ESTIMATING RATES OF LOCAL SPECIES EXTINCTION, COLONIZATION, AND TURNOVER IN ANIMAL COMMUNITIES

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Abstract. Species richness has been identified as a useful state variable for conservation and management purposes. Changes in richness over time provide a basis for predicting and evaluating community responses to management, to natural disturbance, and to changes in factors such as community composition (e.g., the removal of a keystone species). Probabilistic capture–recapture models have been used recently to estimate species richness from species count and presence–absence data. These models do not require the common assumption that all species are detected in sampling efforts. We extend this approach to the development of estimators useful for studying the vital rates responsible for changes in animal communities over time: rates of local species extinction, turnover, and colonization. Our approach to estimation is based on capture–recapture models for closed animal populations that permit heterogeneity in detection probabilities among the different species in the sampled community. We have developed a computer program, COMDYN, to compute many of these estimators and associated bootstrap variances. Analyses using data from the North American Breeding Bird Survey (BBS) suggested that the estimators performed reasonably well. We recommend estimators based on probabilistic modeling for future work on community responses to management efforts as well as on basic questions about community dynamics.

Key words: animal community ecology; capture–recapture models; community dynamics; conservation and management; local colonization; local extinction probability; North American Breeding Bird Survey; species turnover.

INTRODUCTION

Biological diversity is viewed as a state variable reflecting status of the biosphere (Barbault and Hochberg 1992), and is recognized as "central to the productivity and sustainability of the earth's ecosystems" (Christensen et al. 1996:671) and as an important conservation and management objective (e.g., Scott et al. 1993, Mangel et al. 1996). Operationally, species richness is frequently selected as a variable reflecting system state, and is often used as such in management and conservation efforts and in investigations of the effects of human development and disturbance on biodiversity (e.g., Scott et al. 1993, Conroy and Noon 1996, Keddy and Drummond 1996, Wiens et al. 1996). Estimation of rates of change in biodiversity and investigation of factors responsible for change have been identified as important ecological research topics in the Sustainable Biosphere Initiative (Lubchenko et al. 1991). Here, we focus on methods for estimating rates of local extinction, turnover, and colonization, the community-level vital rates responsible for changes in species richness over time.

Advances in ecology and conservation biology de-

pend on the ability to measure or estimate quantities that are relevant to theory, management, and associated hypotheses. At the population level of biological organization, ecologists and managers are interested in such quantities as population size and rates of mortality, recruitment, and movement. Because animal population ecologists and managers can seldom enumerate all of the individual animals in a population or a sampled area, they must estimate these quantities using statistical models that explicitly incorporate the probability of detecting an animal, given that the animal is in the sampled area (Nichols 1992, Lancia et al. 1994). Animal population ecologists and managers have placed strong emphasis on the development and use of appropriate statistical inference procedures that explicitly incorporate unknown animal detection probabilities (see Otis et al. 1978, Seber 1982, Brownie et al. 1985, Burnham et al. 1987, Pollock et al. 1990, Lebreton et al. 1992, Buckland et al. 1993, Lancia et al. 1994, Wilson et al. 1996).

Animal community ecology has not seen parallel development of statistical inference procedures that recognize and explicitly incorporate species detection probabilities. Few animal sampling programs provide community censuses (we define a community census as a complete enumeration of all the species in a com-

munity), leading early ecologists to consider quantitative methods to extrapolate from the number of species observed in samples to the number of species in the sampled community (e.g., Fisher et al. 1943, Preston 1948). This concern for sampling issues was not often found in subsequent ecological literature, and published research in animal community ecology and management contains numerous studies in which species richness (the number of species in an animal community) was equated with the number of species enumerated in a sample. More recently, recognition that not all species are detected by sampling efforts has led to the use of probabilistic estimators of species richness (Burnham and Overton 1979, Derleth et al. 1989, Karr et al. 1990, Palmer 1990, Coddington et al. 1991, Baltanas 1992, Bunge and Fitzpatrick 1993, Hodkinson and Hodkinson 1993, Colwell and Coddington 1994, Solow 1994, Dawson et al. 1995, Thiollay 1995, Walther et al. 1995, Nichols and Conroy 1996, Boulinier et al. 1998). Explicit recognition of detection probabilities has also led to probabilistic approaches to inferring extinction of a particular species from sighting data (Solow 1993, Reed 1996).

Despite the use of such methods for estimating species richness, the incorporation of species detection probabilities into estimation methods has not extended to quantities associated with community dynamics. For example, recently proposed methods for estimating species extinction rates and related metrics require sampling situations in which species are identified and detected in different samples with probability 1 (e.g., Pimm et al. 1993, Clark and Rosenzweig 1994, Rosenzweig and Clark 1994, Burkey 1995, Cook and Hanski 1995). Discrepancies among published estimates of extinction rates (e.g., Budlansky 1994, Heywood et al. 1994) emphasize the need for reliable estimation methods. Recent work on community vital rates other than extinction (e.g., rates of colonization and turnover) is also based on species counts over time, with no effort to deal with detection probabilities <1 (e.g., Hinsley et al. 1995, Mehlman 1997).

If certain sampling situations lead to the detection of all species, then methods based on that assumption are appropriate. However, species detection probabilities sometimes constitute a nontrivial source of variation in species count data (Boulinier et al. 1998), and analyses that ignore this source of variation can lead to invalid inferences about variation in species richness over time and space. For example, local extinction is generally defined as a species detected at time i and not detected at some later time j, whereas local colonization is defined as a species not detected at time i, but detected at a later time j. Consider species present, yet not detected, at sampling period i. If such a species were not present at j, it would represent an unrecorded extinction, whereas if it were present and detected at j, then it would erroneously be recorded as a colonization. Similarly, a species detected at i and present,

yet not detected, at j would be erroneously recorded as an extinction. These errors in recording species extinction and colonization events lead to errors in turnover metrics as well.

In the present paper, we introduce some estimators that should be useful for studying temporal changes in animal communities in sampling situations where not all species are detected. Our personal view is that very few studies can insure species detection probabilities of 1. We consider estimation of species extinction probability, species turnover rate, and number of colonizing species. The estimators are based on capture–recapture models, but the community sampling procedures that produce data for these estimators can be of several possible forms and do not require catching and marking individual animals. We will illustrate some of the estimators using count data from the North American Breeding Bird Survey, BBS (Robbins et al. 1986, Peterjohn and Sauer 1993).

General Approach to Estimation

The estimation approach that we will consider requires sampling an animal community at two different times. We are interested in estimating quantities associated with change in the species composition of the community during the interval. Our estimators require estimates of the number of species in the entire community, and/or in specified subsets of the community, at one or both of the time periods. This estimation requires consideration of species detection probability, which we define for a particular species as the probability that at least one individual of the species is detected in our sampling efforts. Species detection probability can be written as a function of the number of individuals belonging to the species in the area being sampled, and the average detection probability for an individual (e.g., the capture probability parameter of population-level capture–recapture studies). Species detection probability thus depends on both population size and the behavioral attributes of individuals relative to sampling efforts (e.g., activity pattern, vocalization, body size, tendency to enter traps or other sampling devices, etc.) We suspect that species detection probabilities are likely to be <1, and our efforts to deal with such detection probabilities distinguish our methods from other approaches.

Sampling animal communities

Several possible approaches can be used to sample an area for the purpose of estimating species richness and quantities related to changes in richness over time and space (Nichols and Conroy 1996). Quadrat sampling has been especially popular and involves the subdivision of the total area of interest into a number of quadrats or small sampling units. A random sample of quadrats is selected, and the investigator(s) identifies and enumerates species found on each selected quadrat using virtually any set of sampling methods (e.g., direct

observation of animals and their sign [tracks, scats, nests, etc.], auditory identification, trapping and netting with different trap and net types, etc.). It is best to use the same basic set of sampling methods and expend similar effort on each of the sampled quadrats, although models permitting variation in species detection probabilities among the different quadrats are available (see Nichols and Conroy 1996, Boulinier et al. 1998).

Estimating species richness

The result of the sampling efforts is a species list for each quadrat that identifies the species detected. Several different estimators have been proposed for use with such data from quadrat species lists (Burnham and Overton 1979, Heltsche and Forrester 1983, Smith and van Belle 1984, Chao 1987, Mingoti and Meeden 1992, Bunge and Fitzpatrick 1993). In our work on species richness estimation (Boulinier et al. 1998), we have focused on the use of capture–recapture models initially developed for use with data from closed animal populations (see Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991), where ''closed'' populations refer to those in which no animals enter or leave the population between sampling periods.

The estimation models that we have considered include three possible sources of variation in detection probabilities (Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991): variation from one quadrat to another (analogous to temporal variation in capture–recapture modeling at the population level), heterogeneity among species (analogous to heterogeneity among individuals), and variation between the first quadrat sampled and subsequent quadrats (analogous to behavioral response). In our initial work using these models to estimate species richness (Boulinier et al. 1998), we selected a number of BBS routes and ran the corresponding data through program CAPTURE (Rexstad and Burnham 1991), which includes a model selection algorithm to aid the user in selecting the model that most closely corresponds to the data. Model M_h (with detection probabilities that are heterogeneous among species) was by far the most frequently selected model in these analyses of BBS data (Boulinier et al. 1998). This finding was consistent with our a priori expectation that heterogeneity of detection probabilities among species is likely to be substantial when sampling animal communities, and that the models including such heterogeneity are likely to be of most use for estimating species richness.

For all of the examples reported here, we use the jackknife estimator for model M_h proposed by Burnham and Overton (1978, 1979) because it is robust to deviations from underlying assumptions and has performed well both in simulation studies (Otis et al. 1978, Burnham and Overton 1979, Pollock and Otto 1983, Norris and Pollock 1996) and in field trials with known species richness (Palmer 1990, 1991). However, other estimators for model M_h (e.g., see Smith and van Belle

1984, Chao 1989, Lee and Chao 1994, Norris and Pollock 1996) and richness estimators based on other models (e.g., Chao et al. 1992) can also be used in the community-dynamic estimators that we present. The data required for estimation with the jackknife estimator of model M_h are the frequencies, f_h, or numbers of species detected on exactly $h = 1, 2, \ldots, K$ of the sampled quadrats, where K is the total number of quadrats sampled (Burnham and Overton 1978, 1979). The general form of the jackknife estimator for species richness is

$$\hat{N}_k = R + \sum_{h=1}^{K} \alpha_{hk} f_h \qquad (1)$$

where R is the number of species observed, and the α_{hk} are constants (see Burnham and Overton 1978, 1979) corresponding to jackknife estimators of order k ($\alpha_{hk} = 0$ for $h > k$).

Pollock's robust design

The application of closed models to the estimation of species richness is straightforward (e.g., see Boulinier et al. 1998), because it is reasonable to think of a sampled community being ''closed'' to local extinction and colonization for the relatively short periods over which species presence–absence data are collected. However, in order to estimate quantities concerning community change between two sampling periods separated by a long time period (e.g., 10 yr), we require a more general approach. Standard capture–recapture models for open populations (e.g., Pollock et al. 1990, Lebreton et al. 1992) permit such change, but do not deal well with heterogeneous detection probabilities (see later discussion). Thus, we focused on the robust design of Pollock (1982) as a means of developing robust estimators for quantities associated with community change.

Pollock's (1982) robust design involves sampling at two different temporal scales. Primary sampling periods are separated by times that are sufficiently large to expect changes in the population or community from one primary period to the next. In one of our numerical examples, we computed quantities relevant to bird community change occurring between sampling periods spaced 20 yr apart (e.g., the primary sampling periods were 1970 and 1990 and BBS data were obtained from a single survey route during both years). Some number of secondary samples or sampling periods occurs within each primary period. The secondary sampling periods should be sufficiently close together that we would not expect the community to change during the course of the secondary sampling. In our example using data from a single BBS route, secondary samples are represented by the multiple stops made along the route in each of the two years of interest (see later discussion).

There are multiple approaches to estimating quantities of interest from data collected under the robust

design (e.g., Kendall and Pollock 1992, Nichols et al. 1992, 1994, Kendall et al. 1995, 1997). In the community-dynamic work reported here, all of our estimators are based on use of closed-model estimators for species richness, computed over the secondary samples within each primary sampling period. Estimates of parameters relevant to community change are computed as ratios or other functions of closed model richness estimates obtained for different primary sampling periods.

Variance estimation

Here, we present only point estimators for quantities of interest in community dynamics. Because estimates of parameters relevant to community change are computed as ratios or other functions of closed-model richness estimates, it is possible to use the delta method (e.g., Seber 1982) and other approximations to obtain estimators of associated variances and covariances. However, these approximations would be based necessarily on the variance estimates for the closed-model richness estimators; in our examples, they would be based on the variance estimator for the M_h jackknife estimates. These variance estimators themselves do not always perform well, as the coverage of approximate 95% confidence intervals based on the jackknife estimator and its variance has sometimes been poor in simulation studies (e.g., Otis et al. 1978, Burnham and Overton 1979). Therefore, we would not expect approximations that are functions of these variance estimates to necessarily perform well. For this reason, we have chosen to compute bootstrap variance estimates for all of the estimators presented. An outline of our bootstrap computational methods is presented in the Appendix.

ESTIMATORS OF COMMUNITY DYNAMICS

Rate of change in richness

Rate of change in species richness between two sampling periods i and j can be estimated as

$$\hat{\lambda}_{ij} = \frac{\hat{N}_j}{\hat{N}_i} \qquad (2)$$

where N_i denotes species richness at time i and where, typically, $i < j$ (j is the more recent of the two time periods). The estimates of species richness are obtained using species occurrence data in conjunction with closed-model capture–recapture estimators such as those for M_h (e.g., the jackknife estimator of Eq. 1; also see Burnham and Overton 1978, 1979).

If $\bar{p}_i = \bar{p}_j$, that is if the average species detection probabilities are the same for the two periods, then an alternative estimator for rate of change is

$$\hat{\lambda}_{ij} = \frac{R_j}{R_i} \qquad (3)$$

where R_i denotes the number of species actually observed during sampling efforts in period i. Estimators such as Eq. 3, based on the raw count statistics, should have smaller variances than estimators such as Eq. 2, which are based on estimated quantities (e.g., Skalski and Robson 1992). However, the estimator in Eq. 3 will be biased if $\bar{p}_i \neq \bar{p}_j$. A variety of factors could lead to such an inequality in detection probabilities, including temporal changes in observers, habitat, environmental conditions relevant to sampling, and species composition.

Under model M_h, the hypothesis of equal detection probabilities for two samples can be tested using the raw frequency data, f_h, with a $2 \times K$ contingency table χ^2 test of the null hypothesis that the proportions of species found in $h = 1, 2, \ldots, K$ secondary samples are similar for the two primary sampling periods, i and j. Finally, note that the estimated quantity, rate of change in species richness, does not provide information about possible changes in species composition (the identities of the species). The estimators dealing with local extinction, turnover, and colonization do permit inferences about changes in community composition.

Local extinction probability

Survival and reproductive rates are the so-called vital rates responsible for population changes, and the analogous community vital rates are local extinction and colonization rates. We define local extinction probability as the probability that a species present in the community during primary sampling period i is not present at some later period j. We can employ the robust design approach of Kendall and Pollock (1992) and Nichols et al. (1992) to estimate this quantity using the reasoning that underlies open capture–recapture survival estimators (Jolly 1965, Seber 1965). We first condition on the number of species observed in period i (denote this number as R_i), and then estimate the number of these species still present in period j (denote this number as $M_j^{R_i}$). Local extinction probability is then estimated as

$$1 - \hat{\phi}_{ij} = 1 - \frac{\hat{M}_j^{R_i}}{R_i} \qquad (4)$$

where ϕ_{ij} is the complement of extinction probability and denotes the probability that a species present in i is still present in j.

The estimation of $M_j^{R_i}$ is based on closed models with species occurrence data from period j, and can be accomplished using either of two approaches. The most conservative approach is to use only occurrence data for period j (i.e., species presence–absence data over the secondary samples within primary sampling period j) from species also observed at primary period i (i.e., use only $m_j^{R_i}$; members of R_i that are also seen at j). These data are used directly with a closed-population estimator such as Eq. 1 to estimate $M_j^{R_i}$.

The second approach requires the additional as-

sumption that average species detection probabilities at time j are the same for the $M_j^{R_i}$ species that are present in both i and j, and the $N_j - M_j^{R_i}$ species present at j but not at i. If this assumption holds, then we can estimate the number of R_i still present at j as

$$\hat{M}_j^{R_i} = \frac{m_j^{R_i}}{\hat{\bar{p}}_j} \qquad (5)$$

where $\bar{p}_j$ is the average detection probability of all species present at j. This $\bar{p}_j$ is estimated by using occurrence data from all species observed at period j (R_j) in conjunction with program CAPTURE to estimate total species richness at j (N_j), and then using the following estimator:

$$\hat{\bar{p}}_j = \frac{R_j}{\hat{N}_j}. \qquad (6)$$

The first approach for estimating $M_j^{R_i}$ should have smaller bias, but larger variance. The second approach should yield $\hat{M}_j^{R_i}$ with larger bias (perhaps), but smaller variance. A decision about the appropriateness of the second approach can be based on a test for equality of average detection probabilities for species present in primary period j that were and were not detected in period i. This test can be conducted as a χ^2 test for a $2 \times K$ contingency table using the f_h for the two groups of species detected in primary period j: those detected in primary period i ($m_j^{R_i}$) and those not detected in primary period i ($R_j - m_j^{R_i}$). The resulting χ^2 statistic provides a test of the null hypothesis of equal proportions of species detected from the two groups. Whenever the group, $R_j - m_j^{R_i}$, is relatively small, the contingency table test for equal detection probabilities is not likely to be very powerful; in such cases, we recommend the first approach for estimating $M_j^{R_i}$ for use in the extinction probability estimator of Eq. 4.

Local species turnover

The literature of community ecology contains a number of definitions of turnover. Most of these definitions are based on statistics (functions of data) rather than on a specified underlying parameter of interest. Thus, we are faced with different turnover metrics that reflect the different intuitions of their respective devisers about what turnover actually is. Here, we follow an approach that we adopted in paleobiological work with fossil data (Nichols et al. 1986), and define turnover between two times, i and j, where j is the more recent period ($i < j$), as the probability that a species selected at random from the community at time j is a ''new'' species (i.e., it was not present in the community at time i). This turnover parameter arises naturally in the modeling of capture–recapture data (Pollock et al. 1974, Pradel 1996). It is a function of rates of extinction and colonization and reflects dissimilarity between communities at two different points in time. The parameter achieves its maximum value (1) when all of

the species present in period j are new (not present at i) and its minimum value (0) when all of the species present at j are survivors from period i.

Estimation of this turnover parameter is based on an observation by Pollock et al. (1974) about the temporal symmetry of capture–recapture data for open populations. Specifically, they observed that if capture history data are viewed in reverse time order (treating the final sampling period, K, as the initial period and treating sampling period 1 as the final period), then the standard Cormack-Jolly-Seber estimator for survival between two periods estimates the fraction of species in the more recent period that are ''old,'' or survivors from the previous period. The complement of this estimator estimates the proportion of species that are new and were not present in the previous period (Pollock et al. 1974, Nichols et al. 1986, Pradel 1996).

Our estimation of community turnover will thus be accomplished by using the extinction probability estimator of Eq. 4 with data placed in reverse time order. The notation is the same as that for the survival estimator (Eq. 4), except for a change in the subscripting that denotes the change in temporal ordering. We estimate turnover as

$$1 - \hat{\phi}_{ji} = 1 - \frac{\hat{M}_i^{R_j}}{R_j} \qquad (i < j). \qquad (7)$$

The key to the estimation involves $\hat{M}_i^{R_j}$, the estimated number of species observed in j that were also present in i. Estimation is accomplished, as with extinction probability, by conditioning on the subset of species actually observed at j and then estimating the number of these that were also present in i. As was the case with extinction, the estimation of $M_j^{R_i}$ can be accomplished in either of two ways. The most conservative approach, requiring fewest assumptions, involves use of a species richness estimator with species occurrence data for the members of R_j that were also observed in period $i(m_i^{R_j})$. The other approach involves estimating average detection probability for period i, $\hat{p}_i$, from all species observed at i, and then applying this estimate to the number of species observed at i that were also later observed at j (see Eqs. 5 and 6). As was noted in the discussion of extinction probability estimators, the first approach should have smaller bias and larger variance than the second approach. At this point, we recommend that the estimation of turnover be based on the first approach.

Number of local colonizing species

Denote as B_{ij} the number of species not present in the local area at time i that colonize the area between times i and j and are still present at time j. The approach to estimation is similar to that used under the robust design to estimate number of new recruits entering the studied population between two sampling periods (Pollock 1982, Pollock et al. 1990). This approach simply subtracts from the estimated species richness at time j,

the estimated number of surviving species from a previous time, i:

$$\hat{B}_{ij} = \hat{N}_j - \hat{\phi}_{ij}\hat{N}_i \qquad (8)$$

where B_{ij} denotes the number of species not present at time i that entered the community between times i and j and are still present at time j.

Annual extinction and recolonization probabilities

The extinction probability estimator of Eq. 4 estimates the probability that a species present at time i is absent at some later time j, but specifies nothing about the detailed process leading to this event. In the case of previously published turnover and extinction estimators based on census data ($p_i = 1$), this concern for underlying process has been linked to interest in methods for scaling estimators for the length of the interval between census/sampling periods (e.g., Diamond and May 1977, Clark and Rosenzweig 1994, Russell et al. 1995). First-order Markov process models of the general type considered by Simberloff (1969; also see Diamond and May 1977, Clark and Rosenzweig 1994, Russell et al. 1995) provide a reasonable underlying model for community dynamics. This type of model has led to appropriate estimators for local, annual extinction and recolonization probabilities based on census data collected at both annual (Diamond and May 1977, Rosenzweig and Clark 1994) and longer (Clark and Rosenzweig 1994) intervals. Here, we consider estimation under Markovian models in the situation where species detection probabilities are <1.

In order to survive (species survival probability is the complement of extinction probability) between two primary periods, i and j, a species present at i may survive every year between i and j, or it may go locally extinct and then recolonize during this period. Assume a simple situation in which we are interested in changes within a bird community between years i and $i + 2$. We can write

$$\phi_{i,i+2} = \phi_{i,i+1}\phi_{i+1,i+2} + (1 - \phi_{i,i+1})\gamma_{i+1,i+2} \qquad (9)$$

where $\gamma_{i+1,i+2}$ is the probability that a species present in the community at some earlier time (in this case, time i), but not at time $i + 1$, recolonizes the area during the interval $(i + 1, i + 2)$ and is present in the community at $i + 2$.

We can estimate each of the three species survival probabilities in Eq. 9 using the general estimator presented in Eq. 4. We can then solve Eq. 9 for $\gamma_{i+1,i+2}$ to obtain

$$\hat{\gamma}_{i+1,i+2} = \frac{(\hat{\phi}_{i,i+2} - (\hat{\phi}_{i,i+1}\hat{\phi}_{i+1,i+2}))}{(1 - \hat{\phi}_{i,i+1})}, \quad \text{or}$$

$$\hat{\gamma}_{i+1,i+2} = \frac{\dfrac{\hat{M}_{i+2}^{R_i}}{R_i} - \left[\left(\dfrac{\hat{M}_{i+1}^{R_i}}{R_i}\right)\left(\dfrac{\hat{M}_{i+2}^{R_{i+1}}}{R_{i+1}}\right)\right]}{1 - \left(\dfrac{\hat{M}_{i+1}^{R_i}}{R_i}\right)}. \qquad (10)$$

We note that Eq. 9 represents the kind of parameterization that will probably be needed for open-model approaches to the estimation of community-level quantities. Open models are based on capture history data, with row vectors of 0's and 1's representing no capture/detection and capture/detection, respectively. In the usual capture–recapture framework, a "0" appearing between 1's (e.g., the 0 in capture history 101) indicates an animal that is present but not caught in the sampling period. However, in community studies, an interior 0 in a detection history can indicate either a species that is present but not detected (sometimes referred to as a "sampling 0"), or a species that is not present (locally extinct) yet recolonized at a later time (sometimes referred to as a "structural 0"). In this respect, the modeling of species detection history data in the presence of local extinction and recolonization is similar to the modeling of capture–recapture data in the presence of temporary emigration. The robust design (Pollock 1982) provides the information needed to estimate quantities of interest in the presence of temporary emigration (Kendall et al. 1997), and may provide a basis for estimating community parameters from detection history data using parameterizations such as that of Eq. 9.

In the formulation of Eq. 9, our parameters correspond directly to events that are potentially observable for the time scale of our sampling. If assumptions are made about the number of events that can occur between sampling periods, then it is sometimes possible to estimate parameters under alternative models. For example, Clark and Rosenzweig (1994) and Rosenzweig and Clark (1994) consider a Markov model similar to Eq. 9, except that a species present at times i and $i + 1$ can reflect either a species that survived the interval or a species that went locally extinct and then recolonized. Under their formulation, a species absent at i and then present at $i + 1$ reflects only recolonization (e.g., it cannot reflect recolonization, followed by extinction, followed by recolonization), and estimation of both extinction and recolonization probabilities is possible (assuming species detection probabilities of 1 and assuming a stationary Markov process [extinction and recolonization probabilities do not vary over time]). By considering stationary processes and by carefully defining the number of events that can occur during the interval between sampling periods, it is thus sometimes possible to estimate parameters for such models, although this becomes more difficult when $p < 1$. At present, our estimates obtained using the robust design correspond to parameters defined at the same temporal scale at which extinction and recolonization events are observable. However, we require no assumptions about the stationary nature of the underlying Markov process, and permit local extinction and recolonization probabilities to be time specific, as indicated by the subscripting in Eqs. 9 and 10.

TABLE 1. Species detection statistics for Maryland BBS (Breeding Bird Survey) route 25, 1970 and 1990.

Species group	No. species detected	No. species detected on exactly h of the five groups of stops (f_h)				
		f_1	f_2	f_3	f_4	f_5
Total no. species detected (1970), R_{70}	65	15	8	10	12	20
Total no. species detected (1990), R_{90}	55	15	8	13	12	7
No. members of R_{70} detected in 1990, $m_{90}^{R_{70}}$	48	10	6	13	12	7
No. members of R_{90} detected in 1970, $m_{70}^{R_{90}}$	48	7	6	6	9	20

EXAMPLE ANALYSES

We illustrate some of our estimators using data collected as part of the BBS. This survey is carried out every spring on permanent survey routes randomly located along secondary roads throughout the United States and southern Canada. Each route is 39.4 km long and consists of 50 stops spaced at 0.8-km intervals. The observer drives along the route, exiting the vehicle at each stop to record all birds seen and heard within 0.4 km of the stop during a 3-min observation period (Robbins et al. 1986, Peterjohn and Sauer 1993). In the BBS files, data are summarized by groups of 10 stops. Hence, there are five such summary records for each survey route, and for each summary record (each group of 10 stops), we have a species list and the number of individuals counted for each detected species. For our examples, the raw data used to compute our estimates on each survey route are simply the species lists for each of the five groups of stops. We thus treat each group of 10 stops along a survey route as a "quadrat" sampling the area covered by the entire survey route. These five quadrats are the secondary samples of our robust design approach. It is possible to apply our methods to any subset of total species (e.g., defined by taxonomy, foraging habit, etc.), but in our examples, we include all avian species.

All computations were conducted using program COMDYN, developed by Hines et al. (*in press*). Based on the general applicability of model M_h to BBS data (Boulinier et al. 1998), all of the estimators in program COMDYN are based on the jackknife estimators of Burnham and Overton (1978, 1979). Variance estimation in program COMDYN is accomplished using a bootstrap approach (Appendix). COMDYN also includes goodness-of-fit tests of the detection frequency data to model M_h and tests of the null hypothesis that two sets of detection frequency data were produced by the same detection probabilities.

We selected two BBS routes, Maryland route 25 and Wisconsin route 1, and computed estimates relevant to community dynamics between 1970 and 1990. The raw data (Tables 1 and 2) on which all of these estimators are based include simply the number of species detected on 1, 2, . . . , 5 of the route segments, for all species observed in 1970 (R_{70}) and 1990 (R_{90}), for the number of species observed in 1970 that were also detected in 1990 ($m_{90}^{R_{70}}$), and for the number of species observed in 1990 that were also detected in 1970 ($m_{70}^{R_{90}}$).

Model M_h adequately ($P > 0.10$) fit all four sets of detection frequency data in Table 1 for Maryland BBS route 25, 1970 and 1990. The richness estimate for 1990 was smaller than that for 1970, although the 95% CIs for the two estimates overlapped substantially (Table 3). The estimated rate of change based on the richness estimates was 0.88, but the confidence interval for rate of change included values >1. However, the test for equal average detection probability in 1970 (estimate, 0.83) and 1990 (estimate, 0.79) provided little evidence of a difference ($\chi_4^2 = 5.86$, $P = 0.11$), justifying the use of Eq. 3 for estimating rate of change. The resulting estimate of 0.85 was similar to that based on Eq. 2, but was substantially more precise. The 95% CI for the Eq. 3 estimate of rate of change was 0.73–1.00 (Table 3), providing evidence that avian richness declined on the route between 1970 and 1990.

The complement of extinction probability was estimated at 0.84, and the 95% CI included 1.00 (Table 3). The complement of turnover indicated that an estimated 93% of the species present in 1990 were also present in 1970, reflecting an estimated species turnover of 7% (Table 3). Consistent with this fairly low turnover, the estimated number of new species colonizing between 1970 and 1990 and present in 1990 was small (<5 species; see $\hat{B}_{70,90}$, Table 3). The overall conclusion for this route was weak evidence of a decline in species richness, with the number of colonizing species not quite balancing the number of local extinctions.

TABLE 2. Species detection statistics for Wisconsin BBS route 1, 1970 and 1990.

Species group	No. species detected	No. species detected on exactly h of the five groups of stops (f_h)				
		f_1	f_2	f_3	f_4	f_5
Total no. species detected (1970), R_{70}	66	17	19	9	10	11
Total no. species detected (1990), R_{90}	80	23	15	9	12	21
No. members of R_{70} detected in 1990, $m_{90}^{R_{70}}$	57	9	10	6	11	21
No. members of R_{90} detected in 1970, $m_{70}^{R_{90}}$	57	10	17	9	10	11

TABLE 3. Estimates of quantities associated with community dynamics based on avian species seen on Maryland BBS route 25 in 1970 and 1990.

Quantity (θ)	Naive "estimates"†	Estimator	$\hat{\theta}$	$\widehat{SE}(\hat{\theta})$	95% CI
Species richness (1970)	65.0	$\hat{N}_{70}$	78.5	10.4	66.9–104.1
Species richness (1990)	55.0	$\hat{N}_{90}$	69.4	11.1	55.6–94.3
No. members of R_{70} present in 1990‡	48.0	$\hat{M}_{90}^{R_{70}}$	54.7	13.2	35.0–86.0
No. members of R_{90} present in 1970‡	48.0	$\hat{M}_{70}^{R_{90}}$	51.1	6.9	38.5–67.1
Complement of extinction probability	0.74	$\hat{\phi}_{70,90}$	0.84	0.15	0.54–1.00
Complement of turnover	0.87	$\hat{\phi}_{90,70}$	0.93	0.09	0.70–1.00
Rate of change in richness (Eq. 2)	0.85	$\hat{\lambda}_{70,90}$	0.88	0.18	0.61–1.28
Rate of change in richness (Eq. 3)	0.85	$\hat{\lambda}_{70,90}$	0.85	0.07	0.73–1.00
Number of colonizing species	7.0	$\hat{B}_{70,90}$	3.3	12.2	0.0–40.9
Average detection probability (1970)	1.0§	$\hat{\bar{p}}_{70}$	0.83	0.10	0.62–0.97
Average detection probability (1990)	1.0§	$\hat{\bar{p}}_{90}$	0.79	0.11	0.58–0.99

† "Estimates" are based on the assumption that all species are detected.
‡ Confidence intervals for $\hat{M}_j^{R_i}$ can include values $< m_j^{R_i}$, because we consider variation associated with the extinction process ($M_j^{R_i} \sim \text{bin}[R_i, \hat{\phi}_{ij}]$).
§ By assumption.

Model M_h adequately fit ($P > 0.10$) all of the data sets in Table 2 for Wisconsin route 1, 1970 and 1990. Estimated species richness was greater in 1990 than 1970, and there was little overlap between the respective confidence intervals (Table 4). Both estimates for rate of change in species richness were >1.2, and neither confidence interval included 1.00 (Table 4), providing evidence for an increase in richness between 1970 and 1990. The test for similar distribution of detection frequencies ($\chi_4^2 = 3.37$, $P = 0.50$) provided no evidence for different detection probabilities between 1970 (estimate, 0.85) and 1990 (estimate, 0.80).

The estimated $\phi_{70,90}$ reflected only a 7% local extinction probability between 1970 and 1990, but the estimated $\phi_{90,70}$ indicated that 22% of the species present in 1990 were new (not present in 1970). Similarly, the estimator for new species (Eq. 8) indicated >25 species as local colonists between 1970 and 1990 (Table 4). Thus, the data for this route indicated an increase in the number of species, with the number of local colonists exceeding the number of local extinctions.

Tables 3 and 4 also include the naive "estimates" of the quantities of interest obtained, based on the assumption that all species are detected. Many of the naive estimates are biased low The bias of the naive estimate for number of colonizing species may be either positive or negative, depending on the relative detection probabilities and the actual numbers of local extinctions and colonizations. The naive estimate for rate of change in species richness is nearly unbiased when detection probabilities for the two time periods are equal, as in these two examples. Finally, when considering the magnitudes of the difference between the naive and probability-based estimates, it should be noted that higher detection probabilities than those observed will lead to smaller differences, whereas lower detection probabilities will produce even larger differences.

DISCUSSION

The most difficult methodological problem faced by biologists studying animal populations or communities in the field is the inability to detect every animal or species present in a sampled location. Recognition of this problem has led to recent efforts to use capture–recapture models to estimate species richness in studies of animal community ecology (Derleth et al. 1989, Karr et al. 1990, Palmer 1990, Coddington et al. 1991, Baltanas 1992, Bunge and Fitzpatrick 1993, Hodkinson and Hodkinson 1993, Colwell and Coddington 1994, Dawson et al. 1995, Thiollay 1995, Walther et al. 1995, Nichols and Conroy 1996). We agree that these models are well-suited for estimating species richness, and we have found them to be very useful for estimating avian species richness from BBS data (Boulinier et al. 1998).

Our intent here has been to provide suggestions about extending the capture–recapture estimation and modeling framework to the study of animal community dynamics. We have presented several estimators, and estimates computed using some of these in our example analyses seemed reasonable. Precision was not always good, but was consistent with expectations based on other work with capture–recapture models. We note that our examples used all avian species detected on the BBS routes, whereas it would be possible to restrict interest to specific subsets of species (guilds or taxonomic subgroups). However, precision of estimates would be lower with the smaller sample sizes that would necessarily accompany subsetting of the data.

Burnham (1981:325) noted that "Using just the count of birds detected . . . as an index [of] abundance is neither scientifically sound nor reliable." This criticism can be applied to any analysis of counts in which the proportion of individuals (or species) detected is <1. Even extensive monitoring programs such as the BBS have great constraints on any analysis, because

TABLE 4. Estimates of quantities associated with community dynamics based on avian species seen on Wisconsin BBS route 1 in 1970 and 1990.

Quantity (θ)	Naive "estimates"[†]	Estimator	$\hat{\theta}$	$\widehat{SE}(\hat{\theta})$	95% CI
Species richness (1970)	66.0	$\hat{N}_{70}$	77.2	5.5	68.6–89.8
Species richness (1990)	80.0	$\hat{N}_{90}$	99.9	11.4	85.5–129.9
No. members of R_{70} present in 1990[‡]	57.0	$\hat{M}_{90}^{R_{70}}$	61.6	7.7	47.2–74.4
No. members of R_{90} present in 1970[‡]	57.0	$\hat{M}_{70}^{R_{90}}$	62.5	13.8	39.4–84.7
Complement of extinction probability	0.86	$\hat{\phi}_{70,90}$	0.93	0.09	0.72–1.00
Complement of turnover	0.71	$\hat{\phi}_{90,70}$	0.78	0.16	0.49–1.00
Rate of change in richness (Eq. 2)	1.21	$\hat{\lambda}_{70,90}$	1.29	0.17	1.06–1.70
Rate of change in richness (Eq. 3)	1.21	$\hat{\lambda}_{70,90}$	1.21	0.08	1.05–1.37
Number of colonizing species	13.0	$\hat{B}_{70,90}$	27.9	14.1	8.4–62.7
Average detection probability (1970)	1.0§	$\hat{\bar{p}}_{70}$	0.85	0.06	0.73–0.96
Average detection probability (1990)	1.0§	$\hat{\bar{p}}_{90}$	0.80	0.08	0.61–0.94

[†] "Estimates" are based on the assumption that all species are detected.
[‡] Confidence intervals for $\hat{M}_j^{R_i}$ can include values $< m_j^{R_i}$, because we consider variation associated with the extinction process ($M_j^{R_i} \sim bin[R_i, \hat{\phi}_{ij}]$).
§ By assumption.

of the need to model "nuisance" variables that affect the proportion of animals detected and that can bias estimation (e.g., Sauer et al. 1994). The procedures described here have the potential to expand the appropriate use of count data in hypothesis tests, and can be applied to many existing data sets that were formerly considered to be inappropriate for statistical analysis. For example, data gathered in the BBS and other monitoring programs such as the Christmas Bird Count (Butcher 1990) and atlas programs (Robbins 1990) can be used to test hypotheses about changes in species richness and associated community-level vital rates.

Open vs. closed models

All of the community-dynamic estimators presented here are based on capture–recapture models developed for closed animal populations. In our earlier paleo-biological work (Nichols and Pollock 1983*a*, Conroy and Nichols 1984, Nichols et al. 1986), we used primarily open-model estimators, relying on the relative robustness of estimators of turnover and extinction probability to heterogeneity of detection probabilities (variation among different taxa in fossil encounter probabilities). We selected closed models as the basis for the estimators reported here, because of the a priori likelihood, and the strong evidence from BBS data (Boulinier et al. 1998), that detection probabilities are strongly heterogeneous among species. Only capture–recapture models for closed populations permit unbiased estimation in the presence of heterogeneous detection probabilities. However, some open-population capture–recapture estimators are quite robust to heterogeneous capture probabilities (Carothers 1973, 1979). We suspect that sampling variances are likely to be smaller for open-model estimators than for the estimators presented here. The variances associated with many of the estimates computed in our examples were large. Thus, an important topic for investigation will be comparative closed- and open-model estimator

performance in the face of strong heterogeneity. In particular, it will be useful to base such an evaluation on a criterion such as mean squared error that includes both bias and precision.

Potential problems

Although the estimators we have presented should be superior to ad hoc approaches based on species actually detected, our estimators are not without problems. A recurring problem in all statistical modeling involves what to do when the available models do not fit the data. Model M_h was found to be the most frequently selected model, by a wide margin, in analyses of numerous BBS data sets (Boulinier et al. 1998), so we developed program COMDYN basing all estimators on this model (Hines et al., *in press*). In cases where this model does not fit the data well, the data could be run through program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991). If the selected model has available estimators and fits the data reasonably, then resulting estimates can be used with the estimators presented here. If no model fits the data well, then we would recommend relying on the general robustness of the jackknife estimator for model M_h and using this estimator with caution. It may be reasonable to use a quasi-likelihood (see Burnham et al. 1987, Lebreton et al. 1992) approach, computing variance inflation factors based on the goodness-of-fit test results (this is another topic meriting investigation). We emphasize that lack of model fit is not an adequate reason for abandoning an estimation approach and resorting to the use of ad hoc estimators, because model-based estimates will probably perform much better (i.e., exhibit less bias) than ad hoc approaches, even when model assumptions are not met (e.g., see Nichols and Pollock 1983*b*).

Potentially the most serious problem with the community-dynamic estimators we have presented involves the effects of heterogeneity on the ϕ estimators (local

extinction probability, local turnover). The methods that we propose were developed specifically to deal with heterogeneity of detection probabilities. However, detection probability for a species will be a function of the morphological and behavioral characteristics of individuals in the species *and* the number of individuals in the sampled species population. Unfortunately, local extinction probability and probability of having been present at some previous time period (1 − turnover) will probably also depend on the number of individuals in the species. Extinction probability for a population should generally decrease as the number of individuals increases (e.g., Bailey 1964, MacArthur and Wilson 1967, Goel and Richter-Dyn 1974, Gilpin and Soule 1986, Boyce 1992, Burgman et al. 1993), although empirical results are not always consistent with this prediction (e.g., Karr 1990).

Our estimators for ϕ condition on the number of species actually observed at a specific period (Eqs. 4 and 7) and then estimate how many species in that subset are present at a different time. If detection probability for an individual species is closely tied to the number of individuals in that species, then the species on which we condition our estimates (e.g., the members of R_i) will tend to have more individuals, on average, than species present but not observed (e.g., $N_i - R_i$). Thus, the species on which we condition our estimates will also tend to have greater probabilities, on average, of being present in some other sampling period. If we want our inferences to apply to the entire community, then this positive covariance between p and ϕ within species will tend to result in a positive bias in our estimates, $\hat{\phi}$. Heterogeneous survival probabilities also present problems in models for estimating quantities at the population level (Nichols et al. 1982, Pollock and Raveling 1982, Johnson et al. 1986, Rexstad and Anderson 1992, Burnham and Rexstad 1993), and the covariance between survival and recapture/recovery probability is an important determinant of estimator performance (e.g., Nichols et al. 1982). Our initial work on this problem in community analyses suggests that bias is not large, but we will continue to investigate possible bias and methods for bias reduction. Most importantly, we note that ad hoc approaches to estimation share this problem, and the difficulties are magnified because of the absence of an ability to draw inferences about species present, yet not detected. Thus, the approaches presented here are still far preferable to methods that incorrectly assume detection probabilities of 1.

Other quantities

We believe that the estimators presented here will be useful for studying local species extinction, colonization, and turnover. However, we note that our capture–recapture approach can be used to estimate other metrics relevant to these community processes. For example, we believe that our turnover metric (Eq. 7), reflecting the proportion of the species present at time *j* that were not present at a previous time *i,* is a natural turnover statistic and is preferable to other turnover metrics. However, for those who do not share this preference, other statistics such as the widely used turnover index of Diamond (1969) can readily be computed using the estimates of species richness, the number of local colonists, and the local extinction probability presented. Use of capture–recapture estimates to compute such indices avoids the typical assumption of species detection probabilities of 1. In addition, our bootstrap approach can be used to compute associated variances, permitting statistical inference on these indices.

Conclusions

For field situations in which all species present in an area are detected at each sampling occasion, we recommend methods such as those developed by Clark and Rosenzweig (1994) and Rosenzweig and Clark (1994) for estimating local extinction and colonization probabilities. In situations where species detection probabilities are <1, we believe that the estimation methods described here will be useful to community ecologists, managers, and conservation biologists. We recommend use of these estimators for estimating changes in species richness and for investigating potential influences of such factors as environmental change and habitat management on the vital rates that determine such changes.

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APPENDIX

In order to facilitate the understanding of our variance estimation methods, we will describe the specific case of BBS data, but we have encoded general versions of this approach in program COMDYN (Hines et al., *in press*). The first step in computing bootstrap variance estimates is to use the actual data (e.g., from the BBS) to compute the estimate of interest. All such estimates are based on one or more estimates of species richness, sometimes for all of the members of the community and sometimes for specific subsets of species. This estimation of the number of species in the face of unknown species detection probabilities is the source of all of the variation considered in the variance estimates for some of the estimators computed by COMDYN (e.g., $\hat{N}_i$, $\hat{\lambda}_{ij}$, $\hat{p}_i$). For estimating variance of these estimators, each estimate of richness based on the actual data is treated as the true number of species. The observed frequencies of species seen on 1, 2, . . . , 5 of the BBS route segments (denoted as $f_1, f_2, \ldots, f_5$, where f_h denotes the number of species observed on h segments) are then used to estimate multinomial cell probabilities as

$$\hat{\pi}_h = \frac{f_h}{\hat{N}_i} \qquad h = 1, 2, \ldots, 5 \quad \text{and}$$

$$\hat{\pi}_0 = 1 - \frac{\sum_{h=1}^{5} f_h}{\hat{N}_i}. \tag{A.1}$$

These estimated cell probabilities, $\hat{\pi}_h$, correspond to the probability that a species in the community is seen on $h = 0, 1, \ldots, 5$ route segments.

For each bootstrap replicate, we then use the $\hat{N}_i$ and the $\hat{\pi}_h$ to generate a set of multinomial random variables, f_h^*, and use them to compute a new richness estimate, $\hat{N}_i^{**}$. This new richness estimate is then used in the estimator of interest, and resulting "estimates" are the replicates that are used to compute empirical variance estimates

$$\widehat{\text{var}}(\hat{\theta}) = \frac{\sum_{j=1}^{n} (\hat{\theta}_j^* - \hat{\bar{\theta}}^*)^2}{n(n-1)} \tag{A.2}$$

where $\hat{\theta}_j^*$ is the jth bootstrap replicate of the estimated parameter of interest, n is the number of replicates, and $\hat{\bar{\theta}}^*$ is the arithmetic mean of the n replicates. In addition to computing variances, we used the empirical distribution of the bootstrap replicate estimates, $\hat{\theta}_j^*$, to compute our 95% CIs.

The bootstrap variance estimates computed as described can be viewed as conditional on the true value of the estimated quantity. For example, the bootstrap estimate for variance of species richness could be written (using the notation of Jolly 1965) as $\widehat{\text{var}}(\hat{N}_i | N_i)$, indicating that the variance estimate included only the "error of estimation" associated with a detection probability <1, and not any variation associated with the stochasticity of population- or community-dynamic processes that produced the true N_i. Our reasoning for omitting such variation from our variance estimates for species richness is that we are interested in the species actually present at a particular time i, not in a statistic characterizing the distribution of the possible realizations of that random variable.

Our approach to variance estimation is different for turnover and extinction probability, because we are more interested in the underlying probability that a species present at i is still (or was, in the case of turnover) present at j than in the actual proportions that survived (or were survivors). We introduce this additional variation by treating $M_j^{R_i}$ as a random variable, rather than conditioning on the actual $\hat{M}_j^{R_i}$ estimated from the data.

The first step in the bootstrap procedure is the same as for species richness, as described. We treat the estimate, $\hat{M}_j^{R_i}$, as the true number of species present in period j that were survivors from the species observed in period i (members of R_i). We then use the observed frequencies ($f_1, f_2, \ldots, f_5$) with which members of R_i present at j were observed at period j on 1, 2, . . . , 5 of the BBS route segments, to estimate multinomial cell probabilities as

$$\hat{\pi}_h = \frac{f_h}{\hat{M}_j^{R_i}} \qquad h = 1, 2, \ldots, 5$$

$$\hat{\pi}_0 = 1 - \frac{\sum_{h=1}^{5} f_h}{\hat{M}_j^{R_i}}. \tag{A.3}$$

For each bootstrap replicate, we first generate $M_j^{R_i*}$ as a binomial random variable (i.e., $M_j^{R_i*} \sim \text{bin}[R_i, \hat{\phi}_{ij}]$). We then use this $M_j^{R_i*}$, with the $\hat{\pi}_h$ from Eq. A.3, to generate a set of multinomial random variables, f_h^*. These frequencies, f_h^*, are then used to compute a new estimate, $\hat{M}_j^{R_i*}$, which is used in conjunction with the estimators of Eqs. 4 and 7 to compute the bootstrap replicates of the $\hat{\phi}_{ij}$. The bootstrap variance estimates are then computed as in Eq. A.2.

It is possible for some of our estimators to assume values that we judge to be inadmissable, and we had to decide on a way to deal with these in the bootstrap replications. Estimates of $\hat{\phi}_{ij} > 1$ were logically impossible, so when this condition occurred in a bootstrap replicate, we set the estimate to 1. Similarly, estimates of $\hat{B}_{ij} < 0$ were set equal to 0. Finally, the process of generating bootstrap replicates led to the possibility that a richness estimate was smaller than the number of species observed ($\hat{N}_i^{**} < R_i$). In such cases, the bootstrap estimate was set equal to the number of species observed.