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A hidden Markov model for estimating age-specific survival when age and size are uncertain

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Abstract. Estimates of age-specific survival probabilities are needed for age-structured population models and to inform conservation decisions. However, determining the age of individuals in wildlife populations is often problematic. We present a hidden Markov model for estimating age-specific survival from capture–recapture or capture–recapture–recovery data when age is unknown and indicators of age, such as size and growth layer counts, are imprecise. The model is evaluated through simulations, and its implementation is illustrated with maximum likelihood and Bayesian approaches in commonly used software. The model is then applied to genetic capture–recapture data of Florida manatees to estimate age- and time-variant survival probabilities. The approach is broadly applicable to studies aiming to quantify age-specific effects of environmental change and management actions on population dynamics, including studies that rely on minimally invasive methods such as genetic and photo identification.

Key words: age-specific survival; capture–recapture; Florida manatee; genotyping; hidden Markov model; multievent model.

INTRODUCTION

An understanding of population dynamics is necessary to infer causes of changes in population size and structure over time and to inform wildlife conservation and management decisions. Survival probability strongly influences population dynamics, so there is generally interest in estimating variation in survival probabilities across time, across locations, in response to environmental changes or management actions, and across age classes (Clobert and Lebreton 1991). In particular, age-structured population models, including population viability analyses (Morris and Doak 2002), integrated population models (Schaub and Abadi 2011), and fishery stock assessment models (Hilborn and Walters 1992), require estimates of age-specific survival probabilities. These models can be used to identify the most

vulnerable age classes and inform conservation efforts or harvest regulations. Additionally, survival can vary substantially with age, and ignoring the effect of age can lead to misguided management decisions (Coulson et al. 2001). When the age (or life-stage) of individuals sampled from a wildlife population is known without error, conventional capture–recapture methods, including multistate capture–recapture models, can be used to estimate these survival probabilities (Pollock 1981, Nichols et al. 1992). However, the age of sampled individuals is typically unknown unless individuals are first captured and marked soon after birth. This may be unfeasible for many studies or result in a reduced sample size when individuals of unknown age are censored from the analysis.

Previous models developed to estimate age-specific survival probabilities for individuals of unknown age have required that some individuals in the study be of known age (Colchero and Clark 2012, McCrea et al. 2013) or that the duration of the study be considerably longer than the life span of the study species (Matechou

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et al. 2013). Other approaches incorporating size to inform age estimates require a parametric growth model and that individuals be physically captured and measured (Coggins et al. 2006, Reinke et al. 2020). Alternatively, considering age as a latent state may facilitate the use of hidden Markov models (MacDonald and Zucchini 1997) to link discrete observations to uncertain states. Hidden Markov models include multievent models, which extend multistate capture–recapture models by accounting for uncertainty in state assignment (Pradel 2005). These models have been used to estimate survival probabilities while accounting for uncertainty in disease state (Conn and Cooch 2009), sex (Nichols et al. 2004), and reproductive state (Kendall et al. 2012).

Here, we present a multievent model, treating age as a latent state, to estimate age-specific survival probabilities that (1) can be used when the ages of all individuals in the study are unknown, (2) can be applied to long-lived species, and (3) incorporates auxiliary indicators of age that can be obtained with less invasive methods (e.g., observations of behavior, coloration, or relative size). We illustrate this model with genotype-based capture–recapture data on Florida manatees (*Trichechus manatus latirostris*), using relative size as an indicator of age. This model should be applicable to a broad array of study systems where researchers are interested in quantifying differential environmental and management impacts on survival across ages. In particular, it is relevant to capture–recapture studies using genotyping, camera trapping, photo identification, and other emerging, minimally invasive technologies in which animals are not physically captured, measured, or aged.

METHODS

Multievent models are conditioned on the time of an individual’s first capture, and their parameters include: initial state probability, π , given that the state of an individual at first capture may be unknown; state transition probabilities (including survival, S , and conditional state transition probability, ψ), which describe how individuals transition among states between sampling occasions; recapture probability, p ; and state assignment probability, δ , which is the probability of recording a specific observation event, conditional on capture and the individual’s underlying state (Pradel 2005, Conn and Cooch 2009). We use superscripts to indicate state (age) dependence and subscripts to indicate time dependence.

We define N age classes, $\mathbf{a} = \{a^0, a^1, \dots, a^{N-1}\}$, where a^0 denotes individuals alive age 0 (<12 months old), a^1 denotes individuals alive age 1 yr, \dots , and a^{N-1} denotes individuals alive age $N - 1$ yr or older. On sampling occasion t , an individual may be in one of $N + 1$ states, where the additional state denotes dead individuals. We assume that survival and other parameters do not vary with age beyond $N - 1$ yr. The state dynamics and observation processes of multievent models can be represented as matrices, following Pradel (2005). We illustrate

an example with $N = 5$ age classes, which correspond to our manatee example below. All matrices in this model are row-stochastic such that rows are constrained to sum to 1. Initial state probabilities are a row vector:

$$\boldsymbol{\pi}_t = [\pi_t^0 \ \pi_t^1 \ \pi_t^2 \ \pi_t^3 \ \pi_t^{4+} \ 0].$$

Here, individuals cannot be in the dead state at the time of first capture. The transition matrix (from row to column) representing survival from year t to year $t + 1$ is

$$\boldsymbol{\Phi}_t = \begin{bmatrix} 0 & S_t^0 & 0 & 0 & 0 & 1 - S_t^0 \\ 0 & 0 & S_t^1 & 0 & 0 & 1 - S_t^1 \\ 0 & 0 & 0 & S_t^2 & 0 & 1 - S_t^2 \\ 0 & 0 & 0 & 0 & S_t^3 & 1 - S_t^3 \\ 0 & 0 & 0 & 0 & S_t^{4+} & 1 - S_t^{4+} \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}.$$

At each sampling occasion, one of L observation events is possible for each individual. These observation events may denote: the individual’s age if the individual is detected and age is known, an indicator of age (e.g., behavior, coloration pattern, size) if the individual is detected but age is uncertain, or that the individual was not detected. We illustrate an example with $L = 4$ events, where one event denotes that the individual was not detected and the other three denote indicators of age with uncertainty (based on approximate size: small, s, medium, m, or large, l) for when the individual was detected. The matrix of observation event probabilities is then

$$\mathbf{B}_t = \begin{bmatrix} 1 - p_t^0 & p_t^0 \times \delta_t^{s|0} & p_t^0 \times \delta_t^{m|0} & p_t^0 \times \delta_t^{l|0} \\ 1 - p_t^1 & p_t^1 \times \delta_t^{s|1} & p_t^1 \times \delta_t^{m|1} & p_t^1 \times \delta_t^{l|1} \\ 1 - p_t^2 & p_t^2 \times \delta_t^{s|2} & p_t^2 \times \delta_t^{m|2} & p_t^2 \times \delta_t^{l|2} \\ 1 - p_t^3 & p_t^3 \times \delta_t^{s|3} & p_t^3 \times \delta_t^{m|3} & p_t^3 \times \delta_t^{l|3} \\ 1 - p_t^{4+} & p_t^{4+} \times \delta_t^{s|4+} & p_t^{4+} \times \delta_t^{m|4+} & p_t^{4+} \times \delta_t^{l|4+} \\ 1 & 0 & 0 & 0 \end{bmatrix},$$

where the rows represent the states defined above and the columns (from left to right) represent the observations: not detected, detected and recorded as small, detected and medium, and detected and large. Note that $p = 1$ for the occasion when an individual is first captured and marked. Superscripts for δ denote that recorded indicators of age are conditional on the true underlying age.

Extensions of this model can incorporate robust sampling design and carcass recovery data, which we anticipate would lead to gains in the precision of survival estimates (Kendall et al. 2013). A robust design approach can be used when, within a primary occasion, there are multiple secondary sampling occasions during which states do not change (Pollock 1982). Carcass

recoveries can be incorporated by adding newly dead states for each age class and a previously dead state, based on the assumption that carcasses cannot be recovered and individually identified more than 1 yr after an individual has died (Lebreton et al. 1999). For the observation process with carcass recovery data, we add parameters for carcass recovery probability (r) and carcass state assignment probability (ϵ), which are analogous to p and δ . See Appendix S1 for additional details on incorporating robust sampling design and carcass recovery data. Temporary emigration can be modeled by including one or more unobservable states, with corresponding transition probabilities and where p is fixed to 0, for individuals that are temporarily unavailable for recapture (Kendall and Nichols 2002). Extensions to improve parsimony by modeling δ and ϵ as a function of latent age or to account for individual heterogeneity are also possible (Appendix S2).

Implementation and simulation study

Variation in parameters across time, state/age, groups, individuals, or as a function of external covariates can be modeled using generalized linear models, as with other capture–recapture models (Lebreton et al. 1992). Specifically, probabilities within a matrix row can be modeled using a multinomial logit link function. Model parameters can be estimated using maximum likelihood (Pradel 2005, Choquet et al. 2009) or Bayesian (Turek et al. 2016) approaches that have been developed for other hidden Markov models.

Using simulated data based on our starting model (i.e., no robust design or carcass recovery data), we assessed model performance with a maximum-likelihood approach using program E-SURGE (version 2.2.3; Choquet et al. 2009) and with a Bayesian Markov chain Monte Carlo (MCMC) approach using the NIMBLE package (version 0.7.1; NIMBLE Development Team 2019) in program R (version 3.6.0). To reduce MCMC runtime, we used a custom function to calculate the likelihood of each capture history by integrating over all possible latent states, which was then passed to the BUGS model code in NIMBLE (Turek et al. 2016). We used uniform and diffuse normal priors and ran three MCMC chains of at least 2,000 samples after discarding 2,000 as burn-in; the chains were extended until the Gelman-Rubin statistic was <1.3 for all parameters or until 10,000 samples were run. We simulated data for eight sampling occasions, with 100 individuals first captured and marked on each occasion. We set all parameters constant across time, survival as a linear (on the logit scale) function of age, $p^0 = p^1$, and $p^2 = p^3$; otherwise, all parameters varied categorically across age. Code to simulate the data in R and fit the model with NIMBLE are included in Data S1. We ran 1,000 simulations and report the absolute bias, mean absolute error, and coverage (based on 95% credible intervals) for NIMBLE. Because of lack of

automation, we ran only 100 simulations and do not report coverage for E-SURGE.

Manatee example

Tissue samples for genotype-based individual identification were collected from manatees in southwest Florida over 10 winters using a custom biopsy needle. The size class of individuals was estimated at the time of sampling and was recorded as calf, subadult, or adult based on observed behaviors (e.g., nursing) and previous work relating manatee body length to age (Schwarz and Runge 2009). However, manatees were not physically captured and measured during sampling, and length-at-age is likely to vary (Schwarz and Runge 2009), resulting in uncertainty in age. Biopsy samples were also collected from manatee carcasses reported to the Florida Fish and Wildlife Conservation Commission, and carcasses were assigned to one of the same three size classes based on measured or estimated total length. We modeled survival for five age classes ($a^0, a^1, a^2, a^3, a^{4+}$) to align with existing manatee population models (Runge et al. 2017). To implement the robust design, we pooled sampling trips within each winter (primary occasion) into two secondary occasions. See Appendix S3 for more details on manatee sampling and genetic analysis. Capture history data are available (see Open Research).

We fit models to the manatee data using program E-SURGE, which we found more convenient for model construction and selection, and faster in achieving convergence, than Bayesian MCMC methods. Details for implementing the model in E-SURGE are described in Appendix S4. We used Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002) and a build-up approach for model selection (Morin et al. 2020), focusing first on age effects then on time effects and temporal covariates. Candidate models included an age effect for all probabilities and time effects for p , r , ψ (temporary emigration; i.e., the probability that an individual transitioned out of or into the sampling area, given that it survived from the previous year), and S . Temporal covariates included sampling effort and needle design for p , a winter cold severity index for S and ψ , and a red tide severity index for S (see Appendix S3 for details on covariates tested). For S , we considered age as either a categorical or a logit-linear covariate, and we considered both additive and interactive time effects with age (see Appendix S5 for a table of all candidate models).

RESULTS

Simulations

Using simulated data sets, absolute bias was <0.08 for all parameters and <0.04 for all survival probabilities with both E-SURGE and NIMBLE (Table 1). Coverage in NIMBLE was close to the nominal 0.95

TABLE 1. Simulation results for estimating age class-specific survival probabilities when age is unknown using maximum likelihood (program E-SURGE) and Bayesian (R package NIMBLE) approaches.

Parameter	True value	E-SURGE		NIMBLE		Coverage
		Mean	MAE	Mean	MAE	
S^0	0.70	0.70	0.06	0.67	0.06	0.947
S^1	0.79	0.80	0.03	0.77	0.03	0.945
S^2	0.86	0.87	0.02	0.86	0.01	0.957
S^3	0.91	0.92	0.01	0.91	0.01	0.945
S^{4+}	0.95	0.95	0.01	0.95	0.01	0.958
p^0, p^1	0.5	0.56	0.13	0.52	0.10	0.973
p^2, p^3	0.6	0.61	0.04	0.60	0.04	0.956
p^{4+}	0.7	0.70	0.01	0.70	0.01	0.945
π^0	0.1	0.15	0.07	0.09	0.03	0.949
π^1	0.2	0.17	0.06	0.19	0.04	0.948
π^2	0.2	0.20	0.06	0.19	0.04	0.966
π^3	0.2	0.21	0.09	0.21	0.04	0.975
δ^{sl0}	0.8	0.75	0.14	0.81	0.14	0.918
δ^{sl1}	0.6	0.54	0.16	0.60	0.10	0.938
δ^{sl2}	0.2	0.17	0.09	0.24	0.08	0.922
δ^{sl3}	0.1	0.09	0.05	0.13	0.05	0.954
δ^{sl4+}	0	0.00	0.00	0.00	0.00	NA
δ^{ml0}	0.2	0.23	0.13	0.17	0.14	0.875
δ^{ml1}	0.4	0.40	0.11	0.37	0.10	0.936
δ^{ml2}	0.5	0.55	0.10	0.53	0.07	0.948
δ^{ml3}	0.6	0.53	0.15	0.59	0.08	0.951
δ^{ml4+}	0.2	0.20	0.01	0.21	0.01	0.939

Notes: Metrics are mean estimate, mean absolute error (MAE), and coverage. Coverage is not reported for E-SURGE results, which used only 100 simulated data sets, or for probabilities with true value = 0.

(range = 0.88–0.98 for all parameters, 0.95–0.96 for survival probabilities). Mean absolute error for S , p , and δ tended to be greater for younger age classes, which had sparser data in this simulation, than for older age classes.

Manatee example

A total of 2,046 unique individuals were genetically identified from the sampling of live manatees. Our model results suggested that most manatees were age 4 yr or older when first captured ($\pi^{4+} = 0.71$, 95% confidence interval = [0.45, 0.89]), with initial state probabilities equal among the younger age classes in models best supported by the data based on AIC_c (Appendix S5: Table S1). Most manatees (78%) were detected alive only once during the study, and no individuals recorded as a live calf were detected in both secondary occasions in the same winter. Correspondingly, recapture probability estimates were low overall ($p < 0.16$ across all age classes and secondary occasions) and lowest for age 0 manatees ($p^0 = 0.00$ [0.00, 0.01] in all secondary occasions). Of the 2,046 manatees in this study, 119 were recovered dead. Carcass recovery probability was estimated to be 0.25 [0.17, 0.36], and AIC_c did not support models for which

r varied across age or years, likely due to sparse data. Live age 0 manatees were most often, but not always, recorded as a calf ($\delta^{calf0} = 0.65$ [0.45, 0.80]), whereas live age 1, age 2, and age 3 manatees were most often recorded as a subadult (Fig. 1). Live manatees age 4 and older were almost always recorded as an adult ($\delta^{adult4+} = 0.97$ [0.95, 0.98]). Size class assignment probabilities for manatee carcasses had a similar pattern as for live manatees, although estimates were less precise ($\epsilon^{calf0} = 0.82$ [0.01, 1.00]; $\epsilon^{adult4+} = 0.92$ [0.84, 0.97]).

The models with most support based on AIC_c included age as a logit-linear covariate and a red tide effect on survival, and models in which the red tide effect was additive across age classes had more support than models in which the red tide effect was different for each age class (Appendix S5: Table S1). The relative support of models with age as a logit-linear covariate resulted in survival estimates increasing predictably with age, and the red tide effect resulted in lowest survival probabilities

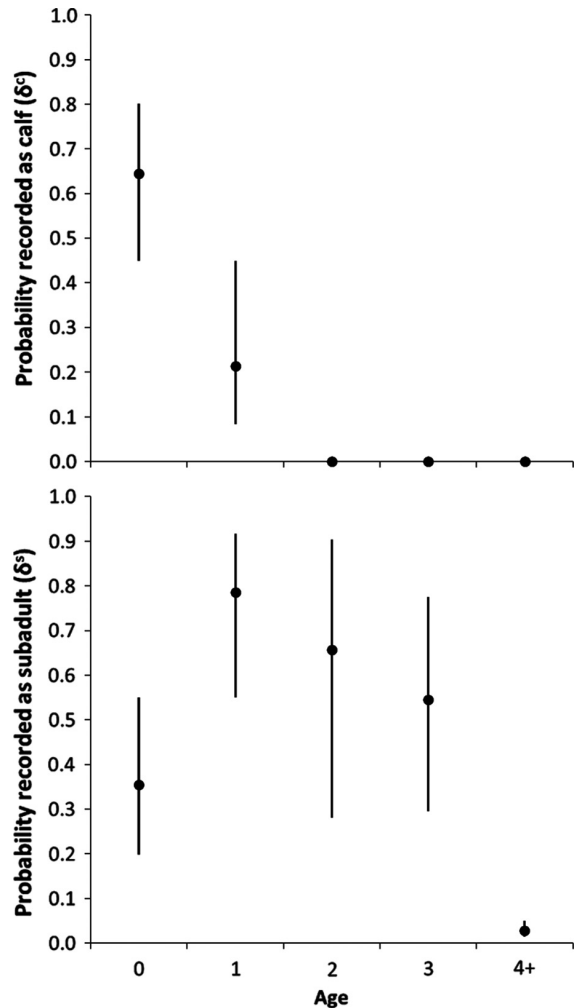


FIG. 1. Estimated probabilities (with 95% confidence intervals) of recording a live manatee as a calf (top panel) or subadult (bottom panel) for five age classes.



FIG. 2. Estimated annual survival probabilities (with 95% confidence intervals) for manatees by age class.

in 2013, a year with extensive red tide concentrations (Fig. 2). Annual survival estimates for age 0 manatees ranged from 0.85 [0.51, 0.97] to 0.89 [0.74, 0.96], and those for age 4+ manatees ranged from 0.88 [0.80, 0.93] to 0.96 [0.93, 0.97] (Fig. 2). Models with temporary emigration were not well supported by the data (Appendix S5: Table S1), and estimates for the probability of moving from inside to outside of the sampling area were generally low (0.09 [0.01, 0.43] in the best supported model that included temporary emigration).

DISCUSSION

Age-structured population models are a useful and common tool for wildlife conservation and management, but it can be difficult to estimate age-specific demographic parameters for these models because the ages of wild animals are often unknown. We have presented a multievent model to estimate age-specific survival probabilities when age is unknown for all sampled individuals. As with other open capture–recapture models, the precision of survival estimates is influenced by the number of marked animals, recapture rates, and duration of the study (Lindberg 2012). In the manatee example, survival estimates were reasonably precise, particularly for the older age classes (CV = 1.2–3.6% for age 4+ manatees), despite low recapture probabilities. We attribute this to a large sample size of individuals and incorporating carcass recovery and robust design data. However, data for the younger age classes were sparse, resulting in less precise survival estimates (CV = 4.7–12.9% for age 0 manatees) and potentially contributing to support for

constrained models with age as a linear covariate. The simulation code we provided can be used to inform study design, including sample sizes, recapture rates (via sampling effort), and the value of ancillary information (e.g., carcass recoveries and robust sampling design), for a desired level of precision and to evaluate parameter estimability.

The number of possible observation events and their ability to differentiate latent age will also likely contribute to the accuracy and precision of estimates. However, the number of state assignment parameters (δ and ϵ) in the model will increase with the number of possible events, which may reduce bias but also increase variance, so constrained models may be advantageous. For example, we fixed to 0 the probability of recording age 0 and age 1 manatees as adults (Appendix S4). Alternatively, using data such as actual size measurements or growth layer counts (Lonati et al. 2019) as imperfect indicators of age can also be considered for extending our model, in which observation events are continuous rather than discrete and assumed to be a parametric function of age (also see Appendix S2 for modeling discrete observation events as a function of age). Such functional relationships could be estimated jointly from capture–recapture studies (Reinke et al. 2020) or estimated from a separate study and used to inform priors in a Bayesian analysis. In any case, including some individuals of known age (i.e., marked soon after birth) in the study is expected to improve estimates (McCrea et al. 2013).

Parameter estimability may also depend on the number of age classes considered relative to the duration of the study (Matechou et al. 2013). In our example,

individuals recaptured at least 4 yr since their initial capture were known with certainty to be in the age 4+ class, likely improving estimates for this age class. However, rather than modeling age as a categorical covariate on survival, parametric curves could be used to reduce the number of model parameters while testing hypotheses regarding whether survival increases with age (e.g., logit-linear model as in our example), senescence (e.g., Gompertz, Weibull), or prime-age survival (e.g., logit-quadratic; Nussey et al. 2008).

The utility of population models is limited when direct estimates of age-specific survival are unavailable. For instance, because it is difficult to estimate age-specific survival from manatee photo identification data, previous manatee population models have generally assumed that the ratio of calf mortality to subadult and adult mortality is constant across regions and years (Runge et al. 2017). In contrast, our model framework and the use of genetic identification allow testing of hypotheses as to how environmental effects and management actions, which vary across space and time, impact survival for different age classes in different ways. For example, although our results supported models where the effect of red tide was additive across age and where cold severity did not affect survival, the approach presented here allowed us to test models where these effects varied across age classes. This model provides an approach for estimating age-specific survival when age is uncertain and can be applied to other species that are monitored with minimally invasive techniques.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3426/supinfo>

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Capture history data are available from the Florida Fish and Wildlife Conservation Commission—Fish and Wildlife Research Institute: <https://doi.org/10.5066/P9TPN4F3>.