data using the negative binomial distribution. *Ecology* **77** 2549–2557.

WHITE, G. C. and BURNHAM, K. P. (in press). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, to appear.

WHITE, G. C. and GARROTT, R. A. (1990). *Analysis of Wildlife Radio-tracking Data.* Academic Press: San Diego.

WHITE, G. C., REEVE, A. F., LINDZEY, F. G. and BURNHAM, K. P. (1996). Estimation of mule deer winter mortality from age ratios. *Journal of Wildlife Management* **60** 37–44.

WILEYTO, E. P. (1995). Expanding Markov-recapture models to incorporate multiple observations. *Environmental Entomology* **24** 1052–1062.

WILEYTO, E. P., EWENS, W. J. and MULLEN, M. A. (1994). Markov-recapture population estimates: a tool for improving interpretation of trapping ex-

periments. *Ecology* **75** 1109–1117.

WILSON, K. R. (1992). An efficiency comparison between capture-recapture estimators derived using maximum likelihood and martingale theory. In *Wildlife 2001: Population*, D. R. McCullough and R. H. Barrett (eds), 102-113. Elsevier: New York.

WILSON, K. R. and ANDERSON, D. R. (1995). Continuous-time capture-recapture population estimation when capture probabilities vary over time. *Environmental and Ecological Statistics* **2** 55–69.

WILSON, R. M. and COLLINS, M. F. (1992). Capture-recapture estimation with samples of size one using frequency data. *Biometrics* **79** 543–553.

WORTON, B. J. (1995a). A convex hull-based estimator of home-range size. *Biometrics* **51** 1206–1215.

WORTON, B. J. (1995b). Using Monte-Carlo simulation to evaluate kernel-based home-range estimators. *Journal of Wildlife Management* **59** 794–800.

WORTON, B. J. (1995c). Modeling radio-tracking data. *Environmental and Ecological Statistics* **2** 15–23.

XIAO, Y. (1996a). A framework for evaluating experimental designs for estimating rates of fish movement from tag recoveries. *Canadian Journal of Fisheries and Aquatic Sciences* **53** 1272–1280.

XIAO, Y. (1996b). A general model for estimating tag-specific shedding rates and tag interactions from exact or pooled times at liberty for a double tagging experiment. *Canadian Journal of Fisheries and Aquatic Sciences* **53** 1852–1861.

YAMAKAWA, T., MATSUMIYA, Y. and KITADA, S. (1994). Comparison of statistical models for expanded Delury method. *Fisheries Science* **60** 405–409.

YIP, P. (1989). An inference procedure for a capture and recapture experiment with time-dependent capture probabilities. *Biometric* **45** 471–479.

YIP, P. (1991a). A martingale estimating equation for a capture-recapture experiment. *Biometrics* **47** 1081–1088.

YIP, P. (1991b). Estimating population size from a capture-recapture experiment with known removals. *Theoretical Population Biology* **40** 1–13.

YIP, P. (1991c). An inference procedure for a capture-recapture experiment in discrete time with variable capture probabilities. *Stochastic Models* **7** 343–362.

YIP, P. (1993). Statistical inference procedure for a hypergeometric model for capture-recapture experiments. *Applied Mathematics and Computation* **58** 225–240.

YIP, P. (1995). Estimating the number of errors in a system using a martingale approach. *IEEE Transactions on Reliability* **44** 322–326.

YIP, P. (1996). Effect of plant-recapture in a capture-recapture experiment. *Communications in Statistics-Theory and Methods* **25** 2025–2038.

YIP, P. and CHAO, A. (1996). Estimating populations size from capture-recapture studies via sample coverage and estimating functions. *Communications in Statistics-Stochastic Models* **12** 17–35.

YIP, P. and FONG, D. Y. T. (1993). Estimating population size from a removal experiment in discrete time. *Statistics and Probability Letters* **16** 129–135.

YIP, P., FONG, D. Y. T. and WILSON, K. (1993). Estimating population size by recapture sampling via estimating function. *Communications in Statistics-Stochastic Models* **9** 179–193.

YIP, P., HUGGINS, R. M. and LIN, D. Y. (1996). Inference for capture-recapture experiments in continuous time with variable capture rates. *Biometrika* **83** 477–483.

ZALE A. V. and BAIN, M. B. (1994). Estimating tag-reporting rates with postcards as tag surrogates. *North American Journal of Fisheries Management* **14** 208–211.

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://www.ruwpa.st.-and,ac.uk/distance/: Maintained by the Research Unit for Wildlife Population Assessment, University of St. Andrews. 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

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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.