

## COMBINING MULTISTATE CAPTURE–RECAPTURE DATA WITH TAG RECOVERIES TO ESTIMATE DEMOGRAPHIC PARAMETERS

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**Abstract.** Matrix population models that allow an animal to occupy more than one state over time are important tools for population and evolutionary ecologists. Definition of state can vary, including location for metapopulation models and breeding state for life history models. For populations whose members can be marked and subsequently re-encountered, multistate mark–recapture models are available to estimate the survival and transition probabilities needed to construct population models. Multistate models have proved extremely useful in this context, but they often require a substantial amount of data and restrict estimation of transition probabilities to those areas or states subjected to formal sampling effort. At the same time, for many species, there are considerable tag recovery data provided by the public that could be modeled in order to increase precision and to extend inference to a greater number of areas or states. Here we present a statistical model for combining multistate capture–recapture data (e.g., from a breeding ground study) with multistate tag recovery data (e.g., from wintering grounds). We use this method to analyze data from a study of Canada Geese (*Branta canadensis*) in the Atlantic Flyway of North America. Our analysis produced marginal improvement in precision, due to relatively few recoveries, but we demonstrate how precision could be further improved with increases in the probability that a retrieved tag is reported.

**Key words:** *bird band recoveries; Branta canadensis; breeding; capture–resight; fidelity; life history states; metapopulation; migration; multisite studies; multistrata models; trade-off; wintering.*

### INTRODUCTION

For many species of interest to population and evolutionary ecologists, individuals can be considered to occupy one of a number of states, based on phenotype or location. These states can be static (e.g., sex) or dynamic, where transitions between states are either deterministic (e.g., age) or probabilistic (e.g., breeding status or location). By uniquely marking individuals, they can be tracked through time as they transition among states. Because in natural settings individuals cannot be detected with probability 1.0, a growing literature is developing on the use of mark–recapture models for multiple dynamic states to estimate state-specific survival and transition probabilities (Arnason 1973, Brownie et al. 1993, Schwarz et al. 1993; see review by Lebreton and Pradel 2002).

With such tools researchers can address many hypotheses in evolutionary ecology and metapopulation ecology. Nichols et al. (1994) and Nichols and Kendall (1995) showed how multistate mark–recapture models (MSMR) could be used to evaluate trade-offs between

current reproductive effort and survival or future reproduction (Clutton-Brock 1988). MSMR models can also be used to evaluate hypotheses about differential gene flow due to natal and breeding dispersal (Spindel et al. 1995, Clobert et al. 2001, Lebreton et al. 2003), or to determine if subpopulations within a metapopulation intermix enough to be managed as a single population (Hestbeck et al. 1991). Finally, MSMR can be useful for estimating the parameters of stage-based projection matrices (Crouse et al. 1987, Caswell 2001), such as in Nichols et al. (1992).

These examples are based solely on recaptures or resightings of individuals within a well-defined sampling period. However, for some populations, especially of harvested taxa such as waterfowl, fish, and sea turtles, recoveries of tags provide a potentially rich (and in some cases the richest) source of data on survival (Brownie et al. 1985, Burnham 1993) and movement (Schwarz et al. 1988, 1993). If tagging and recovery of a migratory population occur in different parts of the annual cycle (e.g., recaptures on breeding grounds, recoveries on wintering grounds), recoveries provide an opportunity to explore hypotheses about migration ecology, such as direction ratios (Baker 1978), or the distribution of harvest (Munro and Kimball 1982). Although the methods of Schwarz et al. (1988, 1993) address the estimation of these movement probabilities, they are based on recoveries alone (i.e.,

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one encounter after tagging) and therefore assume that philopatry to the subpopulation (e.g., breeding population) in which it was tagged is complete.

In this paper we develop a multinomial model that exploits both recapture/resightings from formal sampling periods, and tag recoveries that can occur at any time but often occur during specified harvest seasons. For the remainder of the paper we will equate recaptures and resightings that come from formal sampling periods and simply call them recaptures. We begin with a general model that allows for a set of recapture states and a potentially different set of recovery states. We motivate the development of the model with the example of migratory birds, especially the case where birds are banded in their breeding area immediately before a hunting season, which can provide a substantial number of recoveries. We then compare two approaches to modeling the recovery process, discuss the special case where recapture and recovery states are identical, and discuss the difficulties of generalizing our model to allow for incidental observations. Finally, we illustrate our model by reanalyzing data from the survival and movement study of wintering Canada Geese by Hestbeck et al. (1991), including leg band recoveries.

MODEL DEVELOPMENT

The motivation for the basic model is a migratory metapopulation (e.g., hunted waterfowl), where capture and recapture or resighting effort is expended only on the breeding grounds, in formal sampling periods, and mortalities are reported principally from wintering areas. Consider two breeding areas (A and B) and two wintering areas (1 and 2). We assume that breeding dispersal between areas A and B is a first-order Markov process, along the lines of Arnason (1973) and Schwarz et al. (1993). For example, a bird in breeding area A in year  $i$  will disperse to area B with probability  $\psi_i^{AB}$ , given that it survives to the next breeding season (with probability  $S_i^A$ ), and remains faithful to the metapopulation. Birds from either breeding area winter in areas 1 or 2 with some probability (e.g.,  $\tau_i^{B1}$  = probability that a bird in breeding area B in year  $i$  winters that year in area 1). There is no formal capture or sighting effort in these wintering areas, but birds that die can be found (or retrieved if killed by a hunter) and reported (e.g., with probability  $f_i^1$  if recovered in wintering area 1) to one of the repositories for such data (e.g., USGS Bird Banding Laboratory in Laurel, Maryland, or the Canadian Wildlife Service Bird Banding Office in Ottawa, Canada). For now we assume that death is due to harvesting (e.g., hunting) and that it occurs soon after the recapture period  $i$  (i.e., before any other mortality occurs in the population). We provide other alternatives for modeling the recovery process in a subsequent section. As with movement between capture areas, we assume that movement from recapture to recovery area is dependent only on the location of an

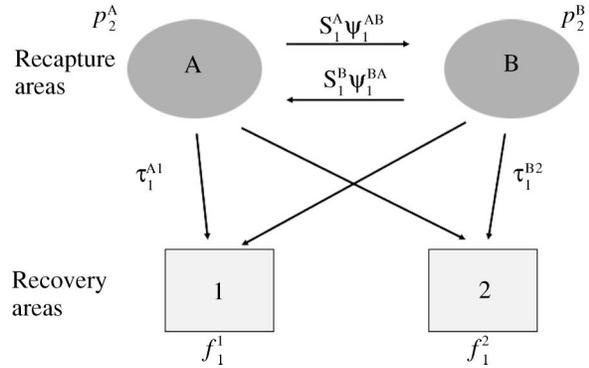


FIG. 1. Diagram of sampling framework for a study that includes multiple states (A and B observable) for capturing animals and other multiple states (1 and 2) for recovering animals. Animals released in capture state  $c$  survive with probability  $S_c^s$  and move to capture state  $s$  with probability  $\psi_c^{cs}$ , where they are captured with probability  $p_{i+1}^s$ ; or after release they are recovered in recovery state  $h$  with probability  $f_i^h$ , having moved there with probability  $\tau_i^{ch}$ .

animal during recapture period  $i$ . This sampling framework is illustrated in Fig. 1.

Based on the sampling framework just described, we can model the encounter histories of animals captured, released, and either recaptured, resighted, or recovered. Consider example histories for three individuals below, followed by their probability structure, conditioned on period of first release;

- A0B100  $S_1^A \psi_1^{AB} p_2^B \tau_2^{B1} f_1^1$
- 00B002  $S_2^B [\psi_2^{BA} (1 - p_3^A) \tau_3^{A2} + \psi_2^{BB} (1 - p_3^B) \tau_3^{B2}] f_3^2$
- A0A0B0  $S_1^A \psi_1^{AA} p_2^A S_2^A \psi_2^{AB} p_3^B (1 - \tau_3^{B1} f_3^1 - \tau_3^{B2} f_3^2)$ .

Each encounter history, consisting of three pairs of columns, represents three capture occasions (columns 1, 3, and 5), along with three recovery periods (columns 2, 4, and 6). The first individual was initially captured in breeding season 1 in area A, then recaptured in breeding season 2 in area B, then recovered between breeding seasons 2 and 3, in recovery area 1. The second individual was first captured in breeding season 2 in area B, but then was not captured in breeding season 3, before dying and being recovered in recovery area 2, just after breeding season 3. Therefore the probability structure for this history includes (in brackets) the possibility that the animal was in either area A or B during capture period 3. In encounter history 3 the animal is captured in area A during breeding seasons 1 and 2, and is captured in area B in breeding season 3. The part of the expression in parentheses indicates the probability that the animal is not recovered after breeding season 3. The model presented in the example histories is more fully developed in the Appendix, using matrix notation.

In order to compute estimates under this model some assumptions must be made. We begin with general as-

assumptions associated with MSMR models. Each animal within a state at a given sampling period has the same probability of being detected, surviving to the next period, and transitioning to another state. We also assume that the fate of each animal with respect to detection, survival, and transition is independent of the next. Finally, we assume that each animal is assigned to the correct state at each capture, and that tags are read correctly, do not fall off (we allude to exceptions to this), and do not affect survival or transition probabilities.

This model is a generalization of previous work. If recovery information is ignored the model collapses to that of Arnason (1973) and subsequent work by Hestbeck et al. (1991), Brownie et al. (1993), and Schwarz et al. (1993). If recapture information is ignored, the model would be similar to those of Schwarz et al. (1993 or 1988), depending on additional assumptions. The model generalizes some aspects of the model outlined by Barker (1995), and represents a special case with respect to other aspects. Barker's (1995) model did not include multiple recovery areas, but did include incidental observations as well as recoveries.

All parameters in our model are estimable, including the last survival probability ( $S_{K-1}^c$ ) and capture probability ( $p_K^c$ ) for each area  $c$ , if (1) the number of recovery areas does not exceed the number of recapture areas, and (2) recoveries are recorded after the last recapture period. With some modification to the tag recovery part, we use this model below in the example of Canada Goose survival and movement.

#### *Parameterization of recovery probability*

Up to this point we have employed the parameterization of the recovery process most often used in the study of hunted or fished animals. For the case of a single state, conditional on an animal living to capture period  $i$ ,  $f_i$  is the probability that the animal is sampled by the recovery process. Recovery is often by hunting or fishing, and if it occurs immediately after the recapture period it can serve as an index to harvest or kill probability. When there is substantial mortality between the release and recovery periods,  $f_i$  is no longer an index to kill probability, but this parameterization is still valid for estimating survival probability. Burnham (1993) used this same parameterization when combining recoveries with recaptures for a single capture state.

Seber (1970) provided a different approach to modeling recoveries, replacing  $f_i$  with  $(1 - S_i)r_i$ , where  $S_i$  is the probability of survival from year  $i$  to  $i + 1$  and  $r_i$  is the probability that the death of a banded animal is reported, given that it dies between recapture periods  $i$  and  $i + 1$ . Regardless of the interpretation of the respective sampling probabilities, in the case of a single banding location, the two approaches are virtually equivalent with respect to survival estimation. This equivalence breaks down in the multistate case where

survival is associated with the state of origin, and recovery probability is a function of the state of destination (e.g., replace  $\tau_2^A f_2^A$  with  $\tau_2^A(1 - S_2^A)r_2^A$ ). Here a parameter that is indexed by recovery area is replaced with a product of parameters that are indexed by both recapture and recovery areas. This could be resolved by indexing recovery probability on the recapture state it occupied immediately prior to recovery, if this is reasonable biologically (e.g., if most of the hazard is in the capture area or along the migratory route therefrom). That creates its own logical problems in some circumstances. If recovery probability itself is truly a function of both the recapture and recovery areas, then perhaps the  $\tau_i^{ch}$  would not be separately interpretable, regardless of which way recovery probability is indexed.

In summary, there are many cases where interpreting  $\tau_i^{ch}$  will be of interest, especially in studies of migration ecology. For these cases we recommend the  $\tau_i^{ch} f_i^h$  parameterization when negligible mortality between recapture and recovery periods can be assumed. Where substantial mortality occurs in this interim we recommend the  $\tau_i^{ch}(1 - S_i^c)r_i^h$  parameterization, based on Seber (1970). We use this latter approach in the "EXAMPLE" section below. If interest is only in improving the precision of  $\hat{S}_i^c$  and  $\psi_i^c$ , not in transition patterns to recovery areas, then the recovery process could be more simply modeled by letting  $\rho_i^{ch} = \tau_i^{ch} f_i^h$ , or by ignoring recovery areas altogether by letting  $\rho_i^c = \sum_h \tau_i^{ch} f_i^h$ .

#### *Common recovery and recapture areas*

In some cases the set of recapture areas and the set of recovery areas might be identical. In the EXAMPLE section below we consider a study focused on wintering areas of Canada Geese, where the hunting season immediately precedes the formal sampling period. In this case the Seber (1970) parameterization of recovery, as described in the subsection immediately above, is the most logical. If we can assume that the geese have reached their winter terminus by the time recoveries are recorded, we can set the  $\tau$ 's equal to the  $\psi$ 's (e.g., if areas A and 1 are equivalent then  $\tau_i^{B1} = \psi_i^{BA}$ ). Alternatively we could use this approach to test hypotheses about when birds have reached their winter terminus. It is tempting to consider the implications when recapture and recovery periods are concurrent. Because of the usual capture–recapture assumption that mortality is negligible during formal recapture periods, it is best to avoid intense harvest periods when designing the recapture part of a study. In some cases this is impractical. For example, where hunting or fishing seasons are long there might be little opportunity to capture or sight animals when harvest is not occurring. This has historically been true for wintering geese, where the best opportunity to sight birds is on the wintering grounds, but hunting seasons are open for most of the wintering period. Where this concurrent sam-

pling is unavoidable, there will likely be some bias in survival (P. B. Conn, W. L. Kendall, and W. A. Link, unpublished data), but the impact on estimates of transition probabilities is not clear.

#### EXAMPLE USING CANADA GEESE

Whereas the initial development of the models presented here was motivated by pre-season banding of waterfowl, wintering banding studies are also common, especially of geese. Hestbeck et al. (1991) used mark-resight data of Canada Geese with uniquely coded yellow neck bands to estimate survival and movement probabilities between three wintering regions in the Atlantic Flyway of the United States. In particular, they investigated movement and site fidelity between the mid-Atlantic (New York, Pennsylvania, New Jersey), Chesapeake (Delaware, Maryland, Virginia), and Carolina (North and South Carolina) regions across consecutive winters from 1984 to 1985 through 1987 to 1988. Hestbeck et al. (1991) demonstrated extensive interannual movements between these coarse-grained areas, primarily from southern wintering grounds to more northerly ones. Their study confirmed that movement was an important component to Canada Goose population dynamics, and helped to explain certain changes in their wintering distributions. They selected a memory movement model MV2 (Brownie et al. 1993) over the Markovian multistate model MV1 (Arnason 1973, Hestbeck et al. 1991) as the best-fitting model to the observed data. Under MV2, movements between patches are modeled as realizations of a second-order stochastic process.

While movement was the main focus of the Hestbeck et al. (1991) paper, the purpose of the present analysis is to investigate possible gains in precision of parameter estimates when incorporating auxiliary band recovery information into the Canada Goose study. As a first step towards this goal, we considered a joint analysis of mark-resight and band recovery data under the Markovian multistate model MV1. While MV2 was previously identified as the best fitting model, its data requirements make it impractical to fit in many circumstances.

Band recovery records for Canada Geese were collected from the USGS Bird Banding Laboratory. We used 680 band recovery records in addition to the 31 826 secondary resightings from the original study. Of the recovery records that we assembled, there were 214 indirect band recoveries (defined here as those recovered two or more hunting seasons after the last resighting).

For simplicity, we treated the geographical areas of recovery as being the strata identified by Hestbeck et al. (1991) for resightings. We used A, B, and C to denote resighting areas in the mid-Atlantic, Chesapeake, and Carolinas, respectively, and 1, 2, and 3 to denote matching recovery areas. Following Hestbeck et al. (1991), we defined the sample period for resight-

ings as occurring between 4 January and 15 February. Only geese banded or observed with yellow neck collars during this time frame were counted as having been resighted in a given year.

We restricted consideration of band recoveries to those reported before 4 January, to avoid problems with modeling the small amount of mortality during the resighting period. A recent study using satellite telemetry suggested that Canada Geese reach the southern terminus of migration by mid to late October (Malecki et al. 2001). Therefore, we defined the sample period for band recoveries as 1 November to 3 January, which roughly corresponds to the longest time period not conflicting with the resighting period in which Canada Geese have reached their final wintering destination. Under this formulation, transitions to recovery areas ( $\tau_i^{ch}$ ) should match up as close as possible to transitions from resighting area to resighting area ( $\psi_i^{cs}$ ). It is then possible to consider a simplified model in which  $\tau_i^{ch}$  is constrained to equal  $\psi_i^{cs}$ . The recovery period could hypothetically be extended to include October, but in this case the transition parameters  $\tau_i^{ch}$  lose biological significance, since a large portion of hunting mortality occurs during migration.

Several important differences remained between the data we used for reanalysis and the data originally used by Hestbeck et al. (1991). For instance, we did not have access to a summer study in 1987 that was used to detect and remove resident geese from the original analysis. Nor were we able to completely duplicate special "coin tosses" that were used to specify single resighting areas for geese that were observed an equal number of times in multiple strata during a given sample period. While this did not occur frequently, it would be impossible to reproduce. Furthermore, records of geese that had contradictory resighting and recovery histories were eliminated from our analysis (e.g., a band recovery occurring before a resighting). A total of 84 capture history records in which birds were shot outside the mid-Atlantic, Chesapeake, and Carolinas areas (most during migration) were deleted from the analysis. Recovery data indicated that few geese emigrated from the three wintering strata, so we expect parameter bias to be low under the assumption of no permanent emigration. Even without incorporating band recoveries into the analysis, parameter estimates we computed using model MV1 differed somewhat, depending on whether we used capture history frequencies that we had compiled or those from the original analysis. In either case, parameter estimates from model MV1 are not directly comparable to estimates presented in Hestbeck et al. (1991), since the latter values reflected estimation under model MV2.

Because there were more than 10 months between the midpoint of the resighting and recovery periods, we modeled recoveries using the  $\tau_i^{ch}(1 - S_i^c)r_i^h$  parameterization. Indirect recovery records were in general very sparse, so only the products  $\tau_i^{ch}r_i^h$  were estimable

TABLE 1. Time- (*i*) and area- (*r*) specific cohort sizes ( $n_i^r$ ), survival probabilities ( $S_i^r$ ), movement probabilities ( $\psi_i^{rs}$ ), and resighting probabilities ( $p_{i+1}^r$ ) for Canada Geese along the Atlantic Flyway.

Parameter	Transition periods ( <i>i</i> to <i>i</i> + 1)							
	1984–1985		1985–1986		1986–1987		1987–1988	
	$\hat{x}$	$d(SE[\hat{x}])$	$\hat{x}$	$d(SE[\hat{x}])$	$\hat{x}$	$d(SE[\hat{x}])$	$\hat{x}$	$d(SE[\hat{x}])$
<b>Mid-Atlantic</b>								
$n_i^A$	900		2332		2825		1619	
$S_i^A$	0.6420	0.0009	0.7060	0.0011	0.6550	0.0012	0.6437	0.0003
$\psi_i^{AA\dagger}$	0.8013	0.0004	0.7998	0.0000	0.7270	-0.0003	0.7135	-0.0002
$\psi_i^{AB}$	0.1987	0.0004	0.2002	0.0001	0.2647	0.0004	0.2833	0.0007
$\psi_i^{AC}$	0.0000	0.0000	0.0000	0.0000	0.0083	-0.0001	0.0063	0.0003
$p_{i+1}^A$	0.6494	0.0008	0.4482	0.0004	0.4743	0.0005	0.5338	0.0010
<b>Chesapeake</b>								
$n_i^B$	2139		3971		4056		2868	
$S_i^B$	0.7417	0.0010	0.6903	0.0008	0.6883	0.0009	0.6934	0.0007
$\psi_i^{BA}$	0.0897	0.0003	0.1233	0.0007	0.0845	0.0003	0.0852	0.0002
$\psi_i^{BB\dagger}$	0.9002	0.0003	0.8665	0.0006	0.8919	0.0003	0.8822	0.0003
$\psi_i^{BC}$	0.0106	0.0001	0.0102	0.0000	0.0236	0.0000	0.0326	0.0006
$p_{i+1}^B$	0.4429	0.0008	0.3713	0.0006	0.3916	0.0008	0.3875	0.0012
<b>Carolinas</b>								
$n_i^C$	711		1136		939		711	
$S_i^C$	0.5471	0.0016	0.6550	0.0012	0.5977	0.0003	0.6566	0.0049
$\psi_i^{CA}$	0.0995	0.0011	0.0374	0.0007	0.0242	0.0004	0.0441	-0.0008
$\psi_i^{CB}$	0.3034	0.0019	0.3451	0.0010	0.2008	0.0008	0.2251	-0.0015
$\psi_i^{CC\dagger}$	0.5971	0.0006	0.6175	0.0001	0.7748	0.0004	0.7308	-0.0023
$p_{i+1}^C$	0.3054	0.0012	0.3549	0.0011	0.4101	0.0006	0.3739	-0.0013

Notes: Resight data and band recovery records were combined in a joint analysis to produce parameter estimates. The difference in estimated standard errors,  $d(SE[\hat{x}])$ , between the combined analysis and an analysis using only resightings of neck collars is presented alongside parameter estimates,  $\hat{x}$ , with positive values representing greater precision for the combined analysis.

$$\dagger \hat{\psi}_i^{rs} = \sum_{g+r} \hat{\psi}_i^{rs}; \widehat{\text{var}}(\hat{\psi}_i^{rs}) = \sum_{r+g} \widehat{\text{var}}(\hat{\psi}_i^{rs}) + 2 \widehat{\text{cov}}(\hat{\psi}_i^{rs}, \hat{\psi}_i^{rs}), \text{ where } s_1, s_2 \neq r.$$

in most cases. In the last time period for recoveries, only the product  $(1 - S_i^r)\tau_i^{rh} r_i^h$  was estimable, since there were no resight data to produce a survival estimate. For the goose example we considered, it was possible to get rough estimates of recovery parameters  $r_i^h$  for every time period except for the last one by using the assumption that  $\tau_i^{cs} = \psi_i^{cs}$ . This assumption requires that the geese have indeed reached their final wintering destination by 1 November. Violation of this assumption would result in the bias of movement probabilities towards northerly wintering grounds.

We used program MSSURVIV (Brownie et al. 1993) to perform analyses for model MV1, which required mark-resight data alone. Changes in the likelihood function due to the introduction of band recovery parameters were incorporated into program MSSRVRCV, a modified version of MSSURVIV. A conversion program, CNVMSRCV, was created to translate capture history frequencies into input files for MSSRVRCV. Copies of these programs are *available online*.<sup>5</sup>

Table 1 contains area- and time-specific cohort sizes and parameter estimates for the analysis including recoveries, and the reduction in standard error that the incorporation of recoveries provided. The increased precision from including recoveries was marginal in this case. Standard errors for estimated survival prob-

ability estimates decreased by an average of 0.0009 (SD = 0.0002) when including supplementary band recoveries. The precision in capture probability estimates increased in 11 out of 12 estimates, and likewise in 27 out of 36 movement probabilities. However, increases in precision in transition probability estimates were sensitive to the assumption that  $\tau_i^{cs} = \psi_i^{cs}$ , most notably in the last two time periods.

It must be noted that the standard errors for both analyses are likely underestimated. Canada Geese often form life pair bonds, and also engage in flocking during migration. These tendencies violate the assumption of independence between individuals (Hestbeck et al. 1991), resulting in data overdispersion (see Burnham and Anderson 2002). To solve this problem, Burnham and Anderson (2002) suggested multiplying sample variances by the variance correction factor,  $\hat{c} = \chi^2/\text{df}$ , where  $\chi^2$  is the goodness-of-fit chi-square statistic of the global model, and df is its degree of freedom. For the Canada Goose models,  $\hat{c} = 3.2$  for the combined analysis and 3.0 for model MV1 using resightings only. If these correction factors are employed, precision gains tend to be more modest or do not exist at all. However, the difference in  $\hat{c}$  was partly a result of pooling over sparse data in the combined analysis. A complete discussion of this problem is beyond the scope of this paper.

<sup>5</sup> (<http://www.mbr-pwrc.usgs.gov/software.html>)

TABLE 2. Mean differences in proportional standard error,  $SE(x)/x$ , for parameter estimates when using a joint analysis combining resightings and band recoveries vs. a traditional analysis using resightings only.

Parameter	$p = p$ $\lambda = \lambda$	$p = p$ $\lambda = 2\lambda$	$p = p$ $\lambda = 3\lambda$	$p = 0.5p$ $\lambda = \lambda$	$p = 0.5p$ $\lambda = 2\lambda$	$p = 0.5p$ $\lambda = 3\lambda$	$p = 0.25p$ $\lambda = \lambda$	$p = 0.25p$ $\lambda = 2\lambda$	$p = 0.25p$ $\lambda = 3\lambda$	$p = 0.1p$ $\lambda = \lambda$
$S_i^A$	0.0012	0.0021	0.0028	0.0052	0.0083	0.0105	0.0126	0.0192	0.0236	0.0418
$S_i^B$	0.0015	0.0025	0.0034	0.0055	0.0085	0.0105	0.0156	0.0214	0.0253	0.0381
$S_i^C$	0.0036	0.0061	0.0081	0.0128	0.0194	0.0237	0.0276	0.0394	0.0466	0.0818
$\psi_i^{AA}$	0.0011	0.0019	0.0023	0.0037	0.0059	0.0070	0.0097	0.0138	0.0158	0.0255
$\psi_i^{AB}$	0.0036	0.0064	0.0087	0.0123	0.0195	0.0248	0.0319	0.0457	0.0549	0.0849
$\psi_i^{AC}$	NA†	NA†	NA†	NA†	NA†	NA†	NA†	NA†	NA†	NA†
$\psi_i^{BA}$	0.0038	0.0068	0.0092	0.0140	0.0219	0.0275	0.0344	0.0493	0.0590	0.0965
$\psi_i^{BB}$	0.0004	0.0008	0.0010	0.0016	0.0024	0.0030	0.0038	0.0054	0.0064	0.0105
$\psi_i^{BC}$	0.0033	0.0059	0.0082	0.0122	0.0195	0.0250	0.0290	0.0442	0.0553	0.0906
$\psi_i^{CA}$	0.0110	0.0204	0.0287	0.0314	0.0543	0.0725	0.0750	0.1223	0.1560	0.2329
$\psi_i^{CB}$	0.0074	0.0128	0.0171	0.0230	0.0352	0.0435	0.0519	0.0727	0.0857	0.1362
$\psi_i^{CC}$	0.0026	0.0046	0.0063	0.0079	0.0128	0.0163	0.0188	0.0280	0.0342	0.0533

Notes: Positive values represent improved precision for the combined approach. Parameter estimates from the original combined approach (Table 1) were used to generate expected  $m_{ij}$  arrays for cases when capture probabilities,  $p$ , and recovery probabilities,  $\lambda$ , were multiplied by scalar factors.

† Estimated movement probabilities from strata A to strata C approached 0, producing unreliable estimates of proportional standard error.

Ignoring problems with variance correction factors, we have shown that simultaneous modeling using mark-resight data and band recovery information can lead to increased precision in multistate parameter estimates. This conclusion is not surprising, since the inclusion of auxiliary data (in this case, dead recoveries) into the joint likelihood for resightings should not result in decreased precision, given that certain maximum likelihood regularity conditions hold (Barker and Kavalieris 2001). However, for the Canada Goose data we considered, gains in efficiency were minimal. We attribute the minimal gain in efficiency here to the small number of band recoveries in comparison to the number of resightings.

We anticipate gains in precision of survival probabilities to be much greater in a variety of real world situations. Estimated recovery probabilities were low ( $<0.07$ ) for all periods and strata. The hunting season was actually closed in South Carolina from 1985 to 1990 (Hestbeck et al. 1991), resulting in a recovery probability for stratum 3 that was effectively zero for the first, fifth, and sixth recovery periods. For Mallards (*Anas platyrhynchos*), and likely for Canada Geese, recovery probabilities have substantially increased following the introduction of 1–800 telephone numbers onto leg bands (Royle and Garretson 2005; J. Dubovsky, J. Hines, and J. Nichols, unpublished data). A higher recovery probability would lead to an increased number of direct and indirect recoveries, and hence contribute more information to the estimation of survival probabilities and transition probabilities. The amount of observer effort applied for resighting marked geese (31 826 secondary resightings over six years) in this study was considerable. This is ideal, but we suspect that there are many studies where recapture/resighting effort is considerably less. Hence, a combined approach may be more useful when resighting effort is

limited in comparison to hunting effort, as would be expected for many exploited populations.

#### Sensitivity of results to sighting probability and reporting probability

To explore the effects of hypothetical increases in recovery probabilities and decreases in resighting effort on the precision of survival and movement estimates, we analyzed combinations of modified Canada Goose resighting and recovery records, using the analytical-numerical method reviewed by Burnham et al. (1987:215, 293). We generated arrays of expected live and dead encounters using parameter estimates and cohort sizes from Table 1 and multinomial cell probabilities from the Appendix (Tables A2b and A3b), but varied capture and recovery probabilities to reflect different levels of sampling effort. Resighting probabilities,  $p$ , were multiplied by factors of 0.10, 0.25, 0.50, and 1.0, and the set of recovery probabilities,  $r$ , was multiplied by 1.0, 2.0, and 3.0. Expected data from each combination of experimental parameters were analyzed using program MSSURVIV (for resightings only) and program MSSRVRCV (for resightings and recoveries). Differences between the mean proportional standard errors were determined for survival and resighting probabilities under the two methods of analysis (Table 2). The mean difference in proportional standard error for strata-specific parameter estimates was calculated by averaging differences over the first four time periods. Only the first four time periods were used because survival in the fifth period is confounded with capture probability when using the traditional analysis and also because transition probabilities showed marked differences between the two types of analysis in the last time periods. This was ostensibly due to the lack of band recoveries in stratum 3 during the final two time periods.

This analysis resulted in varying levels of increased relative precision with the combined method, with greatest decreases in proportional standard error of survival estimates occurring when the number of recoveries comprised a larger proportion of total observations. Transition probabilities also showed decreases in proportional standard error as either resighting effort decreased or recovery effort increased. These results indicate that the combined approach articulated here should be more useful when the amount of recovery effort gets closer to the amount of resighting effort. In either case, the acquisition of tag recovery data is a passive process from the investigator's perspective, based on hunters, fisherman, or others reporting dead animals. This information will thus tend to improve the precision of biologically important parameter estimates such as survival and movement probabilities, with minimal expense.

#### EXTENSION TO USE OF INCIDENTAL OBSERVATIONS

Extending these recapture/recovery models to include incidental observations obtained between recapture periods presents additional challenges. In a single-state case, Barker (1995) modeled incidental observations essentially as "recoveries" that are restored to the population. However, when there are multiple states, an animal that is incidentally observed more than a year after release (e.g., in wintering area 1) presents problems because it is not clear to which state (e.g., breeding) to associate it when it is "re-released" after observation. The states it goes through between physical release and incidental resighting is described probabilistically, as in the recovery case, but that is not sufficient to assign a specific state to it thereafter. Barker (1995) solved this problem by associating survival and movement probabilities with the last state in which it had been captured (which might have been immediately preceding recovery or any number of periods previous). This assumption is convenient but is biologically restrictive, is likely to introduce heterogeneity, and contradicts the Markovian assumption inherent in these models for transitions from recapture state to recapture state. Therefore, except for the case where the state is observed directly at the time of incidental observation (Conn et al. 2004), formal incorporation of these observations and "re-release" of the animal remains an open and difficult problem. In the face of this we outline two options for using these data.

An ad hoc approach would be to treat observations between formal capture periods (e.g., in wintering areas) as recoveries. Information on an animal's survival up to recovery, as well as movement to the recovery area, would be noted. Then the recovered animal would be removed from the cohort "permanently" by ignoring the fact that it is alive until it is recaptured in area A or B during a formal sampling period. At that time it would be re-released into a cohort as a "new" animal. This approach could be juxtaposed with a MSMR ap-

proach that ignores incidental observations entirely (e.g., Spendelov et al. 1995), thus preventing loss of survival and transition information derived from consecutive captures. The relative benefits of the two approaches would depend on the relative number of captures vs. incidental observations, and the relative emphasis on transitions between capture states (e.g., between states A and B in Fig. 1) vs. transitions between capture and recovery states (e.g., from states A or B to states 1 or 2 in Fig. 1).

A formal approach to incorporating incidental observations would be to model the state (e.g., breeding) of a cohort of animals incidentally observed as a finite mixture of all states (e.g., breeding). A mixture parameter would describe the proportion of those incidentally observed between sampling periods  $i$  and  $i + 1$  that occupied each state at time  $i$  (similar to Kendall et al. 2003), which would be estimable if there are some animals whose state (e.g., breeding) is known (because they were captured in the capture occasion immediately preceding their incidental observation). This would involve a Bayes' Theorem development parallel to Barker's (1995, 1997) single-state incidental observation model. As with recoveries, the additional parameters inherent to this approach would be worthwhile, as long as there are a large number of incidental observations.

It is the dispersed nature of incidental observations that requires us to consider such complex models, which model survival only from recapture period to recapture period. When ancillary observations come from truly incidental sources such as the public, this dispersion is unavoidable. However, when they come from haphazard sampling by biologists (e.g., an individual has a look at a concentration of animals while in an area on other business), then the investigator should consider whether this dispersed effort could be concentrated into more formal sampling periods. If this concentration were possible then a MSMR recaptures-only model could be employed to estimate seasonal survival and movement.

#### DISCUSSION

The purpose of combining sources of information to estimate demographic parameters is to be able to estimate parameters that are unestimable using either source independently, or to increase precision for parameters that were already estimable. We have presented a statistical framework for combining multistate recaptures of animals with multistate tag recoveries, the latter being in many cases "free information" provided by the public. We have considered two basic scenarios: where migratory species are captured in one part of their annual cycle and recovered in another, and where capture and recovery areas are the same. We have reanalyzed data from a published study of survival and movement of geese, where recoveries had been ignored. Finally, we have outlined the extension of

these models to incorporate incidental observations between capture periods.

If there are no unobservable capture states, the number of recovery states does not exceed the number of recapture states, and recoveries after the last recapture period are recorded, then all parameters from the combined model can be estimated. The existence of unobservable states (Kendall and Nichols 2002) at the time of capture causes confounding problems, some of which can be resolved, but we address this issue elsewhere.

We anticipate that the combined method developed here will be most useful for those studying species subject to harvest or by-catch, such as game birds, fish, and sea turtles, although European ringing programs also yield recoveries on nonharvested birds. There is great potential for ecologists to exploit this "free" information. As indicated in Table 2, the utility of this information grows as the number of recoveries grows. This is achieved by either raising the harvest probability, or raising the probability that a harvested tag is reported. The use of reward tags (Nichols et al. 1991, Pollock et al. 2001) and toll-free telephone numbers inscribed on tags (Royle and Garretson 2005; J. Dubovsky, J. Hines, and J. Nichols, *personal communication*) can effectively promote the latter.

Maximum likelihood estimation using complex models can result in numerical problems due to multimodality (i.e., multiple peaks in the likelihood function). This problem can be minimized by running an analysis several times, using different starting values, and choosing the one with the maximum resulting likelihood value. In our case one option would be to initially run separate multistate recapture and tag recovery analyses, and use the resulting estimates as initial values for the combined analysis. The multimodality problem deserves further research (Barker and White 2004).

The choice of estimation method must be based on a balance of benefits and costs. More complex models require more data in theory, but it is not always clear how much more. For the practitioner who is most interested only in improving precision, we suggest trying a combined analysis as presented here, and evaluate whether estimated precision has indeed improved over using recaptures or recoveries alone. If the movement from capture states to recovery states is of interest, then the practitioner must either incorporate recoveries or develop a recapture/resighting program in these recovery areas.

Given the combination of data sources described here, it is intriguing to consider extending these methods further, to incorporate other sources of information. Indirect information about movement (see Kendall and Nichols 2004) from stable isotope or genetic data (Waser and Strobeck 1998, Hobson 2002, Webster et al. 2002) could be combined with recapture (Powell 2004) and recovery data in a joint likelihood.

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#### APPENDIX

Probability structure in matrix format (*Ecological Archives* E087-006-A1).