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ON THE USE OF CAPTURE–RECAPTURE MODELS IN MIST-NET STUDIES

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Abstract. Capture–recapture models provide a statistical framework for estimating population parameters from mist-net data. Although Cormack-Jolly-Seber and related models have recently been used to estimate survival rates of birds sampled with mist nets, we believe that the full potential for use of capture–recapture models has not been realized by many researchers involved in mist-net studies. We present a brief discussion of the overall framework for estimation using capture–recapture methods, and review several areas in which recent statistical methods can be, but generally have not yet been, applied to mist-net studies. These areas include estimation of (1) rates of movement among areas; (2) survival rates in the presence of transients; (3) population sizes of migrating birds; (4) proportion of birds alive but not present at a breeding site (one definition of proportion of nonbreeding birds in a population); (5) population change and recruitment; and (6) species richness. Using these models will avoid the possible bias associated with use of indices, and provide statistically valid variance estimates and inference.

Key Words: Capture–recapture, estimation, population size, species richness, survival rate, statistics, transients.

Recent publications that document population changes in migratory birds (Robbins et al. 1989, Hagen and Johnston 1992) have led to great public interest in the population status of birds. Partners in Flight and conservation organizations have attempted to focus this interest into programs for monitoring the status of bird populations and conducting research into the causes of population change in birds. Several monitoring programs, such as Monitoring Avian Productivity and Survival (MAPS; DeSante 1992), use banding data to address questions about population change at both local and regional scales. We believe that banding studies provide the only realistic way of addressing many questions of interest to population ecologists, and careful design of programs will allow estimation of many relevant parameters.

Monitoring and research programs frequently share a common goal: estimation of some demographic parameter for some pre-defined population. Clearly, the initial step in any banding program is definition of the parameter to be estimated and specification of a goal for precision of the estimate. Parameters of interest for both monitoring and research programs include population size, survival, recruitment, species richness, and movement probabilities among multiple study locations. Historically, monitoring programs tended to emphasize estimation of changes in these parameters over time, whereas research programs tended to evaluate differences in these parameters among predefined treatments. However, modern approaches to management require that information from monitoring be nested within a modeling framework, in which the monitoring is used to evaluate the validity of predictions (from models) of the consequences of management actions. The additional rigor associated with adaptive management and modeling exercises provides a strong impetus for designing monitoring programs that can be used to evaluate population responses to management.

There has recently been a great deal of statistical research regarding estimation of demographic parameters from banding studies (Seber 1982; Brownie et al. 1985; Burnham et al. 1987; Pollock et al. 1990; Lebreton et al. 1992; Nichols 1992, 1994; Schwarz and Seber 1999; Williams et al. 2002). Application of these procedures to mist-netting studies will greatly enhance the validity and credibility of the results. In this paper, we discuss methods and designs for estimating population parameters from banding studies. We emphasize capture–recapture methods because they are commonly used for passerine birds.

WHY NOT USE INDICES?

Naïve users of data from mist-net studies often draw inferences about the parameters mentioned above using capture indices. For example, the total number of animals captured is an index to total population size, and the return rate of birds to a location between years is an index to survival rate. The expected values of these indices differ from the actual population values by some unknown proportion, and any hypothesis test must make assumptions about the constancy of the proportions. In general, these constancy assumptions are not tested, and the proportions of animals detected may differ among treatments or over time, invalidating hypothesis tests.

This difficulty with the use of indices is easily documented in any hypothesis test. If the differences between group means can be explained by differences in detection probabilities, then the rejection of the null hypothesis cannot be attributed to the treatment (Sauer and Link *this volume*). For example, if mean captures from two treatments are 11.5 and 14.0, it cannot be established that the 2.5 more birds in one treatment are due to higher capture rates or a larger population in the treatment. In fact, a "better" study in terms of a larger number of replicates will lead to a higher chance of a false result, if the difference in counts is due to differences in capture rates (Barker and Sauer 1995).

We will not discuss the statistical properties of these indices (see Sauer and Link *this volume*), but we note that the methods we discuss here provide a means for testing the assumptions implicit in the use of indices for comparative purposes (Skalski and Robson 1992, MacKenzie and Kendall 2002, Sauer and Link *this volume*). Capture–recapture methods allow us to estimate the proportions of animals detected and test whether the proportions are constant over time or treatments. If the assumption of constancy is concluded to be reasonable, then inferences may be based on the index statistics in some cases (Skalski and Robson 1992, MacKenzie and Kendall 2002). However, if the hypothesis of constant sampling proportions is rejected, then inferences should be based on the capture–recapture model estimates. Interestingly, the use of indices relative to detectability-adjusted estimates continues to be a topic of discussion in the literature. However, we believe that it is time to move past this topic, and we agree with Anderson et al. (2003) that index-based designs are limiting the value of wildlife studies.

A SIMPLE INTRODUCTION TO CAPTURE–RECAPTURE PROCEDURES

All capture–recapture methods require that there are trapping occasions in which animals are captured, previously marked animals are recorded as recaptures, new animals are marked, and animals are released. If there are *k* of these occasions, we can define a capture history for each animal in which a 1 indicates a capture in occasion *i* and a 0 represents no capture of the individual in occasion *i*, as

	Trapping occasion (*i*)				
Animal number	1	2	3	4	.. *k*
9999	0	1	1	0	.. 1

The capture history of animal 9999 reflects that it was not captured in occasions 1 and 4 but was captured in occasions 2, 3, and *k*. The capture history is a fundamental format used in capture–recapture estimation and modeling.

There are two major categories of capture–recapture models (e.g., Seber 1982, White et al. 1982, Pollock et al. 1990, Nichols 1992, Williams et al. 2002). The population is "open" when sufficient time exists between capture occasions to allow animals to leave (via death or movement) or enter (via birth or movement) the population, and open-population estimation procedures estimate parameters such as survival between occasions and population size at trapping occasions. On the other hand, the population is "closed" when little time occurs between capture occasions, and it is assumed that population size is not changing among the occasions. Closed-population estimation procedures are used to estimate population size or density during the trapping occasions. Finally, some studies employ a "robust design" (Pollock 1982, Pollock et al. 1990, Kendall et al. 1995, Schwarz and Stobo 1997, Kendall and Bjorkland 2001), in which an investigator will conduct several trapping occasions during a short period of time, and then repeat the sampling at a future time. The data from the short period of time are usually used with closed-population models to estimate detection probability and population size, and data from the repeated samples are used with open-population models to estimate survival and movement in and out of the study area (Kendall et al. 1997). In addition, the robust design can permit (1) estimation of population size, survival, and recruitment for more periods than standard open population analyses; (2) estimation of components of recruitment; and (3) estimation that is robust to unequal catchability. This design is quite similar to the design employed by MAPS and other constant-effort programs.

Statistical procedures for all of these designs share a common approach. Parameters are defined and used to model the events giving rise to specific capture histories. These parameters are typically defined as probabilities, and are associated with both sampling (e.g., detection probability) and demographic (e.g., survival probability) processes. The events giving rise to a particular capture history are thus used to develop a probability model for that history. The probability models for the different capture histories, together with the numbers of animals observed to exhibit each history (the data), are used to obtain estimates of the model parameters and their variances.

As with all statistical procedures, there are assumptions that must be met for the estimates to be completely valid. There are several basic assumptions, such as the banded sample must be representative of the population and bands must not be lost or misread, that apply to all models (Seber 1982). Then, each model has a specific set of assumptions about how the parameters of interest are defined. For example, survival might be time specific, requiring a separate estimate for each year, or constant over time, requiring only a single estimate. Generally, tests and model selection statistics are available to allow users to assess the validity of the assumptions and determine whether models with different sets of parameters might be more appropriate for the data.

STATISTICAL METHODS AND MODELS

Open Population Capture–recapture Models

For open populations, the basic model, called the Cormack-Jolly-Seber (CJS) model after the individuals who first developed it, considers capture histories in terms of two sets of parameters:

ϕ_i: Probability(survive from trapping occasion i to i+1 | alive and present at time i)

p_i: Probability(captured at trapping occasion i | alive and present at time i)

Note that the vertical bar indicates that the probabilities are conditional, and reflect the probabilities of the event described before the vertical bar given that the event described after the bar occurred. Capture histories can be described in terms of products of these parameters. For example, for animals captured in period 1 and subsequently released, a capture history of 1 0 1 would have associated probability $\phi_1(1 - p_2)\ \phi_2 p_3$. Of course, there will be many different capture histories in any study, and each history can be written in terms of the underlying probabilities. These probabilities form cells in a multinomial distribution, and this multinomial model can be used as a basis for estimating ϕ_i, p_i, and their variances. Due to technical issues of estimation, some of the parameters cannot be separately estimated, and therefore we cannot always estimate survival and capture probabilities for all periods. See Lebreton et al. (1992) for an excellent explanation of the estimation procedure.

This modeling structure, in conjunction with appropriate software such as Program MARK (White and Burnham 1999; www.cnr.colostate.edu/~gwhite/software.html) is extraordinarily flexible. Beginning with the basic CJS model, any number of variations can be implemented. For example, survival or detection probabilities can be modeled as time dependent or constant. Age dependence in parameters can be implemented. In addition, data for groups of animals (e.g., males vs. females or birds found in mature vs. early successional woodlands) can be separately but simultaneously analyzed, to permit comparison of parameters (e.g., Peach 1993, Hilton and Miller 2003, Miller et al. 2003, Peach et al. *this volume*). Finally, survival and capture probabilities can be modeled as functions of covariates. For example, if winter temperature is thought to influence survival, it can be incorporated into the analysis by modeling survival as a function of temperature.

Estimation of population size from capture–recapture data requires a more stringent assumption than is required to estimate survival rate, because both marked and unmarked birds must have similar capture probabilities. Although population size can be estimated directly using program MARK, the Jolly-Seber population size estimation feature in the program is subject to numerical problems. Programs JOLLY (www.mbr-pwrc.usgs.gov/software.html) and POPAN (www.cs.umanitoba.ca/~popan/) provide direct estimates of population size. Alternatively, one could estimate population size indirectly from the number of birds caught in a given time period (n_i) and the estimate of detection probability ($\hat{p}_i$) as $n_i/\hat{p}_i$ (e.g., Williams et al. 2002).

The flexibility of the model structure and the relatively user-friendly nature of software such as MARK can lead to "data snooping," as it is tempting to model parameters as a function of an inordinate number of factors. Given the limited sample sizes that often result from mist-net studies, consideration of too many factors increases the risk of spurious results (i.e., good fit but not repeatable and with little predictive ability). Therefore one is better off taking the time *a priori* to formulate hypotheses about the key causal factors that drive the survival process.

Once an *a priori* set of models (e.g., constant survival, time-dependent survival, survival that is age-dependent and influenced by temperature) is chosen, the significance of these factors (relative to the amount of data available) can be evaluated for certain cases through direct tests (i.e., likelihood-ratio tests when models are nested). Alternatively, information theory criteria like AIC (Burnham and Anderson 1998) can be used to choose the most appropriate of the candidate models, or to average parameter estimates across all candidate models, using relative model selection metrics as weights (Burnham and Anderson 1998).

CLOSED POPULATION CAPTURE–RECAPTURE MODELS

In closed population studies, the goal is to estimate population size (*N*). Because the population size, although unknown, is assumed to be constant over the trapping occasions, the modeling procedure fits alternative models that differ with regard to assumptions about temporal, behavioral, and individual heterogeneity in capture probabilities. Otis et al. (1978) and White et al. (1982) reviewed models for closed populations and developed program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991) to fit four models: (1) M_0: Probabilities of capture are the same for all individuals at all capture occasions; (2) M_h: Probabilities of capture differ among individuals, but do not change over capture occasions; (3) M_t: Probabilities of capture differ over capture occasions, but not among individuals; (4) M_b: Probabilities of capture do not change over capture occasions or individuals, but change the first time an animal is captured (behavioral response), so all unmarked animals have one capture probability and all marked animals a different probability. An extreme case of the latter occurs when individuals are only seen once, then they are never seen again (a "removal" model). Models combining these assumptions also exist, including M_{tb}, M_{th}, M_{bh}, and M_{tbh}. Population size can be estimated under all of these models (Chao 2001). In general, individual heterogeneity in detection probability causes difficulties, unless that heterogeneity is small or can be described completely in terms of covariates. Program CAPTURE can be accessed within program MARK. In addition, MARK itself provides the ability to model closed population data for models M_0, M_t, M_b, and M_{tb}, and model M_h, where heterogeneity consists of two unspecified groups with different capture probabilities between them, but homogeneity within group (Pledger 2000).

For those models where program MARK can be used directly, model selection can be conducted using likelihood-ratio tests or AIC, as described above. Program CAPTURE uses a different model selection procedure based on multivariate statistics, which is not always considered reliable. Stanley and Burnham (1998) were unable to develop a satisfactory model selection algorithm and recommended use of an estimator averaging approach.

TOPICS IN CAPTURE–RECAPTURE ANALYSIS

Developments in capture–recapture analysis over the last decade provide some interesting possibilities for analysis of mist-net data. In this section, we briefly discuss some of these developments and their relevance to mist-net studies of passerine birds.

ESTIMATION OF MOVEMENT RATES

Large-scale banding projects tend to have multiple netting stations scattered over large areas. Sometimes, it is of interest to estimate probabilities of moving among stations. The movement can be seasonal, as occurs when moving from breeding to wintering ranges, or can be between years among locations located on the breeding or wintering grounds, or among stopover sites. In fact, many interesting hypotheses about age-specific site fidelity of passerine birds can be phrased in terms of a movement probability study. Models for estimating movement probabilities have been developed by Arnason (1972, 1973), Hestbeck et al. (1991), Nichols et al. (1993), Schwarz (1993), Schwarz et al. (1993), and Brownie et al. (1993).

Movement probabilities have been estimated for birds using resighting data (e.g., Hestbeck et al. 1991, Nichols et al. 1993), band recovery data (Schwarz 1993), and recapture data (Spendelow et al. 1995, Blums et al. 2003). These models have been used with passerines (Senar et al. 2002), but such uses are relatively rare. The almost complete absence of recapture information of birds banded as juveniles poses a particular challenge for capture–recapture studies of passerine birds.

To estimate movement probabilities among locations, the experimental design requires multiple capture stations, and multiple capture occasions at each station. This design yields data on the locations of captured animals at the various sampling periods at the different stations (c.f. Hestbeck et al. 1991). From these fates, we can define capture histories in which stations are indexed by characters (A = at station A, B = at station B) and these characters replace the "1" in the capture history. For example, a capture history for six periods at two stations could be 0A0BBA. Probabilistic models are developed for such data using the following parameters:

ϕ_i^{rs} = transition probability that an animal alive and at station *r* at time *i* is alive and at station *s* at time $i + 1$.

p_i^s = probability of capture for an animal at station *s* at time *i*.

The parameters ϕ^{rs} and p_i^s can be estimated from these data using the multinomial-based statistical models. Because ϕ_i^{rs} is a parameter that includes two interesting events, survival and movement, it is sometimes useful to decompose the transition probabilities. If survival from i to $i + 1$ depends only on location at i, and not on location at $i + 1$, then we can write the transition probabilities as:

$$\phi_i^{rs} = S_i^r \ \psi_i^{rs}$$

where S_i^r = probability that an animal in location r at time i survives until $i + 1$, and $\psi 0_i^{rs}$ = conditional probability that an animal in location r at time i, is present in location s at $i + 1$, given that it is alive at $i + 1$.

Many interesting ecological hypotheses can be tested using these models (Nichols and Kendall 1995). One elaboration is that sometimes these movement probabilities are not simply a consequence of the location of animals at the most recent time period. Instead, animals may retain memories of where they were in earlier periods and the memories can modify their movements. We can develop a test to see whether transition probabilities depend only on location at time i (a Markovian model), or are influenced by location from earlier time periods (a memory model; see Hestbeck et al. 1991, Brownie et al. 1993). To do this, we add additional parameter subscripts, conditioning on releases at i for which locations at time i-1 are known.

Markovian models can be implemented using programs MARK (White and Burnham 1999) and MSSURVIV (Hines 1994). These programs provide estimates (and associated variances) of location-specific survival, capture, and movement probabilities. Memory models can be implemented in program MSSURVIV. It has been difficult to assess fit of multistate models, but a new goodness-of-fit test has been developed by Pradel et al. (2003) for this purpose.

An example of multistate modeling is provided in Hestbeck et al. (1991) using an extensive mark–resighting study of Canada Geese (*Branta canadensis*). Geese were neck-collared at several locations in eastern North America, and resighted in winter for several years in the Mid-Atlantic states, the Chesapeake Bay region, and the Carolinas. The goal of the study was to look at location changes between years in wintering populations. Estimates of mean annual movement probabilities (Table 1) showed that probability of remaining in the same wintering area was lowest for the Carolina population, and that movement probabilities differed among study areas.

Accounting for Transients

One enduring problem in the analysis of capture–recapture data from mist-net studies has been the separation of resident birds from transients in analysis. Because migration periods are difficult to define, and because they may change yearly, many breeding-season banding programs experience transients early and late in the season, and the presence of these birds can greatly influence the results of the capture–recapture analysis. Several approaches have been taken to minimize the effects of transients in the analysis, such as only analyzing data from the period of greatest population stability, eliminating birds from the analysis if they are never recaptured, and eliminating initial captures of all birds. Unfortunately, these approaches either bias survival rate estimates (if all birds seen only once are eliminated from the analysis) or use data inefficiently (if all initial captures are eliminated). Pradel et al. (1997) have developed a model that avoids these problems by incorporating the proportion of transients among newly released birds as a parameter in the model. Let γ_i = proportion of transients in the sample of unmarked birds at period i. In the model, the survival probability for first-captured animals is a sum of survival rates for transients (ϕ_i^t) and residents (ϕ_i^r), each weighted by its proportion, or:

$$\gamma_i \phi_i^t + (1 - \gamma_i) \phi_i^r$$

The "survival" rate (that is, the chance of surviving and returning to the study location) of transients is 0 by definition. Information exists on the survival rate of residents from previously marked animals in the population. This survival probability (ϕ_i^r) can be estimated from animals seen in at least one previous period, permitting estimation of γ_i in the standard multinomial framework. Pradel et al. (1997) illustrate this method with data from Lazuli Buntings (*Passerina amoena*). Their estimates of resident survival rates are substantially higher with this model than with the standard CJS model. This model is implemented in program TMSURVIV (www.mbr-pwrc.usgs.gov/software.html) and can be implemented in MARK (White and Burnham 1999) as a model with trap response in survival.

Peach (1993) describes two alternative procedures for eliminating transient birds from survival analysis of resident birds, and suggests that defining a group of birds recaptured at least 10 days after initial marking will provide sufficient information for separating the cohort into transients and residents. Hines et al. (2003) formalized the suggestion of

TABLE 1. MEAN ANNUAL MOVEMENT PROBABILITIES WITH ASSOCIATED STANDARD ERRORS FOR CANADA GEESE IN THREE WINTERING LOCATIONS IN THE EASTERN UNITED STATES (HESTBECK ET AL. 1991)

	Location year i+1		
Location year i	Mid-Atlantic	Chesapeake	Carolinas
Mid-Atlantic	0.71 (0.02)	0.29 (0.02)	0.009 (0.001)
Chesapeake	0.10 (0.01)	0.89 (0.01)	0.02 (0.002)
Carolinas	0.07 (0.01)	0.37 (0.02)	0.56 (0.03)

Peach (1993) as an extension of the model of Pradel et al. (1997). A bird first captured in period i, which would normally be assigned to the release cohort of unknown resident status, is instead reassigned to the cohort of known residents if it is recaptured at least x days after initial release in the season of release. Nott and DeSante (2002) applied this approach to data for several species from the MAPS program.

ESTIMATING THE PROPORTION OF BIRDS ALIVE BUT NOT BREEDING (PRESENT) AT A STUDY LOCATION

The proportion of animals in a population that are active breeders is an important demographic parameter, but is extremely difficult to estimate. However, there are several possible approaches to estimation of this proportion, if we are willing to assume that presence of a breeding-age animal in a breeding area is evidence of breeding. This assumption, although not generally appropriate, may be acceptable for some bird species. The expected value of the capture probability estimate from an open population model can be written as $E(\hat{p}_i) = \alpha_i p_i^*$, where α_i = probability that the animal is in the sample area (equivalent to breeding probability), p_i^* = conditional probability that the animal is caught, given that it is in the sample area. Recently, two approaches have been developed to estimate the parameter α_i. Both approaches depend on the ability to estimate p_i^*.

Clobert et al. (1990, 1993, 1994) suggested that if we assume that $\alpha_i = 1$ for adult birds, then $E(\hat{p}_i) = p_i^*$ for all i for adults. Thus, we can estimate α_i for other age classes based on the ratio of $\hat{p}_i$ for the class of interest to $\hat{p}_i$ for adults. Pradel and Lebreton (1999) suggest using a multi-state approach to the same model, which permits the use of program MARK or MSSURVIV for maximum-likelihood estimation (Spendelow et al. 2002, Lebreton et al. 2003).

Alternatively, we can use the robust design to estimate α_i (Kendall et al. 1997). Within a season, closed population models can be used to directly estimate p_i^*. Between seasons, CJS models are used to estimate p_i. The ratio of these estimates can be used as an estimate of α_i in cases where all birds at time i have the same probability of being a breeder. Kendall et al. (1997) also consider a more complicated model in which the probability of an individual breeding at time i depends on whether it bred at time i - 1. Programs MARK and RDSURVIV permit estimation of α_i for robust design data. Fujiwara and Caswell (2002), and Kendall and Nichols (2002) consider the estimation of α_i when robust design data are not available or possible, but their results confirm that the robust design should be used if at all possible.

ESTIMATION OF RECRUITMENT AND POPULATION CHANGE

One of the most interesting new developments in capture–recapture methods is the possibility that the Jolly-Seber approach can be reparameterized to directly estimate the demographic parameters of recruitment rate and finite rate of population change. In the original J-S model, survival and capture probabilities are the primary parameters to be estimated. Population size and recruitment do not appear as model parameters, but can only be estimated as functions of capture and survival rates. However, Pradel (1996) has shown that the model can be reformulated to include any one of these parameters:

$1 - \gamma_i$ = proportion of birds in the population at i that are new (i.e., that entered the population between periods i - 1 and i; this can be viewed as a turnover statistic).

f_i = number of new animals present at i + 1, per animal present at i (this can be viewed as a per capita recruitment rate).

λ_i = finite rate of population increase (N_{i+1}/N_i).

Under some circumstances, γ_i and $1 - \gamma_i$ represent the proportional contributions of survival and recruitment to population growth, an interpretation analogous to elasticities for asymptotic population projection modeling (Nichols et al. 2000).

Uses of the new parameterizations include (1) direct modeling of γ_i or f_i as functions of other study data (e.g., estimates of nest success) or of environmental covariates, which can help provide a mechanistic understanding of the recruitment process; (2) direct incorporation of recruitment rate estimates into population projection models; and (3) use of the λ-parameterization to provide a canonical framework for estimation of population change from capture–recapture and other sources of data. Under situation 3, if another formal estimation method (e.g., variable circular plot, line transect) is used on the mist-net study site, then a joint likelihood can be constructed and λ_i estimated using both data sources. If count data (e.g., point counts) are obtained on the study area, then λ_i can be modeled as a function of these data permitting (1) a test of the hypothesis that the count data really do provide a good "index" of population change and, if they do, (2) use of these data as covariates to obtain a better estimate of λ (Nichols and Hines 2002).

This modeling is relatively recent (Pradel 1996), and few examples exist of its application to mist-net studies (but see Nichols et al. in press). However, we believe the approach of a canonical framework permitting direct estimation of rate of population change using all relevant data (e.g., capture–recapture and point-count) simultaneously, should be preferable to the approach of obtaining separate estimates of λ_i from different data sources and then attempting to combine them or reconcile differences among them.

CAPTURE–RECAPTURE AND MIGRATION BANDING

Banding of birds during migration occurs at many capture stations throughout North America, and data from these stations provide a sometimes controversial view of population changes in birds that breed in the northern regions of North America. Most investigators who attempt to estimate trends in migrating birds use indices to number of birds passing through a banding station (e.g., total number of individual birds captured), but this index is clearly influenced by many environmental variables (Dawson 1990). Though data can be adjusted for some of these variables (e.g., effects of date, weather, and moon phase; Dunn and Hussell 1995, Dunn et al. 1997, Hussell *this volume*), capture probability may be influenced by other factors not measured or accounted for. Capture–recapture methods provide a reasonable alternative to these index approaches, and use of open-population models permits estimation of both the total number of birds passing through a station and residence times of birds at migration stations (Nichols 1996).

Although not commonly done (but see Brownie and Robson 1983, Pollock et al. 1990), it is possible to estimate residence times ("survival") at migration banding stations using standard CJS models. These analyses would use recapture data from the stations to estimate the proportion of animals missed by the sampling, and "survival" rates (primarily the probability of remaining at the station) of marked birds at the station. From these rates an average residence time can be estimated as $-1/\ln(\hat{\phi})$, where $\hat{\phi}$ is the estimate of average survival rate between sample intervals. The total population passing through the station can be estimated as the sum of the CJS estimates of B_i, the number of new animals entering the population between sampling periods (e.g., Shealer and Kress 1994).

Schaub et al. (2001) further generalized the above approach for estimating total stopover duration. They use the method of Pradel (1996) to estimate stopover duration before or after capture, using "recruitment" and "survival" analyses, respectively. They then combine them into total stopover time. They implement this approach in Program SODA (www.cefe.cnrs-mop.fr/wwwbiom/Dyn-Populations/biom-ftp.htm).

The superpopulation modeling approach of Crosbie and Manly (1985) and Schwarz and Arnason (1996) provides an alternative approach to analyzing migration banding data. Under this approach, parameters reflecting entry of new animals into the population are incorporated directly into the model, and total number of individual birds using the station during the entire sampling period (between the first and last samples) can be estimated. If migration banding as described above is conducted for a series of years, the within- and between-year information can be combined to estimate survival rate, as well as the probability that an individual used that particular stopover site in a given year (Schwarz and Stobo 1997, Kendall and Bjorkland 2001).

Of course, these analyses require recapture or resighting data for survival rate estimation, and hence they will only work well when "sufficient" recaptures or observations exist. Even though limited recapture information exists for most species, we feel that these methods have great potential to improve estimation associated with migration banding programs as they provide a means for investigators to directly evaluate the critical assumption of consistency in proportions of animals captured. Innovative applications of methods to increase the number of recaptures (e.g., through resighting procedures) may increase the feasibility of applying capture–recapture methods to a larger number of species, and provide a means for generally estimating the proportion of birds "missed" in capture indices during migration.

SPECIES RICHNESS ESTIMATION

Information on biodiversity has become of increasing importance to conservation, and surveys of species richness are frequently conducted in the Neotropics. Often, the total number of species captured in mist nets, or identified through other sampling procedures, is used as the estimate of species richness. Unfortunately, this estimate is clearly biased, and the extent of the underestimate is a function of both the probabilities of encountering species and the sampling effort. Capture–recapture methods can be used with replicated species list data to directly estimate the total numbers of species present from mist-net and other samples (Dawson et al. 1995, Nichols and Conroy 1996, Boulinier et al. 1998).

To do this, species are treated as individuals, and capture histories can be developed for each species by (1) observing presence–absence of the species at multiple trapping occasions at a single station; (2) observing presence–absence over multiple stations at a single occasion; or (3) recording number of individuals per species at a single station and occasion. The data from approaches (1) and (2) can be analyzed using the closed population models of Otis et al. (1978); models that allow heterogeneity in capture probabilities among species (such as model M_h) are likely to be most useful. In these models, total number of species is estimated, allowing each species to have a different chance of capture.

If data from only a single trapping period are available (scenario 3), a version of the Burnham and Overton (1979) model, M_h, can still be used to estimate total species richness. For this estimator, data are summarized as number of species for which one bird was caught or seen, the number of species for which two individuals were caught or seen, etc., up to the number of species for which five individuals were seen. J. E. Hines has written a program to estimate species richness using the limiting form of model M_h with capture frequency data (Hines et al. 1999). Application of this approach to mist-net data is shown in Karr et al. (1990b).

We view these species-richness estimation methods as providing a useful way of resolving some of the sampling problems that occur in tropical mist-net studies, in which the mist nets do not sample species with equal probability, and counts encounter a different (but not necessarily independent) subset of the bird species present in an area. For these areas, data can be combined from mist-net captures and point counts to get a composite species richness estimate that is free of the bias associated with total number of species captured (Dawson et al. 1995). These methods also permit estimation of parameters associated with community dynamics, such as rate of change in species richness, local extinction rate, and local colonization or immigration rate (Nichols et al. 1998a,b).

CONCLUSIONS

In this paper we have tried to provide some insights into how capture–recapture estimation can be useful in mist-net studies, and describe some new procedures that should be of use to biologists. We emphasize that capture–recapture models form an appropriate structure for thinking about mist-netting studies, and should be considered in the design of any mist-net study. Indices that are not adjusted for the proportion of birds missed by the sampling procedure involve untested assumptions, and capture–recapture provides a way to test these assumptions (Skalski and Robson 1992, MacKenzie and Kendall 2002).

All of the statistical models discussed in this paper are defined in terms of a series of parameters that are assumed to be of importance. Investigators must collect data and use evidence from the data (such as goodness-of-fit tests) to evaluate whether the set of parameters is reasonable for their data sets. Estimation of some parameters, such as number of transients in the population, requires more restrictive assumptions (equal capture probabilities of transients and residents in the transient model) than does estimation of other parameters (e.g., proportion of transients in the sample of unmarked birds does not require this assumption). Before using these models, investigators should evaluate the underlying biological and statistical assumptions implicit in each model. However, we emphasize that these methods will often be preferable to index-based methods, as the latter frequently require much more restrictive assumptions, although these are often left unspecified.

There have been many exciting advances in capture–recapture work over the last decade, and we have discussed advances in the estimation of movement probabilities, survival rates in the presence of transients, populations at migration stopover sites, temporary emigration (breeding proportions), rate of population change, and species richness. User-friendly computer programs exist for application of most of these procedures. Understanding these methods will allow investigators to (1) define the parameters that they want to estimate using a banding study; (2) develop study designs that will allow them to estimate the parameters; and (3) define needed sample sizes, in terms of capture probabilities and number of animals captured and recaptured, that will be needed to achieve prespecified goals of estimate precision and test power. Studies designed with such a focus should permit stronger inferences about avian population dynamics than have been possible previously.