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ESTIMATING SURVIVAL AND TEMPORARY EMIGRATION IN THE MULTISTATE CAPTURE–RECAPTURE FRAMEWORK

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Abstract. The open population Cormack-Jolly-Seber (CJS) capture–mark–recapture model for estimating survival allows for random temporary emigration from the sampling area, but Markovian temporary emigration can bias estimates of survival. We explore a multistate capture–recapture model that has been proposed for coping with Markovian temporary emigration. We provide a comprehensive assessment of the performance of this model using computer algebra and simulation. We found that most model parameters were identifiable unless survival, emigration, and immigration were all time dependent. Simulation results showed that intrinsically identifiable parameters were estimated without bias and that precision of survival estimates was always high. When temporary emigration was Markovian, precision of estimates of emigration, immigration, and recapture probabilities was acceptable; otherwise it was not. Test component 2.Ct of the goodness-of-fit test for the CJS model had good power to detect Markovian temporary emigration. We conclude that the multistate model works well when temporary emigration is Markovian (i.e., when the CJS model should not be used) and when survival and recapture probabilities are high.

Key words: bias; Cormack-Jolly-Seber model; emigration; goodness-of-fit test; immigration; intrinsic identifiability; survival estimation.

INTRODUCTION

Capture–recapture methods are basic tools for estimating survival and breeding probabilities (Williams et al. 2002). The classic Cormack-Jolly-Seber (CJS) model provides unbiased estimates of survival if all individuals have the same recapture probability (Lebreton et al. 1992). However, recapture probability can vary among individuals because some individuals may be absent from the sampling site at one or several sampling occasions. This is known as temporary emigration (Burnham 1993) and may bias estimates of survival probabilities (Kendall et al. 1997). Magnitude and direction of bias depend on the kind of temporary emigration. If all individuals have the same probability of being absent at a given occasion, temporary emigration is random, and estimates of survival are unbiased (Burnham 1993, Kendall et al. 1997). In contrast, if the probability of being temporarily absent depends on whether or not an individual was absent during the previous occasion, temporary emigration is Markovian (''non-random'') and estimates of survival can be biased (Kendall et al. 1997).

Temporary emigration is widespread in animals and plants. For example, sampling is frequently conducted at breeding sites. If marked individuals skip a breeding opportunity (Kendall et al. 1997), they are not present at the breeding site, have a recapture probability of zero, and hence appear as temporary emigrants in capture–recapture data. Also, individuals might be temporarily unavailable for capture, e.g., because they breed, are dormant, in torpor, or hibernate (Tilley 1980, Kendall et al. 1997, Schaub and Vaterlaus-Schlegel 2001, Shefferson et al. 2001).

Currently, sampling under Pollock's robust design is the best way of obtaining unbiased estimates of survival if there is temporary emigration (Pollock 1982, Kendall et al. 1997, Bailey et al. 2004). The robust design requires that individuals are sampled at primary occasions, between which a population is open to gains and losses, and at secondary occasions during which

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the population is assumed to be closed (Williams et al. 2002). Unfortunately, most capture–recapture data are not sampled under a robust design. Therefore, this powerful analytical approach cannot be used, making reliable parameter estimation difficult (Nichols et al. 1987, Kendall et al. 1997, Schmidt et al. 2002, Bailey et al. 2004).

Recently, Fujiwara and Caswell (2002) and Kendall and Nichols (2002) proposed a model for estimating survival and temporary emigration from capture–recapture data that were not collected under the robust design. To model temporary emigration and estimate survival, these authors proposed a multistate capture–recapture model with an ''observable'' and an ''unobservable'' state between which individuals may move. Individuals in the sampling area are in the observable state. Moving out of the sampling area is equivalent to becoming a temporary emigrant and to moving to the unobservable state.

The drawback of such a multistate approach is that estimation of some parameters may be impossible because some are aliased and not separately identifiable. Using the analytical-numerical approach (Burnham et al. 1987) to study parameter identifiability, Kendall and Nichols (2002) found that the model does not perform well when transitions are first-order Markovian. Parameter estimates are only unbiased if transitions between states are deterministic and either transition, survival, or capture probabilities constant. Even then parameter estimates have large coefficients of variation, suggesting problems with parameter estimation. However, the analytical-numerical approach is not fully general, but rather is specific because expected values of capture histories for a restricted set of parameter values are constructed. Kendall and Nichols (2002) encouraged further studies of the behavior of the multistate model because its properties are not yet well understood.

Here, we provide a comprehensive assessment of the performance of this model, give guidance for its use and for the estimation of survival probabilities under temporary emigration. We address three main issues. First, we assess the intrinsic identifiability of the model parameters, where some or all parameters types are either constant, time dependent, and/or group dependent using computer algebra methods to ensure full generality of the results (Catchpole and Morgan 1997, Catchpole et al. 2002).

The second issue is precision and bias of parameter estimates, given that parameters are identifiable. We study these issues under the simplest model where the parameters are identifiable using the analytical-numerical approach. We consider various situations with different survival and recapture probabilities and different propensities of temporary emigration.

Because only Markovian temporary emigration causes bias in CJS survival estimates (Lebreton et al. 1992, Kendall et al. 1997), our third issue is the detection of Markovian temporary emigration. This is critical to the decision as to whether the CJS or the multistate model should be used. We explore the power of test component 2.Ct, which is part of the overall goodness-of-fit test of the CJS model, to detect Markovian temporary emigration. Test 2.Ct was originally developed to detect immediate trap response behavior (Pradel 1993), but may be useful for detecting nonrandom temporary emigration. We use the analytical-numerical approach to study the power of this test to detect Markovian temporary emigration. We conclude by providing guidelines for identifying which model should be used for parameter estimation.

Material and Methods

The multistate model

Kendall and Nichols (2002) considered a multistate capture–recapture model with states ''observable'' and ''unobservable'' between which individuals are allowed to move. Individuals that are in the state ''unobservable'' during a capture occasion cannot be captured because they are unavailable for capture. The transition matrix and associated vectors of survival and capture probabilities for this model, which we term temporary emigration (TE) model, are then

$$\begin{bmatrix} (1-\psi^{OU}) & \psi^{OU} \\ \psi^{UO} & (1-\psi^{UO}) \end{bmatrix}_t \begin{bmatrix} S \\ S \end{bmatrix}_t \begin{bmatrix} p \\ 0 \end{bmatrix}_t \qquad (1)$$

where S_i is the probability that a marked individual has survived from i to $i+1$, ψ_i^{OU} is the probability that a marked individual has emigrated from the study area between i and $i+1$, ψ_i^{UO} is the probability that a marked individual has immigrated (returned) to the study site between i and $i+1$, and p_i is the probability that a marked individual is recaptured at i, given that it is alive and in the observable state at i. The matrix and vector subscript t denotes time dependence. In contrast to the CJS models, the recapture probability in the TE model is conditioned on being observable (on-site recapture probability). Because the transition probabilities depend only on the state in which an individual was before a transition, temporary emigration is a first-order Markov process (herein named Markovian temporary emigration).

Assessing intrinsic identifiability

We used computer algebra to check which parameters are theoretically identifiable (Catchpole and Morgan 1997, Catchpole et al. 2002, Gimenez et al. 2003, Appendix A). The model parameters were considered to be either both group and time dependent (denoted by g × t), time dependent only (t), group dependent only (g; e.g., sexes), or constant (.). Transitions between the observable and unobservable state were considered as one process, thus the parameters ψ^{OU} and ψ^{UO} had always the same structure. In total, 64 different models were checked for intrinsic identifiability.

Analytical-numerical approach

We used the simplest model in which all parameters were intrinsically identifiable $\{S_., \psi^{OU}_., \psi^{UO}_., p_.\}$ to study expected bias and precision of the parameter estimates. We considered eight capture occasions and 500 newly released individuals at each capture occasion and calculated expected values of the 254 possible capture histories for different values of S, ψ^{OU}, ψ^{UO}, and p. We considered situations with high (S = 0.7) and low (S = 0.3) survival probabilities; high (p = 0.8) and low (p = 0.3) recapture probabilities; low (ψ^{OU} = 0.1), medium (ψ^{OU} = 0.5) and high (ψ^{OU} = 0.9) emigration probabilities; and with a wide range (ψ^{UO} = 0, 0.1, 0.2, . . . , 1) of immigration probabilities. For these resulting 132 sets of parameter combinations, we generated capture histories (Supplement 1) and estimated the parameters with the program MARK (White and Burnham 1999) using the model $\{S_., \psi^{OU}_., \psi^{UO}_., p_.\}$. If the number of released individuals is large, resulting maximum likelihood estimates and standard errors represent approximate expected values of the estimators and their standard errors, respectively (Burnham et al. 1987). We then calculated absolute bias (difference of parameter estimate and true value) and coefficient of variation (CV). For comparison, we analyzed the same data using the time-constant CJS model $\{S_., p_.\}$ and calculated absolute bias and CV of the survival rate.

We analyzed these capture histories also with the program U-CARE (Choquet et al. 2001) to compute subtest 2.Ct, which is part of the overall goodness-of-fit test of the CJS model (Lebreton et al. 1992, Pradel 1993). Test 2.Ct tests whether the probability to recapture an individual at $i + 1$ depends on whether it has been captured at i, given that it has survived the interval from i to $i + 1$. We present the type I error probability of test 2.Ct for each situation considered. As the data are generated, this is equivalent to the power of the test (Burnham et al. 1987).

RESULTS

Intrinsic identifiability

Of the 64 models we considered, 52 were intrinsically identifiable (Appendix B). All parameters in these models could be estimated separately, apart from parameters referring to the first and the last time steps in some models. However, it appeared that most parameters were not identifiable when both transition and survival probabilities were time dependent, regardless of whether recapture probability was time dependent or constant (models 1–8 and 21–24). Some interesting exceptions occurred when transition parameters were time and group dependent and survival was time dependent only (models 17–20). If temporary emigration differed among groups, then parameters were identifiable.

The simplest model ($\{S_., \psi^{OU}_., \psi^{UO}_., p_.\}$) was intrinsically identifiable provided there were at least five capture occasions. More complex models required as many as six capture occasions.

Bias and coefficient of variation of parameter estimates

Survival probabilities.—Survival estimated with the TE model was always unbiased (Fig. 1, Appendix C). This is in contrast to the CJS model $\{S_., p_.\}$ where survival probabilities were only unbiased when temporary emigration was random ($\psi^{OU}_. = 1 - \psi^{UO}_.$). Consistent with the results of Kendall et al. (1997), bias was positive when $\psi^{OU} > 1 - \psi^{UO}$ and negative when $\psi^{OU} < 1 - \psi^{UO}$. Bias also increased with increasing probability of emigration.

The CV of survival under the TE model decreased with increasing survival, on-site recapture, emigration, and/or immigration probabilities (Fig. 1, Appendix C), and was often lower than 100%, indicating that the TE model is useful to estimate survival probabilities. This held true also when temporary emigration was random. The CV of survival obtained by the CJS model was smaller, indicating a loss of precision when the TE model is applied.

Transition probabilities.—The TE model yielded unbiased estimates of the emigration and immigration probabilities (Fig. 1, Appendix C). However, the CVs were usually much larger than those of survival, in particular when the temporary emigration pattern was random or nearly so. Generally, CVs of immigration were larger than CVs of emigration. CVs of both parameter types decreased with increasing survival and/or on-site recapture probabilities. Thus, the performance of these parameters is reasonable when survival and on-site recapture probabilities are high and when temporary emigration is clearly Markovian.

On-site recapture probabilities.—On-site recapture probability estimated under the TE model behaved very much the same as the transition probabilities (Fig. 1, Appendix C). An exception can be noticed when emigration was permanent (ψ^{UO} = 0): the CV of the on-site recapture probability was then low (<100%), whereas the CV of the transition probabilities was high. In contrast, recapture probabilities estimated under the CJS model were always biased low, unless emigration was permanent in which case bias was zero (result not shown).

The main conclusions about bias and precision of parameter estimates hold true also when some parameters were time dependent (Appendix D). However, as more parameters were estimated, the CV of the estimates increased compared to that of the model where the parameters were constant across time.

Detection of Markovian temporary emigration

Subtest 2.Ct of the overall goodness-of-fit test of the CJS model appeared to be a good indicator for the pattern of temporary emigration. The power of subtest 2.Ct increased the more temporary emigration deviated

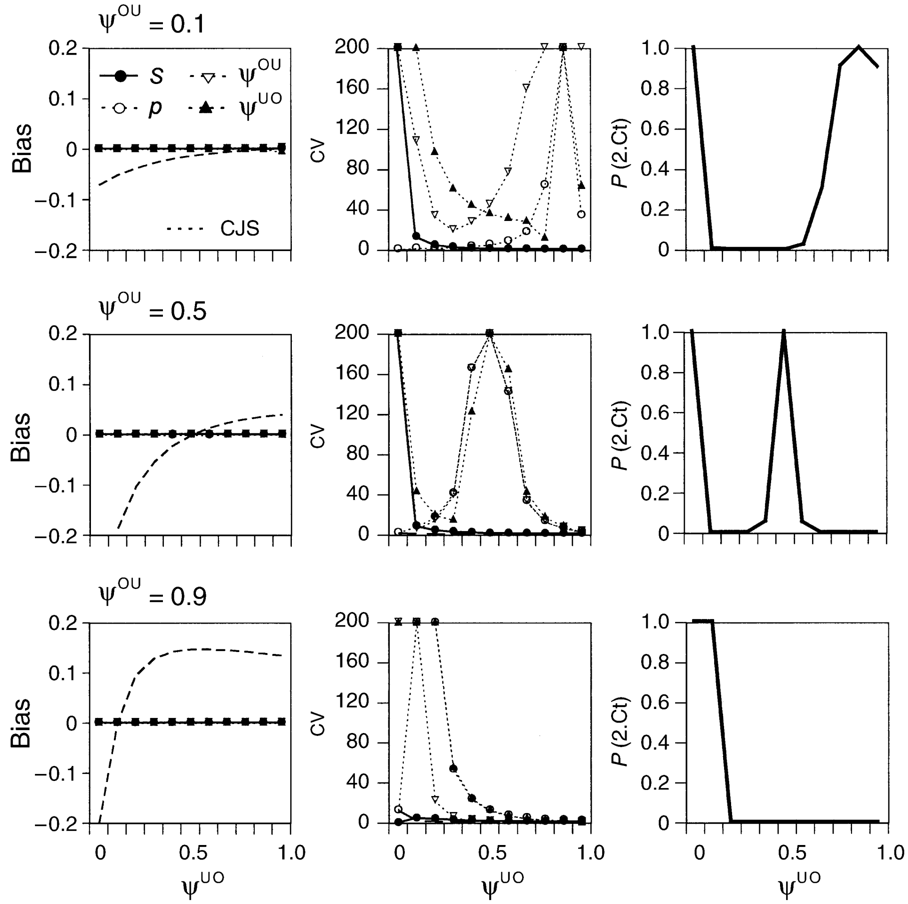

FIG. 1. Asymptotic absolute bias and coefficient of variation (CV) of parameter estimates, and the P value of the goodness-of-fit χ^2 test component 2.Ct for the TE model $\{S_., \psi^{OU}_., \psi^{UO}_., p_.\}$. The model is evaluated for a survival probability of 0.7, an on-site recapture probability of 0.8, and under different conditions with respect to emigration (ψ^{OU}) and immigration (ψ^{UO}). Temporary emigration is random when $\psi^{OU} = 1 - \psi^{UO}$, and emigration is permanent when $\psi^{UO} = 0$. The lines in the graphs are truncated at ±0.2 (bias), at 200% (CV), and at 150 (χ^2). In the charts showing the bias, often only the survival rate is visible. The bias in the other parameters is the same as that of the survival rate when not visible. CJS refers to the survival rate estimated with the Cormack-Jolly-Seber model $\{S_., p_.\}$. Evaluation of models with other survival and on-site recapture probabilities can be found in Appendix C.

from randomness and with increasing survival and on-site recapture probabilities (Fig. 1, Appendix C).

Discussion

Temporary emigration is a common phenomenon in animal and plant populations and can lead to biased estimates of survival in capture–recapture models. When temporary emigration occurs, the classic Cormack-Jolly-Seber model should not be used. Here we show that a recently proposed multistate model with an unobservable state (Fujiwara and Caswell 2002, Kendall and Nichols 2002) can be used as an alternative analytical approach when there is temporary emigration because estimates of survival are unbiased and fairly precise. Estimates of transition probabilities also were unbiased but had good precision only when temporary emigration was clearly Markovian. Thus, in the very situation where temporary emigration causes bias when the CJS model is used for parameter estimation, the TE model has its strength. Hitherto, these parameters could be estimated without bias only when data were sampled under a robust design (Pollock 1982, Kendall et al. 1997). Yet, many capture–recapture data have not been sampled under the robust design. The TE model offers new possibilities to estimate and adjust for Markovian temporary emigration and can substantially enhance the value of sampled data. For example temporary emigration was presumed repeatedly in amphibian data, rendering statistical analyses difficult (Nichols et al. 1987, Kendall et al. 1997, Schmidt et al. 2002, Bailey et al. 2004).

The TE model performs well generally, but a discussion of some of its weaknesses and assumptions seems appropriate. We showed that most parameters in 52 out of 64 variants of the TE model are intrinsically identifiable. It is not necessary to make transitions deterministic (Kendall and Nichols 2002, Fujiwara and Caswell 2002), but this may increase precision of parameter estimates. However, in models where both survival and temporary emigration probabilities were time dependent, no parameter of interest was generally identifiable. If a nonidentifiable model is selected as the best one (e.g., $\{S_t, \psi_t^{OU}, \psi_t^{UO}, p_t\}$), one might calculate the model averaged estimates of the models that are identifiable and that capture some of the variation in the parameters (i.e., $\{S_., \psi_t^{OU}, \psi_t^{UO}, p_t\}$ and $\{S_t, \psi_.^{OU}, \psi_.^{UO}, p_t\}$). However, such an approach is not yet established and warrants further investigation. Another solution might be to use the estimates of the best model with identifiable parameters (Burnham and Anderson 2002).

The precision of parameter estimates in the TE model is reduced relative to the CJS model. This is due to the fact that on-site recapture, emigration and immigration probabilities are combined in a single parameter (recapture probability) in the CJS model, hence fewer parameters are estimated. Precision of all parameter estimates under the TE model increased the more that temporary emigration deviated from randomness. Under these circumstances the bias of parameter estimates under the CJS model increases. In the trade-off between unbiased and imprecise vs. biased and precise estimates we prefer the unbiased and imprecise estimates and hence the TE model.

As for robust design models (Kendall et al. 1997, Schwarz and Stobo 1997, Kendall and Bjorkland 2001, Lindberg et al. 2001; but see Bailey et al. 2004), the TE model assumes that individuals that are present and temporarily absent have equal survival probabilities. Theoretically, this assumption could be relaxed by allowing for a state-specific survival probability (model $\{S_t^O, S_t^U, \psi_t^{OU}, \psi_t^{UO}, p_t\}$). However, only a submodel where several parameters were assumed constant $\{S_.^O, S_.^U, \psi_t^{OU}, \psi_t^{UO}, p_.\}$ was intrinsically identifiable, rendering this approach not very useful.

Detecting nonrandom temporary emigration

A test to detect Markovian temporary emigration is important because the choice of the model for parameter estimation and precision of the parameter estimates depends on whether temporary emigration is random or Markovian. We found that the goodness-of-fit test 2.Ct, which was developed to detect immediate trap-response behavior (Pradel 1993), is useful for detecting Markovian temporary emigration. Although immediate trap-response behavior is biologically different from Markovian temporary emigration, both give similar results in this goodness-of-fit test. Under Markovian temporary emigration individuals that are present (but not necessarily caught) at i have a different probability to be at the site and being caught at $i + 1$ $[(1 - \psi_i^{OU}) \times p_{i+1}]$, than individuals that were not at the site at i $[\psi_i^{UO} \times p_{i+1}]$. Thus, if the on-site recapture probability would be 1, test 2.Ct would be an exact test to detect Markovian temporary emigration. Still the power to detect Markovian temporary emigration is reasonable when on-site recapture probabilities are lower, provided that survival and temporary emigration probabilities are high. Generally, the probability of detecting Markovian temporary emigration with test 2.Ct increases with increasing on-site recapture and survival probabilities (Fig. 1, Appendix C).

The reason for a significant test 2.Ct could be Markovian temporary emigration, or alternatively immediate trap-response behavior. The latter may be distinguished statistically from the former by a significant directional test as implemented, for example, in the program U-CARE (Choquet et al. 2001) or by knowledge of the capture methods and the biology of the species under study.

Temporary emigration and capture–recapture data: Which model should be used for parameter estimation?

When temporary emigration is suspected and a new study is planned, we clearly recommend Pollock's (1982) robust design for data collection and parameter estimation. Compared with the TE model considered here, Pollock's robust design models have several important advantages (Kendall et al. 1997, Williams et al. 2002). Parameters are estimated with higher precision (Kendall and Nichols 2002), modeling is more flexible, and random temporary emigration as well as other quantities such as recruitment and population size also can be estimated.

However, many existing data sets have not been collected under the robust design and Markovian temporary emigration is detected during data analysis. In this situation, there are several possibilities to take temporary emigration into account and to get unbiased estimates of survival probabilities.

First, one should check whether the data cannot be arranged such that they conform to the robust design. This is often possible because the population does not necessarily need to be closed during the secondary capture occasions (Schwarz and Stobo 1997, Kendall 1999, Kendall and Bjorkland 2001). For example, a modified version of the robust design allows estimation of the parameters of interest if animals are captured while entering or leaving a breeding site (Bailey et al. 2004), as is often the case in studies of amphibian populations (Schmidt et al. 2002).

The second possibility is to use the TE model. As we showed, this model yields unbiased estimates of the survival and on-site recapture probabilities as well as estimates of the emigration probabilities. Furthermore, it is possible to test hypotheses about variation in these parameters. This works particularly well when temporary emigration is clearly Markovian, and thus in the situation where the CJS survival estimate is biased most strongly.

Third, one may fit an immediate trap-response model (Pradel 1993, Schmidt et al. 2002). In the immediate trap response model, the probability of being present at the current occasion is based on whether an animal was caught at the previous occasion. In contrast, in the TE model, the probability of being present at the current occasion depends on whether the individual was present at the previous occasion. Thus, the immediate trap response model only approximately adjusts for temporary emigration. The only advantage over the TE model is that the immediate trap-response model works with four capture occasions whereas the TE model requires at least five capture occasions.

Fourth, one might consider using the CJS model given that survival estimates often are not strongly biased (Kendall et al. 1997). However, as we have shown, bias may be strong, especially when emigration probability is high (Fig. 1, Appendix C).

Conclusion

We explored the multistate temporary emigration model of Kendall and Nichols (2002) and, based on goodness-of-fit tests, provide guidelines when it should be used instead of the classic CJS model. We show that most parameters are identifiable in most models and that identifiability problems can in some cases be avoided when multiple groups of individuals are analyzed that share some parameters. Parameters are estimated without bias and with high precision when temporary emigration is Markovian. Markovian temporary emigration is a common phenomenon that can bias estimates of survival. The multistate temporary emigration model allows estimation of many parameters of biological interest.

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APPENDIX A

A description of a MAPLE session for assessing the intrinsic identifiability of the temporary emigration models is available in ESA's Electronic Data Archive: *Ecological Archives* E085-061-A1.

APPENDIX B

A table with the assessment of the intrinsic identifiability of different temporary emigration models is available in ESA's Electronic Data Archive: *Ecological Archives* E085-061-A2.

APPENDIX C

Figures showing the evaluation of bias and precision of parameters estimated with different time-invariant temporary emigration models are presented in ESA's Electronic Data Archive: *Ecological Archives* E085-061-A3.

APPENDIX D

A brief description of the evaluation of bias and precision of parameters estimated with time-dependent temporary emigration models is available in ESA's Electronic Data Archive: *Ecological Archives* E085-061-A4.

SUPPLEMENT 1

Files allowing the construction of expected values for the temporary emigration model are available in ESA's Electronic Data Archive: *Ecological Archives* E085-061-S1