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Mark-Recapture Models for Estimation of Demographic Parameters

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Summary

Population ecologists require robust estimates of survival and other demographic parameters for understanding the ecological and evolutionary drivers of wildlife population dynamics. Live encounter data from individual animals marked with unique tags or natural marking patterns are a key source of information for many species. Imperfect detection and losses to emigration can be challenging issues when tracking mobile organisms under natural conditions. Mark-recapture models utilize encounter histories for marked individuals where consecutive sampling occasions are coded with detection or nondetection data. Alternative models can then be fit as fixed-effect models with maximum likelihood methods in a frequentist framework, or as hierarchical models with random effects in a Bayesian framework. The Cormack–Jolly–Seber (CJS) model conditions upon first capture and uses forward-time modeling to estimate apparent survival corrected for the probability of encounter. More complex models extend the basic CJS model to estimate additional parameters. Time-since-marking models estimate apparent survival corrected for losses due to transients, age effects, and other factors. Temporal symmetry and Jolly–Seber models combine forward- and reverse-time modeling to estimate recruitment and population change without the need to parameterize a full matrix model. Robust design models adopt a nested sampling approach and are useful for investigating the dynamics of temporary emigration due to regional movements, dormancy, and intermittent breeding. Multistate models extend the single-state CJS model to multiple categorical states and provide state-specific estimates of apparent survival and transition rates among sites, demographic classes, disease status, or other states. Extended multistate models allow for unobservable states or situations where state classifications may be uncertain. Other models combine live encounters from marked individuals with different types of auxiliary data. Mark-resighting models add counts of unmarked individuals to estimate total abundance. Joint models add data on dead recoveries or supplementary resightings to estimate true survival and site fidelity. Integrated population models combine live encounters with count and fecundity data to estimate immigration rates and population change. Mark-recapture models are powerful tools because they correct for imperfect detection and imperfect availability, they can control for transients, social structure, and other potential sources of heterogeneity, and they also allow joint analysis across independent datasets. Demographic parameters are estimated with less bias and greater precision, thereby providing a stronger foundation for addressing key questions in population biology, evolutionary ecology, and wildlife management.

7.1 Introduction

Estimation of demographic parameters is central to the population biology of wildlife species, with important applications for understanding the ecology of population dynamics, the evolution of life-history strategies, and for making management and conservation decisions. Survival is particularly difficult to estimate for wildlife populations because the timing and causes of mortality are usually unknown for free-living animals, and because imperfect detection is the rule rather than the exception in most field studies (Kellner and Swihart 2014). Marked animals are often difficult to detect due to the logistics of field effort, low densities, wide-ranging movements, or secretive behavior (Mazerolle 2015). Despite challenges for estimation, survival is often identified as the demographic parameter with the greatest impact on the *finite rate of population change* (λ, Doherty et al. 2004; Schorcht et al. 2009). Adult survival is often an important driver for long-lived vertebrates or declining populations, whereas juvenile survival can have greater impacts in short-lived species or growing populations (Oli and Dobson 2003; Stahl and Oli 2006; Vélez-Espino et al. 2006). The relative influence of survival rates and other demographic

parameters is determined by both their mean value and variance, and demographic parameters that have a large effect on the rate of population change often have relatively low variance (Gaillard and Yoccoz 2003; Rotella et al. 2012; Péron et al. 2016). Estimation of the variance of survival rates is complicated because the maximum variance declines to zero when a probability approaches the boundary value of one (Morris and Doak 2004), and because temporal variation includes the *process variance* of biological interest, but also *sampling variance* which adds undesirable statistical noise (Gould and Nichols 1998; Ryu et al. 2016). The predicted impacts of conservation or management actions are determined by both the mean and the variance of demographic parameters in a population model. Hence, a central goal in population biology is to obtain parameter estimates that are *unbiased* with estimates that are close to the true value of a demographic parameter, but also have good *precision* with a low variance.

Estimation of survival rates and other demographic parameters for wildlife populations generally require one of four different types of data: age ratios from unmarked individuals, live encounters of marked individuals, dead recoveries of marked individuals, or intensive monitoring of animals marked with radio transmitters or other tags (Williams et al. 2002). *Age ratios* can be estimated from the standing age distribution of a population or by tracking cohorts through time, and may be the only demographic data available in a short-term study (Hernández-Matías et al. 2011). Calculation of survival from age distributions requires that the population has a stable age distribution, the rate of population change is either stable or stationary, and all age classes have an equal probability of encounter. All of these assumptions are likely to be violated in field studies of wildlife populations (Conn et al. 2005). *Dead recovery* data require that observers retrieve and report markers from animals that are harvested or found dead of natural causes. Dead recovery data can be a valuable source of information for harvested species, but are less useful for nongame species unless a large number of markers can be retrieved and reported (Robinson et al. 2009; Arnold et al. 2016). *Radio telemetry* data can be analyzed with time-to-event models to estimate survival and hazard rates (Zens and Peart 2003; Murray 2006, Chapter 6), and also provide insights into animal movements and space use (Chapters 13–14). The disadvantages of telemetry methods are mainly logistical considerations: transmitter size may limit battery life, attachment techniques should avoid impacts on survival, and financial costs of transmitters and tracking may limit sample size for a field study. Of the four sources of information, *live encounter* data are arguably the most widely used source of information for estimating survival and other demographic parameters for wild populations of animals and plants.

7.2 Live Encounter Data

Live encounter data include a variety of different types of information that can be collected for wildlife populations. In a mark–recapture study based on tagging, the field methods start with live capture and unique marking of individual animals. Standard techniques for physical marking vary among different groups of animals: numbered stickers for butterfly wings, injected tags for fish based on PIT (passive inductance transducers) or RFID (radio-frequency identification) technologies, toe-clipping or branding for amphibians and reptiles, neck collars, wing-tags or leg-bands on birds, and ear-tagging or tattoos for mammals (Silvy et al. 2012). In some species, natural marking patterns can be used to identify unique individuals without application of external tags: distinctive vocalizations of songbirds, spots of sharks and salamanders, notches in the tail flukes of whales, or coat patterns of wild cats (Vögeli et al. 2008; Bendik et al. 2013; Lee et al. 2014; McClintock 2015). Another noninvasive approach for tracking individuals is molecular genotyping based on DNA isolated from shed hair and feathers, or scat (Lukacs and Burnham 2005).

The basic assumptions of marking techniques are that handling and marking do not negatively affect animal survival or behavior, marks are read without error, and marks are retained for the duration of the field study. Once a uniquely marked individual has been released, observers monitor subsequent survival by attempting to find the same individual again. Assumptions of the detection process are that fates of marked individuals are independent, and that all marked individuals have the same probability of recapture. Live encounters of a marked individual or *detections* can include physical recaptures to read the mark, resighting of individuals with binoculars or a spotting scope, or registering the tag as the animal comes near a camera or other recording device. Detections can be recorded in several formats, including detection only, counts of the number of detection events, or information on the state of an individual. If an individual is successfully detected, the true state is usually unambiguous because the organism is observed to be alive or dead. Uncertainty arises for *nondetections* of marked individuals because they could be dead, emigrants from a study plot, alive but not available for encounter, or present but overlooked by the observer.

A mark-recapture study requires defining the *spatial* and *temporal* scale of the project relative to the movements and expected lifespan of the study organism (Lindberg 2012). Population studies often have one or more *study plots* of fixed size – a series of meadows for an alpine butterfly, a systematic trapping grid for rodents, a linear array of weirs for a stream fish, or a valley ecosystem for a resident predator. In most mark-recapture

models, marked individuals are marked and encountered within the same network of study plots. In joint models, individuals are marked at a study plot of fixed size, but dead recovery data or resighting data can be taken from the extended range of a migratory population. Mark-recapture models that estimate number of immigrants or probability of recruitment usually require that the boundaries and size of the study area remain constant for the duration of the project. If a study area is enlarged midway through a project, newly captured individuals in the expanded zone cannot be distinguished from new immigrants.

Efforts to detect marked individuals are spread across two or more *occasions*. The time-step might be days for a short-lived insect, weeks or months for a rodent, or years for most vertebrate populations. Two sampling occasions permit estimation of return rates, but three to four occasions are the minimum needed to use mark-recapture models. Longer time series with six or more occasions are needed to model temporal covariates and to estimate the process variance of demographic parameters without the confounding effects of sampling variance. Mark-recapture models perform best if sampling is systematic with *equal intervals* between consecutive sampling occasions. However, systematic sampling may be impractical for remote field sites where logistics of site access are difficult, or for ectothermic animals which are only active during suitable environmental conditions. Most mark-recapture models can also accommodate *unequal intervals* among different sampling occasions. In *closed* models, the interval between occasions is relatively short, and population size is assumed to be constant and unchanging. Closed population models offer some advantages for estimation of abundance because encounter rates can be modeled more effectively, without a need to estimate survival or recruitment. In *open* models, the duration of the interval between sampling occasions is long enough to accommodate the dynamic processes, such that the number of marked individuals can increase due to gains from recruitment or immigration, or decrease due to losses from death or permanent emigration. Sampling should be instantaneous; gains and losses occur within long intervals but not during the short sampling occasions, although mark-recapture models can be robust to violations of this assumption (O'Brien et al. 2005).

Mark-recapture models are mainly used to estimate demographic parameters for marked individuals in populations, but can also be applied at different ecological levels. If encounter histories are coded for detections of species instead of individuals, the same set of mark-recapture models can be used to study community dynamics including species richness, persistence, colonization, and turnover (Dorazio et al. 2006; Zipkin et al.

2010). Noninvasive methods of detection may be preferable for threatened or secretive species where physical capture is undesirable or impossible. Detections or counts of animals from vocalizations, tracks, or other signs of animal activity (Pellet and Schmidt 2005; O'Connell et al. 2006; Richmond et al. 2012) can be used to estimate occupancy, abundance, and population dynamics (Dail and Madsen 2013; Chapters 3–4). Mark-recapture models for unmarked individuals can also be used to estimate survival and other dynamic rates for open populations (Zipkin et al. 2014). Here, I focus on mark-recapture models for estimating survival and other demographic parameters in field projects where at least some portion of the study population is individually marked or otherwise identifiable.

7.3 Encounter Histories and Model Selection

A starting point for any statistical analysis of live encounter data is to identify the mark-recapture model that best matches the sampling design of a field project, and will yield estimates of demographic parameters that are corrected for imperfect detection and other sources of heterogeneity (Horton and Letcher 2008; Lindberg 2012, Figure 7.1). The next step is to assemble encounter histories for the sample set of uniquely marked individuals. In a matrix of encounter histories, each row corresponds to a different individual and each column corresponds to a different sampling occasion. The cells of the resulting matrix are then coded with information from live encounter data (L), or some combination of live encounter and dead recovery information (LD). Live encounters in a single state are based on the L format and encounter histories are coded as: $1 =$ an observer detected a marked individual as a recapture or resighting, or $0 =$ an observer did not encounter the individual (Box 7.1). In a multistate model, detections are coded as categorical states: $B =$ breeder, $N =$ nonbreeder, and $0 =$ not detected. If the categorical states are the number of unmarked young attended by a marked parent, detections might be coded as digits: $3 =$ three young, $1 =$ one young, and $0 =$ no young detected. For joint models based on an LD format, codes would include: $10 =$ a live encounter, $01 =$ a dead recovery, $02 =$ a supplemental observation, or $00 =$ not detected by any method.

Once encounter histories are assembled, the next step is to select the intrinsic and extrinsic variables to be included in the starting global model. Selection of important covariates is conducted a priori to guard against the possibility of spurious or irrelevant results (Chapter 2). Covariates can be discrete or continuous, as well as static or dynamic. Variables that affect demographic
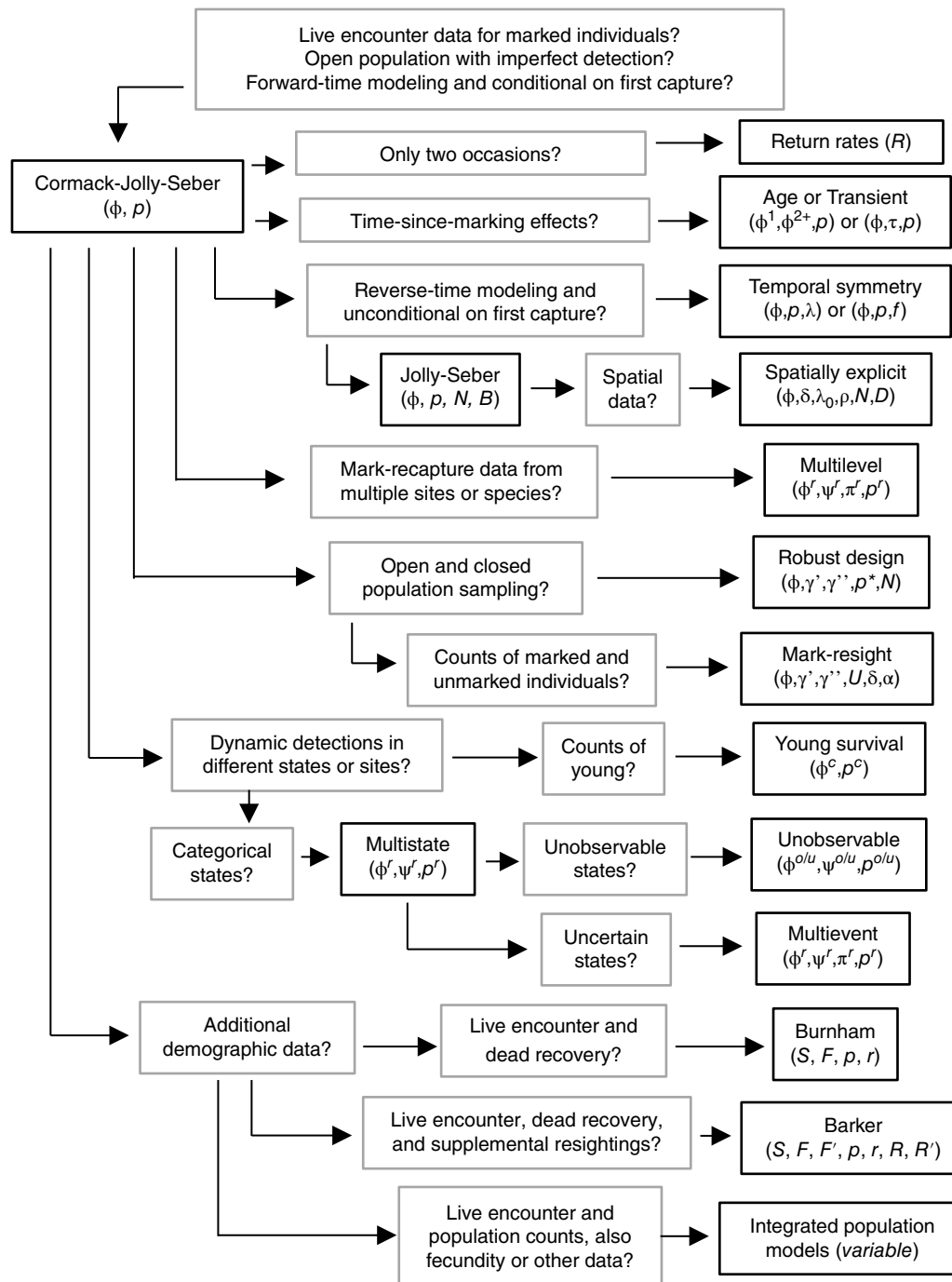
Figure 7.1 Conceptual diagram for open population models based on live encounter data for marked individuals. The *Cormack–Jolly–Seber model* is a fundamental model that estimates apparent survival (ϕ), corrected for the probability of encounter (p). If only two sampling occasions are available, *return rates* can be estimated as the product of the two parameters ($R = \phi\, p$). A large family of mark-recapture models are based on different extensions of the CJS model. If individuals are not detected after first capture, the *time-since marking model* estimates age-specific apparent survival (ϕ^n), whereas the *transient model* estimates the probability of transience (τ). *Temporal symmetry models* combine forward and reverse-time modeling to add estimates of realized population change (λ) or seniority (ζ). The *Jolly–Seber (JS) model* uses the complete encounter histories and estimates the population size of marked individuals (N), and number of immigrants (B). *Spatially explicit models* add spatial data on animal locations to also estimate recruitment (ρ) and density (D), adjusted for spatial detectability (δ) and encounters per individual (λ_0). *Multilevel models* use hierarchical approaches to model CJS data from multiple sites or species. *Robust design models* subdivide primary sampling occasions into secondary closed periods, and can be used to partition the probability of encounter into temporary emigration (γ) and true detection ($p*$). *Mark-resighting models* extend the robust design model by adding counts of unmarked individuals, and estimate transitions for observable (γ'') and unobservable individuals (γ'), abundance adjusted for the number of unmarked individuals (U), with corrections for individual heterogeneity (δ) and resighting (α). *Multistate models* code detections as different categorical states (r), and provide state-specific estimates of ϕ^r and p^r, along with the probability of changing states (ψ^r). If detections are coded as counts of unmarked young attending a marked parent, the *young survival model* gives age-specific estimates of ϕ^c and p^c. Multistate models for *unobservable states* are possible but usually require additional constraints to avoid parameter redundancy. *Multievent models* handle uncertainty in state classification, and include estimates the probability of assignment to a state (π). In the Burnham and Barker *joint models*, live encounter data are combined with dead recovery data and supplementary resighting data to decompose apparent survival into true survival (S) and movement (F, F'), corrected for the probabilities of recovery (r) and resighting (R and R'). *Integrated population models* combine mark-recapture data with counts of population size, fecundity, age ratios, or other types of demographic data to conduct an integrated demographic analysis.

Box 7.1 Encounter Histories and Parameter Index Matrices

The starting point for any capture-mark-recapture analysis is to assemble the detection–nondetection data for uniquely marked individuals into encounter histories. The rows of the file are the information for *individual* animals and the columns are the *sampling occasions*. The status of the animal is then recorded for each individual at each sampling occasion. In the case of the Cormack–Jolly–Seber (CJS) model for live encounter data, a single value is recorded for animal status at each occasion (LLLLLLL) with the two possible codes being detected alive (1) or not detected (0). Consider the following encounter history for one individual animal:

$$1101010 \tag{7.1}$$

The field study had seven sampling occasions, which produces an encounter history with seven columns. The values of one in the encounter history indicate that the animal was detected on occasions 1, 2, 4, and 6, whereas the zeros show it was not observed on occasions 3, 5, and 7. Given detections on occasions 2 and 6, the individual was definitely alive but was not detected on occasions 3 and 5. Inspecting the encounter histories can be a useful starting point for an analysis. If any encounter histories contain gaps with zeros nested within a string of ones, then the probability of encounter will be less than one. The fate of the animal on the last occasion is ambiguous: the individual could have been alive but not detected, or it might be dead.

The CJS model estimates two parameters, the probability of apparent survival (ϕ) and the probability of encounter (p). Depending on the data included in the encounter histories, the latter parameter can also be called the probability of capture or the probability of resighting. For a sample of n occasions, the CJS model calculates $n-1$ estimates of apparent survival and $n-1$ estimates of the probability of encounter.

$$
\begin{array}{ccccccc}
t_1 & t_2 & t_3 & t_4 & t_5 & t_6 & t_7 \\
1 & 1 & 0 & 1 & 0 & 1 & 0 \\
& \xrightarrow{\phi_1} & \xrightarrow{\phi_2} & \xrightarrow{\phi_3} & \xrightarrow{\phi_4} & \xrightarrow{\phi_5} & \xrightarrow{\phi_6} \\
& p_1 & p_2 & p_3 & p_4 & p_5 & p_6
\end{array}
\tag{7.2}
$$

Apparent survival is estimated for the *intervals* between consecutive occasions, whereas the estimates of encounter apply to the *sampling occasions*. In the CJS model, encounter rates are not estimated for the first occasion

(t_1) because no animals were released before the start of the field study and none are available for recapture.

One possible summary of this model would be to collect all of the subscripts or *parameter index* numbers into separate vectors for each parameter.

$$
\begin{array}{cc}
\phi & p \\
1\ 2\ 3\ 4\ 5\ 6 & 1\ 2\ 3\ 4\ 5\ 6
\end{array}
\tag{7.3}
$$

In the above example, the index numbers correspond to different intervals and occasions. However, apparent survival and encounter are independent parameters and they might be renumbered consecutively to avoid confusion.

$$
\begin{array}{cc}
\phi & p \\
1\ 2\ 3\ 4\ 5\ 6 & 7\ 8\ 9\ 10\ 11\ 12
\end{array}
\tag{7.4}
$$

If the index numbers are different for each interval or occasion, then the parameter estimates from the model will be different among occasions or *time-dependent*.

One row of index numbers would be sufficient if a single batch of animals was marked and released on the first occasion of the field study. In an open population model, subsequent years of field work would include recapture or resighting effort, but also new capture events with marking and release of individuals on later occasions. If we add additional rows for animals first marked on the second and later occasions, our summary diagrams then become triangular *matrices*.

$$
\begin{array}{cccccc|cccccc}
\phi & & & & & & p & & & & & \\
1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 & 11 & 12 \\
& 2 & 3 & 4 & 5 & 6 & & 8 & 9 & 10 & 11 & 12 \\
& & 3 & 4 & 5 & 6 & & & 9 & 10 & 11 & 12 \\
& & & 4 & 5 & 6 & & & & 10 & 11 & 12 \\
& & & & 5 & 6 & & & & & 11 & 12 \\
& & & & & 6 & & & & & & 12
\end{array}
\tag{7.5}
$$

The triangular matrices are known as *parameter index matrices* or PIMs, and are one approach for describing the structure of a mark-recapture model and fitting alternative models in software packages such as Program `Mark`.

performance often include *group* effects such as sex, colony, or breeding status, *time* effects for environmental conditions that vary temporally, *time-since-marking* effects that change with time since first capture such as transience, age, or experience, and *individual covariates* such as body size and other morphometric traits (Grosbois et al. 2008; Fredericksen et al. 2014). Different sets of variables can then be combined in *additive* models with main effects only, or in *factorial* models with main effects and their interactions. As a rule of thumb, the maximum number of parameters in a starting model is usually capped at $n/10$, where n is the effective sample size, calculated as the number of captures and recaptures in a set of encounter histories based on live encounters or dead recoveries (Burnham and Anderson 2002, p. 245). The parameter count of a model (K) can be reduced by modeling parameters without any temporal variation, as a temporal *trend*, or as a *linear* or *nonlinear* function of explanatory covariates (Gimenez et al. 2006).

A common situation in mark-recapture analyses is that the detection or count data may be *overdispersed* due to lack of independence or heterogeneity among marked individuals, and the starting global model may not be a perfect fit to the encounter histories. A necessary first step is to use goodness-of-fit (GOF) procedures to calculate a *variance inflation factor* ($\hat{c}$) to correct for possible overdispersion caused by a lack of fit between the starting model and the encounter histories. The variance inflation factor approaches an asymptotic value of one if the starting model is a perfect fit with no overdispersion. If an estimation procedure returns a value of $\hat{c} < 1$, then the parameter is usually set to one. Values of $\hat{c} = 1$–3 are typical for most mark-recapture datasets, and higher values may indicate structural problems. A variety of procedures are available to estimate $\hat{c}$ for CJS and multistrata models, but not for more complex models, such as multievent models (Pradel et al. 2005; Choquet et al. 2009a; Kendall et al. 2013). Calibrated simulations have been used to test GOF for integrated population models, and might be an option for other mark-recapture models too (Besbeas and Morgan 2014). Last, if GOF tests are not available to test for overdispersion or to estimate $\hat{c}$, sensitivity analyses for model rankings can be conducted by varying $\hat{c}$ across a range of plausible values (e.g. $\hat{c} = 1$–3 by 0.5).

Mark-recapture analyses are often conducted in an information theory framework with the tools of model selection (Burnham et al. 2011; Lindberg et al. 2015, Chapter 2). If alternative models are fit with maximum likelihood estimation (MLE), model selection is based on different variants of Akaike's Information Criterion (AIC, AICc, or QAICc) or Bayes Information Criterion (BIC), which are tools for identification of parsimonious models (Burnham and Anderson 2004; Grueber et al. 2011, Chapter 2). Picking an information criteria depends on the goals of a study: AIC for exploratory analysis of model complexity in an observational study, and BIC for confirmatory analysis of the single-best model in a controlled experiment (Aho et al. 2014). Differences in information criterion values are used to calculate model weights (w_i), and ratios of model weights or Bayes factors can be used to calculate relative levels of support between different models. Caution should be taken when comparing models that differ by a single parameter because the minimum AIC model may retain an uninformative covariate (Arnold 2010). AIC and BIC are also less suitable for comparing hierarchical models with random effects, and tools for model selection in a Bayesian framework are an emerging field (Barker and Link 2015; Hooten and Hobbs 2015, Chapter 5).

Model testing starts with a global model, and proceeds by dropping variables to fit a series of reduced models which can be viewed as a suite of alternative hypotheses (Chapter 2). For a simple analysis, an *all-combinations* approach might be used to test candidate models that include all possible combinations of a limited set of explanatory variables. However, the number of possible models increases exponentially as additional explanatory variables or demographic parameters are added to the set of candidate models. In a *step-down* approach, terms are dropped from the global model in an iterative manner starting with the encounter rates or other nuisance parameters associated with the sampling process, proceeding to the demographic parameters of biological interest, and then with a final step that adds terms back to explore additional models close to the best model (Sandercock and Jaramillo 2002). In a *single-factor* approach, each parameter is modeled separately while retaining full model complexity for all other parameters in the model, and then highly ranked structures for each parameter type are combined in a composite model (Grosbois and Tavecchia 2003). The order that parameters are modeled may not be critical because model selection strategies seem to have little effect on bias or precision of parameter estimates (Doherty et al. 2012). Still, if computation times or issues with convergence are a consideration, the best approach may be to fit a concise set of 4–20 biologically plausible models and be less concerned with multimodel inference.

Once model testing has been completed, several procedures can be used to obtain parameter estimates. If a single model in the candidate set receives majority support ($w_i > 0.8$), then parameter estimates might be taken from that top-ranked model. If a subset of models each receive some support ($w_i > 0.3$), then *model-averaging* can be

used where each set of parameter estimates is combined with the model weight, and then used to obtain a weighted average with an unconditional variance that also includes uncertainty due to model selection. An issue that arises is that demographic parameters or covariates may only appear in a subset of models in the candidate set (Grueber et al. 2011). Under the *natural average method*, parameters are averaged across the subset of models in which the parameter is present, after rescaling the model weights to sum to one. Under the *zero method*, missing parameters are set to zero in models where the parameters are absent, thereby shrinking predictors toward zero if models without the effect have strong support. The *relative importance* of a parameter is sometimes calculated by summing the weights across models where the parameter appears, but simulations have shown that sums of weights can be unreliable for assessing the importance of predictor variables (Galipaud et al. 2014). Model averaging can also lead to flawed parameter estimates if the predictor variables are correlated, but can be addressed with tests for multicollinearity and by standardizing predictor variables for their covariance structure (Cade 2015).

7.4 Return Rates

Return rates (R) are a good starting point for understanding the value of mark-recapture models. If a sample of individuals is marked on an occasion at a sampling site, the return rate is the proportion of marked individuals encountered the following year, or during some block of future years. Return rates are challenging to interpret because the probability of capturing an individual animal in two consecutive years is a function of four independent probabilities: *true survival* (S), *site fidelity* (F), *site propensity* (δ), and *true detection* ($p*$, Box 7.2). Return rates are a minimum estimate of true survival because they are the product of four probabilities ($R = S \times F \times \delta \times p^*$). If return rates are high ($R > 0.9$), then true survival and the other three probabilities must also be high (≥ 0.9). Difficulties arise in the interpretation of low or moderate return rates ($0.2 < R < 0.6$), and with comparisons of return rates among different groups or years. If any of the last three parameters are <1, return rates are negatively biased as an estimate of true survival. A low return rate of 0.4 could be the result of poor survival, weak site fidelity, or a

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Box 7.2 Definitions of Demographic Parameters in Cormack–Jolly–Seber Models

Return rates have been widely used in population biology as an index of survival. If a group of individuals are marked one year at a sampling site, the "return rate" (R) can be calculated as the proportion of marked individuals encountered the following year, or during some block of future years. Return rates are difficult to interpret because they are the product of four independent probabilities ($R = S \times F \times \delta \times p^*$):

True survival (S): the probability that an individual survives between two sampling occasions. The complement of survival includes losses to mortality ($1 - S$).

Site fidelity (F): the probability that an individual returns to the same sampling area, conditional upon true survival. The complement of site fidelity includes losses to permanent emigration ($1 - F$).

Site propensity (δ): the probability that an individual is available for encounter in the same sampling area the next occasion, conditional upon survival and site fidelity. The complement of site propensity includes losses to temporary emigration ($\gamma = 1 - \delta$).

True detection (p^*): the probability that an observer detects the individual under field conditions, conditional upon survival, site fidelity, and availability for encounter. The complement of true detection is imperfect detection ($1 - p^*$).

Cormack–Jolly–Seber (CJS) models are an improvement over return rates because they use encounter histories of marked individuals to estimate two independent probabilities:

Apparent survival ($\phi = SF$): the probability that an individual survives between two sampling occasions and returns to the sampling area. The complement of apparent survival includes losses to mortality or permanent emigration.

Encounter rate ($p = \delta p^*$): the probability that an individual is detected under field conditions given that is available for encounter in the sampling area. The complement of the probability of encounter includes individuals not available for detection and individuals that were present in the sampling area but not detected.

Extended mark-recapture models can be used to decompose the demographic parameters even further. Joint models combine live encounter with dead recovery data and can be used to decompose apparent survival into true survival and site fidelity. Conversely, robust design models can be used to separate temporary emigration from the probability of true detection. An integrated model that combines live encounter data, supplementary observations, and a robust design framework can estimate all four parameters separately (Kendall et al. 2013).

variety of other combinations of the four parameters. Given the expected problems of bias and interpretation, return rates should be avoided if possible. On the other hand, return rates may be the only estimator available if the duration of a project is 2–3 years. In that case, return rates may be used as a crude index of true survival, but assumptions must be made about the remaining three probabilities. If site fidelity, site propensity, and true detection are assumed to be equivalent among groups or years, then differences in return rates might be due to variation in true survival. Similarly, temporal trends in return rates may be compared among different locations if the distributions of the other probabilities are assumed to be stationary over time.

7.5 Cormack–Jolly–Seber Models

The *Cormack–Jolly–Seber* (CJS) model is a fundamental model for analysis of live encounter data, and many other models for live encounter data are extensions of the CJS model (Figure 7.1). The CJS model conditions upon first capture and uses forward-time modeling to estimate two demographic parameters for a population of marked individuals: *apparent survival* (ϕ) corrected for the *probability of encounter* (p, Box 7.2). Apparent survival is less biased as an estimator of true survival compared to return rates because it is the product of two instead of four parameters ($\phi = S \times F$). Like return rates, if apparent survival is high, then both S and F must be high. CJS models can be used to estimate true survival for sessile organisms if movements are limited and site fidelity is effectively one ($\phi = S$ if $F \approx 1$). Conversely, CJS models can also be used to estimate site fidelity if true survival rates are expected to be high during a short-term study ($\phi = F$ if $S \approx 1$). The probability of encounter ($p = \delta \times p^*$) is usually regarded as a nuisance parameter because it corrects for imperfect detection (p^*), but p can also be of biological interest if the dynamics of temporary emigration lead to low site propensity ($\gamma = 1 - \delta$).

CJS and other mark-recapture models require live encounter data from at least three sampling occasions because internal gaps in the encounter histories are used to estimate the probability of encounter (e.g. `101`, Box 7.1). Individuals that are newly marked on the last occasion of a field study do not contribute to parameter estimates in a CJS model (e.g. `001`), and the terminal field season of a field project is best spent trying to recapture or resight marked individuals. CJS models can be fit to encounter histories with a multinomial likelihood using MLE in a frequentist framework (Lebreton et al. 1992),

or with a state-space likelihood and Markov chain Monte Carlo (MCMC) methods in a Bayesian framework (Gimenez et al. 2007; Royle 2008). Alternative models with different structures can be defined with model statements, parameter index matrices (PIMs), or design matrices (DM) in the different software tools (Box 7.3).

One issue that arises with the CJS model and many other mark-recapture models is that the intrinsic model structure may prevent estimation of a desired parameter. In a fixed-effects CJS model with time-dependence in both ϕ and p, it is not possible to estimate p for the last sampling occasion because no capture data are available from occasions following the end of the project. If ϕ and p cannot be estimated separately for the last interval in a time series, then the product of the last two transition rates is estimated as a single parameter (ϕp). The terminal parameters of ϕ or p are *nonidentifiable* because they cannot be estimated separately, and the model is then considered *parameter redundant* because the likelihood is expressed as a function of fewer parameters than the original count (Gimenez et al. 2003; Hubbard et al. 2014). The terminal product of ϕp can be decomposed if some constraint is applied to the CJS model: by modeling ϕ or p as constant over time or as a random effect in a hierarchical model. Nevertheless, n years of study may yield $n - 2$ estimates of apparent survival, and each additional year adds another annual estimate. Longer time series are needed to model apparent survival as a function of annual covariates, to estimate components of variance, and to estimate additional demographic parameters in more complex models.

7.6 The Challenge of Emigration

Capture, marking, and monitoring of individually marked animals for a population study are labor-intensive activities. Logistics and cost often constrain field projects to sampling on a fixed-area study plot that encompasses a random or representative sample of individual territories or home ranges. Marked individuals may be detected with intensive area-search sampling (Efford 2011; Royle et al. 2011), or with grids or webs of live traps, hair snares, or camera stations (O'Connell et al. 2006; Monterroso et al. 2014). If a fixed-area study plot is located in contiguous habitat, the plot boundaries may not be a barrier to movements. Movements can lead to *permanent emigration* where marked individuals disperse away from the study plot and never return, whereas during *temporary emigration*, the dispersing individuals may leave or be unavailable for encounter for some period but then return again to the study plot in the future.

Box 7.3 Alternative Approaches to Fitting Candidate Models in `RMark` **and Program** `Mark`.

Fitting mark-recapture models with formulae in `RMark`, or with parameter index matrices (PIM) and design matrices (DM) in Program `Mark`. Model effects are constructed with model statements in `RMark`. With PIMs, shared or different index numbers are used to pool or separate estimates for different groups or times. Each row is a cohort that was first captured on different sampling occasions. In DMs, dummy variables are used to code separate effects for the intercept, groups, time, or interactions. The example is based on six transitions for seven sampling occasions, and two groups for sex.

RMark	PIMs	DM

Constant model
formula =
~1
	1 1 1 1 1 1
	  1 1 1 1 1
	    1 1 1 1
	      1 1 1
	        1 1
	          1
		$\begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \end{bmatrix}$

Group model
formula =
~sex
	1 1 1 1 1 1
	  1 1 1 1 1
	    1 1 1 1
	      1 1 1
	        1 1
	          1
	2 2 2 2 2 2
	  2 2 2 2 2
	    2 2 2 2
	      2 2 2
	        2 2
	          2
		$\begin{bmatrix} 1 & 1 \\ 1 & 1 \\ 1 & 1 \\ 1 & 1 \\ 1 & 1 \\ 1 & 1 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \end{bmatrix}$

Time model
formula =
~time
	1 2 3 4 5 6
	  2 3 4 5 6
	    3 4 5 6
	      4 5 6
	        5 6
	          6
		$\begin{bmatrix} 1 & 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$

Factorial model
formula =
~sex * time
	1 2 3 4 5 6
	  2 3 4 5 6
	    3 4 5 6
	      4 5 6
	        5 6
	          6
	7 8 9 10 11 12
	  8 9 10 11 12
	    9 10 11 12
	      10 11 12
	        11 12
	          12
		$\begin{bmatrix} 1 & 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 \\ 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$

Emigration can lead to bias in the demographic parameters estimated with CJS models. If emigration is temporary and random, only the probability of encounter is biased, whereas nonrandom temporary emigration leads to bias in both apparent survival and the probability of encounter (Schaub et al. 2004a). If emigration is permanent, apparent survival is biased low as an estimate of true survival because losses to mortality cannot be distinguished from losses to permanent emigration (Ergon and Gardner 2014; Schaub and Royle 2014). Emigration limits the utility of CJS models for estimating true survival for any group of animals with low site fidelity, such as juvenile age classes with strong natal dispersal or species that use ephemeral habitats (Paradis et al. 1998; Zimmerman et al. 2007; Roche et al. 2012). If long-distance dispersers cannot be detected, measures of dispersal distance are truncated by the longest axis of a fixed-area study plot, and dispersal distance will also be underestimated (Cunningham 1986; Koenig et al. 1996).

A variety of mark-recapture models and study designs have been proposed for estimation of *true survival* instead of apparent survival. In some cases, the size of the study plot remains fixed and the different types of emigration are handled with model structure or auxiliary data. If dispersing individuals are transients or migratory individuals that permanently emigrate from a study plot, *time-since-marking* or *transient* models can be used to estimate apparent survival that is corrected for losses of individuals that are never encountered after first capture. If dispersing individuals are temporary emigrants that are likely to return, *robust design* models can be used to estimate apparent survival corrected for losses to temporary emigration (Horton and Letcher 2008). Marked individuals with home ranges close to the boundary of a study plot may be more likely to emigrate, and modeling ϕ or p as a function of distance to plot edge may improve parameter estimates from CJS models (Boulanger and McLellan 2001; but see Marshall et al. 2004). Losses to emigration may be less important in linear habitats such as streams or coastal beaches. In terrestrial habitats, circular or square study plots that minimize perimeter-area ratios may help to reduce losses to emigration. Estimation of survival can also be improved if a subset of the marked population is marked with radio transmitters or transponders to track movements (Powell et al. 2000). *Multistate* or *robust design* models can be used for joint analysis of encounter data for marked individuals with or without radio transmitters to model survival corrected for imperfect detection and emigration from a fixed-area study plot (Devineau et al. 2010; Horton et al. 2011; Bird et al. 2014).

Movements of marked individuals within a study plot are another source of data that can be used to estimate true instead of apparent survival. One approach is to make post hoc corrections to adjust apparent survival for losses due to local movements. *Area-ratio methods* correct for bias by comparing observed movement distances vs. random pairs of locations within the study plot to estimate a probability of detection for different dispersal distances (Zeng and Brown 1987; Baker et al. 1995). Area-ratio methods are flexible and can accommodate study plots of diverse sizes and shapes, or various dispersal distributions. Unfortunately, area-ratio methods can perform poorly for survival estimation if adjustments for rare long-distance dispersal events cause survival to be overestimated (Cooper et al. 2008). Still, Taylor et al. (2015) showed that post hoc corrections for local breeding dispersal led to less-biased estimates of apparent survival for arctic-breeding sandpipers. *Spatially explicit* models include information on locations of marked animals in analyses of demographic parameters (Borchers 2012). Most attention has been on use of closed population models for estimation of abundance (Efford 2004; Royle and Young 2008), but new applications for open populations have also been developed (Gardner et al. 2010, Chapter 5). Last, *spatial CJS models* (sCJS) allow joint analysis of capture and spatial data, and may yield estimates of true survival if local dispersal movements are relatively short compared to the spatial scale of a fixed-area study plot (Schaub and Royle 2014; Weiser et al. 2018).

Losses to emigration can also be reduced by expanding the size of a fixed-area study plots. One study design is to conduct captures and marking in a core study area but search for marked individuals in an expanded *buffer zone* (Marshall et al. 2004). Inclusion of additional detections from an expanded buffer zone can increase return rates and estimates of apparent survival (Reed and Oring 1993; Cilimburg et al. 2002; McKim-Louder et al. 2013). The challenge with buffer zones is that the total search area increases exponentially with potential dispersal distance and quickly becomes unmanageable. Zimmerman et al. (2007) modeled the effects of plot size on bias in CJS models and found that apparent survival of juvenile owls increased linearly among plots ranging in area from approximately 80 to 1400 km^2, suggesting unbiased estimates of survival would require even larger plots.

Another possible sampling design is to use a *distributed network* of study plots that can potentially detect both short and long-distance dispersal movements. Inclusion of spatial data on animal captures allows survival and emigration to be jointly estimated from movements both within and among fixed-area study plots (Schaub and von Hirschheydt 2009; Gilroy et al. 2012; Ergon and Gardner 2014; Lagrange et al. 2014). A network approach has been successfully used for birds of conservation concern where multiple research groups are working with the same

species, populations are small with a high proportion of marked individuals, and patches of suitable habitat are discrete (Cooper et al. 2008; Gilroy et al. 2012; Roche et al. 2012). Distributed networks of study plots are also a feature of national programs for constant effort banding of landbirds in Europe and North America (Saracco et al. 2008; Robinson et al. 2009). Repeated captures and information from neighboring stations can be combined in a hierarchical model to investigate spatial variation in survival and residency on the study plots (Saracco et al. 2012). Moreover, correction factors for the difference between apparent and true survival can be calculated as the difference between estimates of the finite rate of population change based on demographic rates versus population counts (Ryu et al. 2016). At the broadest possible spatial scale, *joint models* can be used to decompose apparent survival into true survival and site fidelity if the live encounter data come from a fixed-area study plot, but other sources of information such as dead recovery or supplementary resighting data are taken from a larger geographic area such as a regional flyway (Bacheler et al. 2009; Bowerman and Budy 2012; Kendall et al. 2013; Lok et al. 2013).

7.7 Extending the CJS Model

The CJS model provides the foundation for most mark-recapture models for live encounter data. *Time-since-marking* and *transient* models are also CJS models, but use a different model structure to estimate apparent survival separately for different intervals after first capture. *Temporal symmetry* and *Jolly–Seber* models are based on the same set of encounter histories as the CJS model but do not condition upon first capture, and include both forward- and reverse-time modeling. Other mark-recapture models for open populations extend the CJS model by including various kinds of *auxiliary data* in the encounter histories. Use of auxiliary data usually requires additional sampling but allows apparent survival and other demographic parameters to be estimated with less bias and greater precision (Kendall et al. 2006, 2013; Schaub and Abadi 2011).

Multilevel models use data from multiple populations of one species or multiple species at a single site in a random effects framework, thereby expanding CJS models based on a single population of one species to multiple higher levels. *Spatially explicit* models incorporate spatial data with the locations where marked individuals are encountered, allowing joint analysis of movement and capture-recapture data. The auxiliary data in a *robust design* model come from dividing the primary occasions of a CJS model into shorter secondary periods when the population is assumed to be closed to gains or losses. CJS

models are based on live encounters of marked individuals, but *mark-resight* models incorporate auxiliary data with counts of unmarked individuals. The CJS model is a single-state model that is coded with detections and non-detections, and the *young survival* model extends the detections to include counts of young. Similarly, *multistate* models include categorical information about the state of an individual when it is detected, such as information about site, breeding status, physiological condition, or different methods of detection. Multistate models with *unobservable states* handle the special situation where individuals in some states cannot be encountered, whereas *multievent* models address situations where an individual cannot be assigned to a state with certainty. *Joint* models are based on CJS models but also allow inclusion of auxiliary data on dead recoveries or supplemental resightings that are recorded during the intervals between sampling occasions. Last, *integrated population* models are a flexible approach for development of customized models that allow joint modeling of mark-recapture data with population counts, and other demographic data on the components of fecundity, age ratios in harvest bags, or known fate survival data.

7.8 Time-since-marking and Transient Models

A common feature of live encounter data is that a subset of marked individuals are never detected again after first capture, with encounter histories characterized by detection at only one occasion (e.g. `1000`, `0100`, Box 7.1). In this case, apparent survival of newly marked individuals will be lower in the interval after first capture (ϕ^1) than returning individuals detected in subsequent intervals (ϕ^{2+}). In a sample of animals marked as young, apparent survival may be lower after first capture if juveniles have lower true survival or site fidelity than adults ($\phi^1 < \phi^{2+}$). The same difference can occur in a sample of animals marked as adults, if capture and handling negatively affect survival or site fidelity, if a sample includes transients, or if capture rates are heterogeneous. If any of these effects are present, ϕ^{2+} from a time-since-marking model may be less biased as an estimate of true survival than ϕ from a standard CJS model where ϕ^1 and ϕ^{2+} are pooled (Johnston et al. 1997; Korfanta et al. 2012).

Time-since-marking and transient models are CJS models that control for losses to mortality or permanent emigration that occur during the interval after the first capture occasion. The encounter histories are coded in the same manner as for standard CJS models, but the model structure is more complex to estimate additional parameters. The model structure is set up so that ϕ^1 and ϕ^{2+} are estimated separately, along with the

encounter rate (p). The structure can be termed a *time-since-marking* model if a sample includes individuals of unknown age, or an *age* model if the sample is known-aged individuals. A *transient* model can be applied in situations where losses after first capture are likely due to inclusion of transients captured as unmarked individuals (Pradel et al. 1997). The probability that an unmarked individual is a transient at time t (τ_t) is then estimated as a derived parameter: $\hat{\tau}_t = 1 - \hat{\phi}_t^1 / \hat{\phi}_t^{2+}$. The proportion of transients in the population ($\hat{T}_t$) can then be estimated as $\hat{T}_t = \hat{\tau}_t[N_t/(N_t + m_t)]$, where N_t and m_t are the numbers of newly marked and recaptured individuals at time t (Jessopp et al. 2004). Multistate versions of the transient model include τ_t as a parameter in the likelihood (Schaub et al. 2004b), allowing greater flexibility for modeling transient dynamics as a response to temporal covariates.

A common pattern in time-since-marking models is that apparent survival rates are often ranked: juveniles after first capture < adults after first capture < adults in subsequent intervals (Sandercock 2006). Unfortunately, the ecological causes are often difficult to distinguish because age, handling effects, and capture heterogeneity are all expected to produce the same general pattern of $\phi^1 < \phi^{2+}$. Thus, a prudent approach before starting any CJS analysis is to examine the relative frequency of individuals that were encountered on one versus multiple sampling occasions. If a set of encounter histories is dominated by individuals encountered on only one sampling occasion, time-since-marking effects should probably be included in the set of candidate models. A minimum of four occasions are needed to estimate the extra parameters of the time-since-marking or transient models, and the terminal parameters of each age class may be nonidentifiable in models with full time dependence (Hubbard et al. 2014).

7.9 Temporal Symmetry Models

CJS models condition upon first capture and proceed forward in time, whereas *temporal symmetry* models analyze the encounter histories with both forward- and reverse-time modeling (Pradel 1996; Nichols and Hines 2002; Nichols 2016). Temporal symmetry models do not require additional sampling and can be based on the same set of encounter histories as standard CJS models. With addition of reverse-time modeling, temporal symmetry models use the complete encounter histories and can be considered an alternative parameterization of a Jolly–Seber (JS) model (see below, Cooch and White 2018). Forward-time modeling yields estimates of apparent survival (ϕ) and encounter rates (p).

Modeling of the same encounter histories from the last capture backwards gives a seniority probability (ζ) as a reverse-time analogue of ϕ, which is defined as the probability that an individual did not enter the population between the previous and current occasion. Forward-time modeling assumes that capture probabilities are homogeneous among marked animals. In the temporal symmetry and JS models, reverse-time modeling extends the assumption of equal catchability to marked and unmarked individuals.

The temporal symmetry model has three alternative parameterizations. The *seniority* or ζ-parameterization (ϕ_t, p_t, ζ_t) yields separate estimates of ϕ and ζ corrected for p. Alternatively, the *lambda* or λ-parameterization is perhaps the most useful model (ϕ_t, p_t, λ_t), where ϕ and ζ are combined to estimate the finite rate of population change $\hat{\lambda}_t = \hat{\phi}_t / \hat{\zeta}_{t+1}$. Here, λ can be modeled as a function of environmental covariates, and the variance of λ can be used to estimate risk of extinction (Nichols and Hines 2002). In the *recruitment* or *f*-parameterization of the temporal symmetry model (ϕ_t, p_t, f_t), ϕ and ζ are again combined but instead to estimate the per capita rate of recruitment $\hat{f}_t = \hat{\phi}_t (1 - \hat{\zeta}_{t+1}) / \hat{\zeta}_{t+1}$. Bayesian versions of the temporal symmetry model allow the parameters to be modeled as random effects (Saracco et al. 2008; Tenan et al. 2014).

Temporal symmetry models allow estimation of λ from live encounter data alone, without the need to determine abundance from population censuses or estimate demographic rates to parameterize a matrix model (Sandercock and Beissinger 2002; Pradel and Henry 2007; Currey et al. 2011; Schorr 2012). In temporal symmetry models, λ is a realized estimate of population change that includes gains from recruitment and is based on the demographic classes included in the encounter histories. Seniority parameters are comparable to elasticity values from a matrix model in identifying sensitivity of $\hat{\lambda}$: survival has a greater effect on $\hat{\lambda}$ if $\hat{\zeta} > 0.5$, whereas recruitment has a greater effect on $\hat{\lambda}$ if $\zeta < 0.5$ (Nichols et al. 2000; Korfanta et al. 2012).

Temporal symmetry models require longer time series than CJS models to estimate ζ as an additional parameter. Time dependence in ϕ and p creates inestimable terms in the first and last intervals, and n occasions yields $n - 3$ estimates of $\hat{\lambda}$ (Dreitz et al. 2002). Modeling can be tricky because model fit for p affects parameter estimates for ϕ and ζ, and vice versa. Modeling p as a trend or a function of a covariate may induce a pattern in λ or the other model parameters (Tenan et al. 2014). Estimates of λ from temporal symmetry models are also sensitive to changes in sampling area. An increase in the size of a fixed-area study plot could increase the numbers of newly marked individuals which would affect estimates of recruitment

into the population. Last, numerical simulations suggest that $\hat{\lambda}$ is robust to the effects of individual heterogeneity in capture, but behavioral responses to trapping and failure to account for losses at capture can bias estimates (Hines and Nichols 2002; Marescot et al. 2011).

7.10 Jolly–Seber Model

The JS model is an open population model that estimates four demographic parameters from the encounter histories: the probability of *apparent survival* ($\phi = S \times F$), the probability of *encounter* ($p = \delta \times p^*$), *abundance* or population size (N), and *net recruitment* or the number of new individuals entering the population (B, Pollock et al. 1990). The JS model is similar to a CJS model but is an unconstrained model, and the apparent survival and encounter parameters are not equivalent between the two classes of models. CJS models condition upon first capture and assume that marked individuals have the same probability of capture. Like a temporal symmetry model, the JS model uses the complete encounter histories including the leading zeros before first capture. The JS model extends the assumption of equal probability of capture to both marked and unmarked individuals, which allows the complete encounter histories to be used in the estimation of N and B. Thus, ϕ and p from a CJS model apply to marked individuals only, but to both marked and unmarked individuals in a JS model. The difference between the parameters in the CJS and JS models is subtle but has practical implications for study design. In a CJS model, different field methods can be used for marking and recapture, and individuals marked on the last occasion can be discarded because they do not contribute to the parameter estimates. If capture and marking are costly, the final season of a field project might be devoted to resighting efforts only. In a JS model, the same field methods should be used for marking of unmarked individuals and detections of marked individuals to meet the assumption of equal catchability. Individuals should still be captured for marking on the last occasion because leading zeros in the encounter histories will also contribute to parameter estimation in the analysis.

Several parameterizations of the JS model are available but differ in number of sources of data, how recruitment is modeled, and whether estimation is conditional upon individuals detected in the study area (Madon et al. 2011; Cooch and White 2018). Criteria for choosing a particular model include whether or not losses at capture are present, and what combination of demographic parameters are desired as model output, including

abundance, net recruitment, per capita recruitment (f), and the finite rate of population change (λ). JS models can be useful for modeling patterns of recruitment into a population, and for separating gains from in situ recruitment vs. immigration (Collier et al. 2013). Unfortunately, individual heterogeneity and other issues often lead to bias in estimates of N and B from JS models (Chapter 5). If estimation of abundance is the goal of a mark-recapture analysis, mark-resight or closed population models may be better methods with additional options for control of problems due to heterogeneity of capture (Abadi et al. 2013).

7.11 Multilevel Models

Mark-recapture data collected from natural populations are often structured at multiple levels: individuals in a population with different probabilities of survival or capture, different populations of the same species, or related species in the same guild or community. Here, replication among sites or species provides a type of auxiliary data that can be used for parameter estimation. Under a frequentist framework, groups are either pooled in a constant model or treated as a fixed effect with a separate parameter estimates for each population or species. An assumption of homogeneity is required if groups are pooled, whereas fixed-effect models can be problematic if data are sparse for a subset of groups. Multilevel models offer a useful compromise because groups retain their individual identity but information is shared among groups during the estimation process (Cam 2012). A Bayesian framework allows groups to be modeled as random effects and at different ecological scales: individual heterogeneity, multipopulation, or multispecies.

If individual identity is treated as a random effect, heterogeneity in survival can be used to investigate patterns of senescence or other questions with *frailty* models (Marzolin et al. 2011; Cam et al. 2013). Individual heterogeneity in catchability can affect bias and precision of estimates of apparent survival and abundance, but may be handled with *finite-mixture* models or as a random effect in *multilevel* models (Cubaynes et al. 2012; Abadi et al. 2013; Péron et al. 2016). Multipopulation studies can treat time as a random effect to investigate spatial patterns of synchrony (Grosbois et al. 2009), or site as a random effect to calculate overall estimates of survival from multiple populations of a single species (Papadatou et al. 2011; Jansen et al. 2014; Weiser et al. 2018). Last, multilevel models can be used to treat species as a random effect to investigate patterns of synchrony

in apparent survival among species in a community (Lahoz-Monfort et al. 2011; Papadatou et al. 2012), or to compare different communities (Lloyd et al. 2014).

7.12 Spatially Explicit Models

Spatially explicit capture-recapture models provide a robust methodology to combine live encounter data with location of capture information for joint estimation of demographic parameters (Efford 2011; Borchers 2012). Encounters can be based on standard methods for live capture or resighting, or alternatively, camera traps or other devices that record proximity of marked individuals to a sampling location. Location data for encounters can be recorded with different sampling designs, including coordinates of a site within a trap grid, angle, and distance from a point count station or line transects, or as a location within the boundaries of a fixed-area study plot. A general feature of spatially explicit models is that the spatial scale of a trap grid or study plot should be larger than the home range of the study organism.

Closed population models estimate abundance (N) corrected for the probability of capture (p). In *spatially explicit* models for estimation of abundance, detections of individuals at known sampling sites provide information on the probability of detection at the center of a home range (g_0). Animal distributions can be viewed as a point process model where range centers are assumed to be distributed at some density (D). The locations of individual activity centers are usually unknown but the mean distances between recaptures on different occasions can provide information on the scale of spatial movements (σ). For example, Gardner et al. (2010) generalized a JS model to include spatial data for a grid of camera traps, and estimated abundance of activity centers (N_t), density per unit area (D_t), and the per capita recruitment rate (ρ), adjusted for detectability (δ), and the expected number of encounters per individual at a given trap station (λ_0). Spatially explicit models can be fit in either a MLE or Bayesian framework, or with other methods (Efford 2004). Another challenge for spatially explicit models is that estimates of N are required for the likelihood but the true abundance is unknown. This issue can be addressed by *data augmentation* where the data set is supplemented with a large number of encounter histories for individuals that were never captured and have all zeros. These additional encounter histories are used to calculate recruitment, and thereby estimate the proportion of additional individuals that were present but never captured.

Spatially explicit models for open populations allow inclusion of spatial data of locations in the individual encounter histories. Schaub and Royle (2014) developed a sCJS model that includes a kernel for dispersal movements, which allows estimation of apparent survival corrected for local movements within a fixed-area study plot. Raabe et al. (2014) extended the CJS model to include spatial data for detections of stream fish in a linear array of weirs. A spatial version of a robust design model has also been proposed by Ergon and Gardner (2014). Spatial CJS models can be effective at correcting for bias due to permanent or temporary emigration (Weiser et al. 2018), but simulations suggest that parameter estimates may be sensitive to the statistical distributions used to model dispersal movements (Ergon and Gardner 2014). Estimates of dispersal kernels from mark-recapture data suggest that use of Gaussian kernels can lead to parameter bias (Fujiwara et al. 2006). Nevertheless, spatially explicit models for open populations have great potential for improving demographic analyses because auxiliary data on animal locations are often recorded in population studies but the information is not typically included in mark-recapture analyses.

7.13 Robust Design Models

Robust design models differ from CJS models in that additional sampling is required at the outset of a field project, and primary sampling periods are subdivided into shorter secondary sampling occasions. Robust design models assume that the population is open to gains and losses among *primary* sampling periods but closed to change within *secondary* sampling occasions (Kendall et al. 1997; Fujiwara and Caswell 2002; Schaub et al. 2004a). Like CJS models, encounter histories are coded: 1 = detected and 0 = not encountered. Robust design models control for both imperfect detection and imperfect availability by modeling a *superpopulation* with marked individuals moving in and out of the sampling area where they can be encountered. Survival rates are assumed to be the same for individuals both inside and outside of the sampling area. Standard robust design models can perform well if the assumption of closure is not met (Kendall 1999). Open robust design models relax the assumption of geographic closure to allow staggered entry and exit of individuals from a breeding population (Schwarz and Stobo 1997; Kendall and Bjorkland 2001), or the assumption of demographic closure to allow mortality between the secondary sampling occasions (Bailey et al. 2004a).

In a CJS model, the probability of encounter (p) is the product of site propensity (σ) and the true probability of detection (p^*). If true detection is close to unity, then the encounter rates are effectively an estimate of site

propensity ($p = \sigma$ if $p^* = 1$). In a robust design model, the open population part of the model gives the same p as a CJS model, whereas the closed captures provide estimates of $p*$ and abundance (N), or alternatively, the number of individuals never captured (f_0). Closed population models were first used to estimate abundance for a single closed period and the original notation used a capital M to denote different model structures (Otis et al. 1978). A variety of closed population models can be used to model p^* during the secondary occasions of a robust design model, including a null model (p or M_0), time dependence (p_t or M_t), behavioral effects (p vs. c, or M_b), heterogeneity of capture with finite-mixture models (p_π sensu M_h), or different combinations of the effects. Robust design models usually estimate the probability of *temporary emigration* as the complement of site propensity ($\gamma = 1 - \delta$, but see Kendall et al. 2013).

A variety of alternative models can be used to model the probability of temporary emigration. If movements are random and not affected by previous events, temporary emigration at occasion t is calculated as: $\hat{\gamma}_t = 1 - \hat{p}_t / \hat{p}_t^*$. If movements are nonrandom, the probability of temporary emigration is modeled as a function of an individual's status on the previous occasion. Temporary emigration is estimated separately for absent individuals that remained unavailable for capture (γ_t') versus individuals that were present but dispersed away from the sampling area (γ_t'', Kendall et al. 1997). Individuals may be unavailable for capture either because they have dispersed away the sampling area, such as marine animals that have left breeding sites to be at sea, or because marked individuals are hidden in refugia where they cannot be sampled, such as fossorial animals in belowground burrows. The parameter γ_t' has been termed "immigration," but the probability that an absent individual re-enters the sampling area is calculated as the complement: $\delta' = 1 - \gamma'$. Alternative models for movement among the different segments of a superpopulation include no temporary emigration ($\gamma' = \gamma'' = 0$), random emigration ($\gamma' = \gamma''$), nonrandom emigration ($\gamma' \neq \gamma''$), or even-flow models with balance between immigration and emigration ($1 - \gamma' = \gamma''$, Cooch and White 2018). Depending on model structure, robust design models quickly become complex with estimation of multiple parameters for the transitions between primary periods in the open part of the model (ϕ, γ',γ''), and also for the secondary sampling occasions in the closed part of the model (p, c, N or f_0). Estimation of these additional parameters may require long-term datasets with large samples of marked individuals.

Robust design models have two advantages compared to the CJS model. One issue for both models is parameter estimation during the last interval if demographic parameters are time-dependent. Under random temporary emigration, robust design provides estimates of ϕ and p for all intervals in a time series because p^* is available for all occasions. If temporary emigration is nonrandom, then the last movement parameters γ_t' and γ_t'' are still confounded with survival (Peñaloza et al. 2014). As in the CJS model, constraints would have to be applied to the robust design model to estimate survival for the last interval. Robust design models can yield estimates of ϕ and p with less bias and greater precision than CJS models if temporary emigration is present. Temporary emigration causes heterogeneity in encounter rates because individuals that are present have a nonzero probability of encounter, whereas temporary emigrants are unavailable for capture and probability of encounter is zero. Under random temporary emigration, estimates of ϕ and p from CJS models are relatively unbiased but precision is reduced. Under nonrandom temporary emigration, estimates of ϕ and p from standard CJS models can be strongly biased if $\gamma_t' \neq \gamma_t''$ (Kendall et al. 1997, Peñaloza et al. 2014).

The demographic processes that lead to temporary emigration remain poorly understood in ecology. Empirical applications of robust design models include investigations of regional movements and partial migration (Dinsmore et al. 2003; Jahn et al. 2010; Cantor et al. 2012), dormancy or use of refugia where animals are not available for capture (Schaub and Vaterlaus-Schlegel 2001; Bailey et al. 2004b), as well as variation in breeding propensity among animals at reproductive sites (Kendall and Nichols 1995; Kendall and Bjorkland 2001; Sedinger et al. 2001; Schmidt et al. 2002). Breeding propensity can be imperfect ($\sigma < 1$) because of delayed maturity among juveniles or subadults, intermittent breeding among adults, or early reproductive failure that causes emigration before detection. The closed portion of a robust design model also provides estimates of abundance, and can be used to estimate population gains from in situ recruitment vs. immigration (Nichols and Pollock 1990). However, estimates of abundance from the closed part of the model are restricted to the number of marked individuals available for capture in the fixed-area study plot (N or f_0). Thus, estimates of abundance from robust design models may be an underestimate of total population size unless a high proportion of the population has been marked, or in the special case where individuals have been identified by natural marks (Cantor et al. 2012; Lee et al. 2014).

7.14 Mark-resight Models

Mark-resight models take their name from early field studies where marked individuals were released on one occasion and then resighted on multiple occasions.

A single release event might be more cost-effective if capture and marking are expensive procedures, and less invasive if capture events pose a risk to sensitive species of wildlife. "Mark-resight" is a confusing term because the CJS and joint models can also be based on encounter histories with resightings of marked animals. The fundamental difference among different types of models is that counts of *unmarked individuals* are included as inputs for the likelihood function in mark-resight models. Mark-resight models can also allow *batch marking*, where all captured individuals are marked with the same tag as a group, instead of marking each individual with a unique tag. Even if individual tags were used, mark-resight models can include partial information for individuals that were seen as marked but were not individually identified. Mark-resight models improve upon closed population and robust design models by allowing estimation of the total abundance for the marked and unmarked individuals that are observable in the fixed-area study plot (N), and also the nonobservable individuals that are part of a larger superpopulation (N^*). A hybrid model that combines mark-resighting and closed population models has been used to estimate abundance of bobcats (*Lynx rufus*, Alonso et al. 2015). Similarly, a combined mark-resighting and robust design model has been used to estimate survival and total abundance for open populations (McClintock and White 2009).

Three estimators for mark-resight data include the logit-normal estimator (LNE), the immigration–emigration logit-normal estimator (IELNE), and the zero-truncated Poisson log-normal estimator ([Z]PNE, McClintock and White 2012). The LNE and IELNE estimators can be used with batch marks instead of individually marked animals, but have the restrictive requirements that the total number of marked individuals must be known, and sampling with replacements is not allowed. Number of marks is rarely known in field studies of open populations, with the possible exception of situations where all animals are marked immediately before release, or if all marked individuals receive radio collars with mortality switches. Double-counting of individuals may be difficult to avoid if sampling is partitioned into multiple occasions and animals are mobile. Still, if the model assumptions can be met, the IELNE estimator produces estimates of the total superpopulation because geographic closure is not required.

The robust design version of the (Z)PNE estimator is perhaps the most useful model for open populations. The (Z)PNE estimator requires individually identifiable marks and geographic closure, but is a better fit to modeling of open populations because it does not require the number of marks to be known and allows sampling with replacements within secondary occasions. Ideally, individual identity should be obtained on most encounters of marked individuals in the field (>90%). If partial sightings are common, extended mark-resight models allow for individual heterogeneity in detection and control for uncertainty in individual identification (McClintock et al. 2014). Encounter histories for marked individuals do not condition upon distinct secondary occasions and instead tally the total number of individual sightings per primary occasion (Cooch and White 2018). If a marked individual is not detected on a primary occasion, separate codes are used if the animal is known to be alive (+0) or of unknown fate (–0). Additional input includes counts of unmarked animals, marked individuals sighted but not identified, and number of marked individuals in the population (if known). Like the robust design model, the (Z)PNE estimator provides estimates of ϕ, γ', and γ'', but also provides estimates of the number of unmarked individuals (U) and total population size ($N = U + n$) that are corrected for variation in resighting rates (α, σ, and λ). The (Z)PNE estimator has been used to estimate demographic parameters for sharks (Lee et al. 2014), migratory sandpipers (Lyons et al. 2016), and river dolphins (Ryan et al. 2011).

7.15 Young Survival Model

The *young survival* model extends the CJS model by coding detections as counts of group size (Lukacs et al. 2004; Cooch and White 2018). Like the CJS model, the young survival model estimates apparent survival (ϕ) corrected for probability of encounter (p). The young survival model was developed to monitor groups where one or more individuals are individually marked but the remainder of the group is unmarked. Group size must be known at the start of the encounter history, but if group size is one, then the young survival model is equivalent to a CJS model. Survival rates of the different unmarked individuals within each group are assumed to be equivalent. Groups should be independent, and the model cannot be used in field situations where fission or fusion of social groups leads to changes in numbers that are not due to mortality.

The young survival model has been to model chick survival for precocial birds where an individually marked parent attends a brood of unmarked young (Dreitz 2009; Brudney et al. 2013). Detection is often imperfect because broods are mobile and young can escape observers by hiding or moving away. However, hatchlings may be too small to be marked, tags might affect risk of mortality, or individual tags may be too expensive. Thus, an advantage of the young survival model is that chick survival can still be estimated even if the young are not individually marked. If the dependent young are unable to survive without parental care, then the model will estimate true survival because all losses result in mortality. A high maximum group size leads to many possible transitions between groups of different size, which can reduce

the precision of parameter estimates (Cooch and White 2018). It may not be possible to use the model if the maximum group size is large but the sample size of family groups is relatively small. Still, the young survival model can be useful for estimating juvenile survival for species where litter or brood sizes are small (≤3–4 young) and detection of mobile young is imperfect (Kendall et al. 2003; Ryan et al. 2011; Tarwater et al. 2011).

7.16 Multistate Models

Multistate models provide a particularly flexible modeling approach that have been widely used in population ecology (Sandercock 2006; White et al. 2006; Lebreton et al. 2009), and can be set up as mark-recapture (Boxes 7.2 and 7.3) or multievent models (Box 7.4). The term multistate refers to the coding of detections as dynamic categorical states that potentially change between consecutive occasions. The Arnason–Schwarz (AS) model is a multistate version of a CJS model because both models are conditional on first capture, but multistate versions of the JS model can also be unconditional (Brownie et al. 1993; Lebreton et al. 2009; Pledger et al. 2013). Many types of survival models, including the CJS, transient, robust design, dead recovery, and time-

to-event models can also be set up as multistate models (Lebreton et al. 1999; Schaub et al. 2004a, 2004b; Gauthier and Lebreton 2008; Lebreton et al. 2009; Devineau et al. 2014).

A CJS model is a single-state model because the encounter histories are coded as 1 = detected, or 0 = not encountered. In a multistate model with two states (r), detections might be coded as A = state A versus B = state B, and 0 = not encountered. The estimates of apparent survival from a CJS model (ϕ) can then be decomposed into *state-specific estimates* of apparent survival and changing states ($\phi = \phi^r \psi^r$). A multistate model with two states will have a minimum of six parameters: state-specific estimates of apparent survival (ϕ^A and ϕ^B) and probability of encounter (p^A and p^B), as well as the transitional *probability of changing states*, such as from state A to B (ψ^{A-B}) or from B to A (ψ^{B-A}). The total number of parameters increases rapidly with addition of more states ($K = r^2 + r$), with 12 parameters for $r = 3$ states, 30 parameters for $r = 5$ states, and so forth. Standard assumptions of multistate models are that apparent survival does not depend on a previous state, all individuals make the transition at the end of the interval, individuals do not temporarily emigrate to states where they cannot be detected, and that observers can correctly assign individuals to states. The different

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Box 7.4 Fitting Multistate Models with Elementary Matrices

Multievent models are defined by elemental matrices that specify three sets of probabilities: initial states (**Π**), transitions (**Φ**), and conditional events (**B**). Initial states are a vector but **Φ** and **B** can each be one or more matrices in a Markov chain. Multievent models differ from standard mark-recapture models because the dead state (D) is explicitly included as a terminal state even if dead individuals are never observed. The usual conventions are that the dead state is the last column in **Π** and **Φ**, whereas not detected is the first column in **B**. Intermediate states may not be the same as initial states, and elementary matrices need not be square but each matrix row sums to one and is row-stochastic.

A standard multistate model might include two observable states for breeders (B) and nonbreeders (N). Initial states (**Π**) for the B, N and D states would be:

$$\mathbf{\Pi}_t = \begin{bmatrix} \pi^B & 1-\pi^B & 0 \end{bmatrix}, \tag{7.6}$$

where π^B and $1 - \pi^B$ are the probabilities that an individual is a breeder or nonbreeder at first encounter, and 0 indicates that none of the individuals are dead at the start. Two transition matrices (**Φ**) summarize the state-specific rates for the B, N, and D states:

$$\mathbf{\Phi}_t^{r(\phi)} = \begin{bmatrix} \phi^B & 0 & 1-\phi^B \\ 0 & \phi^N & 1-\phi^N \\ 0 & 0 & 1 \end{bmatrix} \text{ and}$$

$$\mathbf{\Phi}_t^{r(\psi)} = \begin{bmatrix} \psi^{BB} & 1-\psi^{BB} & 0 \\ 1-\psi^{NN} & \psi^{NN} & 0 \\ 0 & 0 & 1 \end{bmatrix}, \tag{7.7}$$

where ϕ^r is the state-specific probability of apparent survival and ψ^r is the probability of changing states. The top rows indicate that an individual must survive, remain in the same state, or change states. The right column absorbs individuals that die or permanently emigrate, whereas the bottom row indicates that lost individuals never return to the population. The columns of the conditional events matrix (**B**) summarize the state-specific probabilities of encounter for three possible events: not detected, detected as a nonbreeder, or detected as a breeder:

$$\mathbf{B}_t^r = \begin{bmatrix} 1-p^N & p^N & 0 \\ 1-p^B & 0 & p^B \\ 1 & 0 & 0 \end{bmatrix}. \tag{7.8}$$

assumptions are relaxed in modified multistate models that model transitions as a function of states previously occupied (Rouan et al. 2009), subdivide events during transitions (Grosbois and Tavecchia 2003), include temporary emigrants as an unobservable state (Kendall 2004; Schaub et al. 2004a), or account for uncertainty in state assignment (Pradel 2005).

Dynamic categorical states have been used to investigate four basic types of information: location, age or stage classes, disease or physiological state, and alternative sources of encounter data. *Location data* are based on detections of marked individuals at discrete geographic sites such as ecoregions, islands, breeding colonies, or core vs. peripheral habitat patches. In these cases, state-specific estimates of apparent survival might be used to identify the habitat strata with the best demographic performance (Serrano et al. 2005; Low et al. 2010). Movement rates can be modeled as a function of distance, colony size, or habitat conditions to better understand the effects of connectivity in spatially structured populations (Brown et al. 2003; Breton et al. 2006; Roche et al. 2012). Movement rates can also be estimated for a core study plot with a contiguous buffer zone (Powell et al. 2000; Devineau et al. 2010; Horton et al. 2011), or between staying in a site or moving elsewhere in a network of sites (Lagrange et al. 2014). If a network of study sites represents the entire known distribution for a metapopulation, apparent survival may approach true survival because losses will be due to mortality and not permanent emigration.

Multistate models can also be used to model demographic variation among different *age or stage classes*. Demographic classes are important sources of heterogeneity that can be treated separately in a multistate model but are pooled in a CJS model. In the case of breeding status, encounter histories might be coded as B = breeder, N = nonbreeder, and 0 = not detected (Sandercock et al. 2000). With sufficient data, strata might be extended to multiple classes: juveniles, nonbreeders, inexperienced breeders, or experienced breeders (Schaub et al. 2011; Rotella et al. 2012), or to a combination of breeding status and site (Anderson et al. 2012). Alternatively, stage classes might be based on social dominance (subordinate vs. dominant, Cohas et al. 2007), reproductive output (unsuccessful vs. successful, Schaub and von Hirschheydt 2009), migratory status (resident vs. migrant, Grayson et al. 2011), or sociality (solitary vs. groups, Genton et al. 2015). Multistate models based on stage classes yield state-specific estimates of ϕ and p, and ψ becomes the probability of maturation or changing stage class. If age or experience accrue over time, the transitional probabilities of returning to a younger or inexperienced state can be fixed to zero. Multistate models based on breeding status have been used to test for the cost of reproduction,

as a life-history tradeoff between reproduction and survival (Nichols et al. 1994; Nichols and Kendall 1995). Observational methods are not the best approach to test for tradeoffs because breeders or experienced individuals may have high reproductive success, high survival, and strong site fidelity (Sandercock et al. 2000; Sanz-Aguilar et al. 2008; Schaub and von Hirschheydt 2009). Multistate models can also be used to test for demographic responses to manipulated treatments in an experimental context, but relatively few studies have used this approach (Doligez et al. 2002; Lyet et al. 2009).

Multistate models are a useful tool for investigating *disease dynamics* in wild populations (Cooch et al. 2012). Here, encounter histories might be coded as U = uninfected, I = infected, and 0 = not detected. Determination of disease state can be determined by external appearance, immunoassays, or molecular tests of different tissues. Depending on disease latency and test sensitivity, the U-state can be a heterogeneous mixture of uninfected individuals and individuals that are infected but still asymptomatic (Conn and Cooch 2009). If disease negatively impacts survival or activity, infected individuals may have lower state-specific estimates of apparent survival ($\phi^I < \phi^U$) or encounter ($p^I < p^U$, Faustino et al. 2004). Alternatively, encounter rates might be higher for infected individuals if behavioral changes increase detection by observers (Senar and Conroy 2004). Here, the transition rates provide estimates of the probability of infection (ψ^{U-I}) and potential recovery (ψ^{I-U}), and asymmetry between the infection and recovery rates can provide an index of disease virulence ($\psi^{U-I} > \psi^{I-U}$). Multistate models allow the transitions to be modeled as a function of environmental covariates, such as the relationship between infection rates and prevalence of a disease in a population (Lachish et al. 2007; Ozgul et al. 2009).

Multistate models have also been used to investigate the effects of *body mass or size* on survival. Body mass and size are usually continuous variables which must be converted to states based on quartiles or standardized scores (i.e. z-values, Letcher and Horton 2008; Boulanger et al. 2013; Monticelli et al. 2014). Ordinal covariates such as rank scores of body condition are often pooled to a few states too (Miller et al. 2003). Multistate models based on size or mass classes yield state-specific estimates of ϕ and p, and larger, mobile individuals might be predicted to have higher survival or a lower probability of encounter. The transition ψ becomes the probability of growing or regressing into a different stage class. Multistate models were a useful method for modeling mass and size because early mark-recapture models could not handle continuous covariates that were also dynamic (Nichols and Kendall 1995). However, pooling is potentially problematic because information may be lost when continuous

variables are collapsed into categorical bins. Improved methods for including individual covariates in CJS models now allow ϕ and p to be modeled as a function of covariates that are both continuous and dynamic (Cooch and White 2018).

A final application for multistate models is for combining multiple sources of information such as different marker types, live encounter with dead recovery data, or both (Kendall et al. 2006; Besnard et al. 2007; Juillet et al. 2011). Different marker types might include a standard mark (band, tag, or molecular identity) vs. an additional auxiliary mark such as a neck collar (Reed et al. 2005) or a radio tag (Powell et al. 2000; Boulanger et al. 2004). Here, the encounter histories might be coded as M = detected with a standard mark, A = detected with an auxiliary mark, or 0 = not detected. If neck collars or radio tags negatively impact animal performance, apparent survival or encounter rates may be lower for individuals with auxiliary marks ($\phi^A < \phi^M$). Additionally, the transition rates can provide an estimate of marker loss (ψ^{A-M}). In the case of combining live encounter and dead recovery information, encounter histories might be coded as A = alive, D = newly dead, or 0 = not detected (Lebreton et al. 1999; Gauthier and Lebreton 2008; Devineau et al. 2014). A third possible state of dead for multiple years is unobservable and not necessary to include. To investigate competing risks of mortality, codes for dead recoveries can be expanded to multiple sites (Kendall et al. 2006), or to different causes of mortality such as predation, harvest, or collisions (Schaub and Pradel 2004). The transition rates of the multistate model then become estimates of cause-specific mortality rates for the different sources of mortality (ψ^{A-D}) and encounter rates are calculated separately for the live encounters (p^A) and cause-specific dead recoveries (p^D or r, Bischof et al. 2009). For example, Besnard et al. (2010) used multistate models to show that monthly risks of harvest mortality were up to three times higher than natural mortality in hunted populations of Gray Partridge (*Perdix perdix*).

The main limitation of multistate models is that the number of state-specific parameters and transitions increases exponentially with the number of states, especially in *memory* models where the parameters are also dependent on previous states. In practice, most multistate models are limited to ~2–4 categorical states, although networks with multiple sites can still be modeled with two states for staying at a site ("here") or dispersing ("elsewhere," Lagrange et al. 2014). Model complexity can also be reduced by fixing parameters to zero for any impossible transitions that cannot occur, such as regression of adults to juveniles (ψ^{A-J}) or resurrection from dead to alive (ψ^{D-A}). Complex multistate models can have problems with parameter redundancy as an intrinsic function of model structure, or due to *extrinsic* problems with sparse data if the encounter histories do not include all possible transitions (Fujiwara and Caswell 2002; Gimenez et al. 2003; Bailey et al. 2010; McCrea et al. 2012). Complex multistrata models can also be difficult to fit with MLE methods due to problems with convergence and multiple solutions for the likelihood function (Lebreton and Pradel 2002; Pradel et al. 2008). Problems with model fitting can be addressed by using different sets of random values as starting values, or by using *simulated annealing* as an optimization algorithm that uses random jumps to sample the likelihood function (White et al. 2006).

7.17 Multistate Models with Unobservable States

One challenge for multistate models is when one or more states are *unobservable* (Kendall and Nichols 2002; Kendall 2004; Schaub et al. 2004a). Unobservable states are a feature of herbaceous plants where belowground rhizomes or corms may be dormant (Shefferson et al. 2003; Kéry et al. 2005), and among long-lived vertebrates where nonbreeders are unobservable due to delayed maturity among juveniles or intermittent breeding among adults (Fujiwara and Caswell 2002; Kendall et al. 2009; Stauffer et al. 2013). Two states might be coded as O = observable and U = unobservable, and more complex models may have multiple observable or unobservable states (Converse et al. 2009; Bailey et al. 2010). By definition, $p^O > 0$ but $p^U = 0$, and the state U does not appear in the encounter histories. The multistate model has the potential to give state-specific estimates of apparent survival (S^O and S^U), but the two parameters may not be identifiable unless constrained to be equal (Henle and Gruber 2018). The transition rates are equivalent to a robust design model with non-random movements where ψ^{U-O} is immigration (or $1 - \gamma'$) and ψ^{O-U} is temporary emigration (or γ'', White et al. 2006). If $\psi^{U-O} = 0$, then emigration is not temporary but is permanent. Conceptually, multistate models with unobservable states can be used to model temporary emigration as *absent* (ψ^{U-U} and $\psi^{O-U} = 0$), *random* ($\psi^{U-U} = \psi^{O-U}$), *nonrandom* ($\psi^{U-U} \neq \psi^{O-U}$), or balanced in a model with *even-flow* dynamics ($\psi^{U-O} = \psi^{O-U}$). One potential advantage is that multistrata models can still be used even if a field study lacks the secondary sampling periods needed for a robust design model (Schaub et al. 2004a). Unfortunately, unobservable states can cause problems with intrinsic parameter redundancy, such that not all parameters may be identifiable in multistate models (Hunter and Caswell 2009; Bailey et al. 2010; Cole 2012), and may

affect bias and precision for the parameter estimates (Henle and Gruber 2018).

Issues of parameter redundancy can be resolved by setting constraints on the structure of multistate models (Kendall and Nichols 2002; Kendall 2004). Three alternatives include setting survival to be equal for the different states ($S_t^O = S_t^U$), setting transitional probabilities to be time-constant ($\psi_c^{U-O} \neq \psi_c^{O-U}$), or by placing constraints on a subset of the transitions, for example if breeders become obligate nonbreeders when interbirth intervals are greater than a year ($\psi^{O-O} \equiv 0$, Fujiwara and Caswell 2002; Reed et al. 2003; Monk et al. 2011). Alternatively, constraints on p may be preferred if the probability of encounter has less biological interest. Multistate models for herbaceous plants have included three states: dormant (D), vegetative (V), and flowering plants (F). Dormant life-stages are unobservable ($p^D \equiv 0$), and the dormant state is not included in the encounter histories. Encounter rates for aboveground life-stages of a sessile plant can be arbitrarily set to one ($p^V = p^F \equiv 1$, Kéry et al. 2005), or can be estimated with closed population models (p^V and $p^F > 0.97$, Shefferson et al. 2003). Encounter rates of mobile animals are unlikely to be close to unity, and different methods are required.

One approach for investigating dynamics of unobservable states is a combined *multistate open robust design* model for open populations (MSORD) with a multistate framework for estimating state-specific demographic parameters coupled with a robust design component for estimating encounter rates. Encounters on secondary occasions can include repeated recaptures in the *robust gateway* model (Bailey et al. 2004a; Church et al. 2007), or resightings only in the *less-invasive robust design* (Kendall et al. 2009). Problems with parameter redundancy can still arise with these models, and survival of individuals in the observed and unobserved states is usually constrained to be equal (Kendall and Bjorkland 2001; Bailey et al. 2009). Despite the increased complexity of the combined MSORD models, empirical applications have provided insights into the sex-specific costs of breeding (Muths et al. 2013; Stauffer et al. 2013; Rendón et al. 2014), reproductive strategies of failed and successful breeders (Converse et al. 2009), and the key environmental drivers that affect these life-history transitions (Church et al. 2007; Grayson et al. 2011).

7.18 Multievent Models with Uncertain States

Another challenge for multistate models arises when individuals cannot be assigned to categorical states with confidence. Uncertain states differ from unobservable states because *uncertain states* can still be detected, whereas unobservable states are not available for capture (δ or $p^* < 1$). Uncertain states can arise for two non-exclusive reasons (Conn and Cooch 2009). Under *misclassification errors*, marked individuals may be assigned to an incorrect state, such as a genotype or species (Lukacs and Burnham 2005; Runge et al. 2007). Under *partial observability*, marked individuals are detected but states remain ambiguous because of difficulties in determining sex (Nichols et al. 2004), disease status (Conn and Cooch 2009), breeding status (Sanz-Aguilar et al. 2011), or association with dependent offspring (Kendall et al. 2003; Taylor and Boor 2012). Early attempts to deal with uncertain states included adding an additional unknown state to the encounter histories (Wood et al. 1998; Conroy et al. 1999; Faustino et al. 2004), or using auxiliary data to develop state assignment matrices that could be used as model constraints (Fujiwara and Caswell 2002; Lebreton and Pradel 2002). Censoring of unknown observations or including unknowns as an additional state are undesirable solutions because both procedures affect the bias and precision of parameter estimates from multistate models (Faustino et al. 2004; Nichols et al. 2004; Conn and Cooch 2009).

Like unobservable states, uncertain states can also be handled with a combined MSORD. In mammals, large-bodied females can be relatively easy to detect but it be harder to determine if a female is attending dependent offspring. In a population study of manatees (*Trichechus manatus*), Kendall et al. (2003) sampled marked females twice per year and recorded three states: female with calf (C), lone female with no calf (N), or undetected (0). Females had imperfect detection ($p = 0.48$), but if a female was detected, then the probability of detecting her calf was also imperfect ($\delta = 0.72$). Estimates of the transitional probability of becoming a breeder were biased low in a standard multistate model ($\hat{\psi}^{N-B} = 0.31$) compared to a model controlling for uncertain states ($\hat{\psi}^{N-B} = 0.61$). Nichols et al. (2004) used a similar model to address uncertainty in sex determination. One feature of these models is that probability of classification is often hierarchical; a female with a calf cannot be misclassified as a lone female, and unsexed juveniles mature to become known sex adults, but cannot regress to an unknown state.

Uncertain states can also be handled with *multievent* models, which belong to the family of *hidden Markov models* (HMM, Pradel 2005, 2009; Choquet et al. 2009b; Conn and Cooch 2009). The models are *hidden* because the latent state dynamics are only partially observable and *Markov* because individuals move independently among a finite set of states in an ordered series

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Box 7.5 Fitting Multievent Models with Elementary Matrices

Multievent models can also handle situations where the state assignments are *uncertain* in a multistate model. Desprez et al. (2014) used a multievent model to investigate costs of first-time breeding in an animal population with three latent states: prebreeders (P), new breeders (N), and experienced breeders (E). Dead (D) was also included as a state in the elementary matrices. In the field, individuals were observed in four possible states: not detected, detected as a prebreeder, detected in an unknown state, or detected as an adult (new or experienced combined). All individuals were first marked as prebreeders and the initial states (Π) for the P, N, E, and D states were then:

$$\Pi_t = \begin{bmatrix} 1 & 0 & 0 & 0 \end{bmatrix}. \qquad (7.9)$$

The transition matrices (Φ) summarized the state-specific rates for the P, N, E, and D states:

$$\Phi_t^{r(\phi)} = \begin{bmatrix} \phi^P & 0 & 0 & 1-\phi^P \\ 0 & \phi^N & 0 & 1-\phi^N \\ 0 & 0 & \phi^E & 1-\phi^E \\ 0 & 0 & 0 & 1 \end{bmatrix} \text{ and } \Phi_t^{r(\psi)} = \begin{bmatrix} 1-\psi^{PN} & \psi^{PN} & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}, \qquad (7.10)$$

where ϕ^r and ψ^r are the state-specific probabilities of apparent survival and the probability of changing states. Prebreeders had an imperfect probability of becoming a new breeder (ψ^{PN}) whereas new or experienced breeders automatically transitioned to becoming experienced breeders.

The model had two conditional events matrices (**B**). The columns of the first matrix summarized probabilities of encounter (p^r) for the four latent states as three possible events: not detected, detected as a prebreeder, or detected as an adult. The columns of a second matrix then summarized the probability of classification (δ^r) for each of the three events as four possible observation codes: not detected, detected and classified as a prebreeder, detected in an uncertain state, or detected and classified as an adult:

$$\mathbf{B}_t^{r(p)} = \begin{bmatrix} 1-p^P & p^P & 0 \\ 1-p^A & 0 & p^A \\ 1-p^A & 0 & p^A \\ 1 & 0 & 0 \end{bmatrix} \text{ and } \mathbf{B}_t^{r(\delta)} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & \delta^P & 1-\delta^P & 0 \\ 0 & 0 & 1-\delta^A & \delta^A \end{bmatrix}. \qquad (7.11)$$

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of events. Multievent models are defined by elemental matrices that specify three sets of probabilities: initial states (Π), transitions (Φ), and conditional events (**B**, Box 7.5). Like the challenges for multistate models with unobservable states, multievent models face problems of parameter redundancy and the possibility of multiple optima. Multievent models provide a flexible framework for developing custom models to investigate capture heterogenity (Crespin et al. 2008; Péron et al. 2010), memory models for movements (Rouan et al. 2009), or patterns of breeding propensity and mate fidelity (Cubaynes et al. 2011; Sanz-Aguilar et al. 2011; Culina et al. 2013; Desprez et al. 2014).

7.19 Joint Models

Joint models combine live encounter data collected at sampling occasions with auxiliary data on dead recoveries or supplemental resightings taken from intervals between occasions (Burnham 1993; Barker 1997, 1999). Live encounters are usually taken from a fixed-area study plot at set sampling occasions, whereas dead recoveries and supplemental resightings are collated opportunistically from other sites and at any time of year. In Program Mark, the encounter histories are coded in a LD format where each type of information is recorded separately for each occasion (Cooch and White 2018). Thus, the code 11 is released alive but recovered dead in the following interval, 12 is released alive and resighted in the following interval, 10 is a live encounter only, 01 is a dead recovery only (not allowed on the first occasion), 02 is an observation only, and 00 is not detected. A key advantage of using information from dead recoveries and supplemental observations is that losses to permanent emigration are reduced if the auxiliary data are taken from a large geographic area (Horton and Letcher 2008). Many mark-recapture models require systematic sampling at discrete occasions with regular intervals to meet the assumption of instantaneous sampling. A second advantage is that auxiliary data can be collected at any time, which may be a better sampling design for field projects where marked individuals are sampled opportunistically at irregular or continuous intervals instead of discrete occasions (Ruiz-Gutiérrez et al. 2012; Barbour et al. 2013; Kendall et al. 2013).

The Burnham model combines live encounter and dead recovery data to estimate four parameters: true survival (S), site fidelity (F), probability of encounter for live individuals (p), and the probability of reporting (r) for dead individuals. Similarly, the Barker model combines live

encounters, dead recoveries, and auxiliary observations to estimate S, p, and r, and four additional parameters: the probabilities of resighting for individuals that survive or die during an interval (R, R'), and probabilities that an individual in the population is at risk of capture or not (F, F'). Joint models can also be parameterized as multistate (Lebreton et al. 1999; Kendall et al. 2006) or multievent models (Kendall et al. 2013). If dead recoveries are not available, the reporting parameters can be fixed to zero ($r \equiv 0$) and the Barker model can be based on live encounters and auxiliary observations alone (Collins and Doherty 2006; LeDee et al. 2010). If most data are live encounters with relatively few auxiliary observations, then site fidelity and resighting parameters might be modeled as constants without time dependence (Ruiz-Gutiérrez et al. 2012). Extended versions include models that allow for continuous covariates (Bonner 2013), control for marker loss (Conn et al. 2004), and include a robust design framework (Lindberg et al. 2001; Barker et al. 2004; Kendall et al. 2013).

The main challenge for use of joint models is that multiple sources of information must be available for individually marked animals. Burnham and Barker models have been widely used with harvested species where live and dead individuals are routinely encountered (Doherty et al. 2002; Blums et al. 2005; Sandercock 2006), but applications to nongame species are also possible (LeDee et al. 2010; Lok et al. 2013; Cohen et al. 2014). Joint models effectively decompose apparent survival into the component probabilities, thereby providing separate estimates of true survival (S) and site fidelity (F). Thus, joint models have also allowed for variation in the two demographic parameters to be modeled as a function of demographic classes, environmental conditions, and other explanatory factors.

7.20 Integrated Population Models

Integrated population models provide a powerful modeling approach for joint analysis of live encounters with counts or abundance from population surveys, along with other available sources of demographic data, such as productivity data from nest monitoring, dead recoveries or age ratios from harvest monitoring, or known fate survival models (Gauthier et al. 2007; Schaub and Abadi 2011; Zipkin and Saunders 2018). In a traditional population model, each dataset might be analyzed separately with different statistical models, and the estimates of fecundity, survival, and recruitment would then be combined in a matrix population model (Chapter 8). Integrated population models can be more efficient because they allow simultaneous analysis of all available information, explicitly handle uncertainty, and can be

used to estimate immigration and other demographic parameters that are not part of the input datasets (Abadi et al. 2010a; Schaub et al. 2013; Chapter 9). Integrated models are also flexible enough to cope with messy features of long-term monitoring programs such as gap years of missing data, datasets that vary in temporal overlap or duration, as well as predictions into the future.

Integrated population models are developed in three steps: defining an age- or stage-structured population model that links population size to demographic rates, defining separate likelihood functions for each available dataset, and creating a joint likelihood for an integrated model as the product of all component likelihoods (Schaub and Abadi 2011). The population model is usually a projection matrix where the matrix elements are comprised of lower-level demographic parameters including fecundity, apparent survival, and immigration. Individual likelihoods can be simple for parameters measured without error such as direct counts of number of young. To control for imperfect detection in survey counts or apparent survival, state-space formulations split the likelihood for each dataset into separate components for the latent state dynamics and the observation process. If input datasets are independent, the joint likelihood for the integrated model is then calculated as the product of the component likelihoods. If input datasets are not independent, simulations suggest parameter estimates may still be robust (Abadi et al. 2010b) or could be tackled with spatially explicit integrated population models (Chandler and Clark 2014). The joint likelihood can be illustrated conceptually as a directed acyclic graph (DAG), with nodes and arcs similar to the life-cycle diagram of a matrix population model (Schaub and Abadi 2011; Chapter 9).

7.21 Frequentist vs. Bayesian Methods

Mark-recapture models can be fit to encounter histories with different modeling approaches, including MLE in a *frequentist* or *information theory framework*, or MCMC methods in a *Bayesian framework*. The methods have different advantages and disadvantages but often converge to identical results given the same set of encounter histories and mark-recapture model. Maximum-likelihood models are usually limited to fixed-effects models but have the advantage that less computation time is needed and a suite of alternative models can be fit to a dataset relatively quickly. Fitting mark-recapture models in a Bayesian framework can be challenging but offers several advantages. Hierarchical models in a Bayesian framework are a good framework for modeling explanatory factors as

random instead of fixed effects, and may perform better with sparse data (Gimenez et al. 2007; Calvert et al. 2009). Random-effect models can be used to investigate individual heterogeneity (Cam et al. 2013), calculate the process variance of a demographic parameter (Rotella et al. 2012), examine the functional relationship between two demographic parameters without the confounding effects of sampling variance (Link and Barker 2005; Sedinger et al. 2010), or jointly analyze data from multiple sites or species (Papadatou et al. 2011, 2012; Jansen et al. 2014).

Another advantage of Bayesian models is greater flexibility in developing customized models that may be a better fit to the sampling design of a field study, such as cases where states are unobservable or uncertain (Pradel 2005), or integrated population models that combine live encounter data with population counts and other demographic information (Gauthier et al. 2007; Schaub and Abadi 2011; Zipkin and Saunders 2018). Early integrated population models were analyzed with MLE methods based on complex integrals and process equations that had to be approximated by normal distributions (Gauthier et al. 2007). Integrated population models are now usually fit with MCMC in a Bayesian framework (Schaub and Abadi 2011, Chapter 9). The Bayesian framework requires definition of prior distributions for model parameters but allows use of binomial distributions for probabilities and Poisson or negative binomial distributions for count data, and may be more efficient for sparse datasets (Véran and Lebreton 2008; Schaub et al. 2012).

MLE and Bayesian methods differ in model selection procedures. In MLE methods, model selection procedures can be based on AIC (or AIC*c* or QAIC*c*) or BIC. In Bayesian models, model selection can be based on the Deviance Information Criterion (DIC) where a model with a low DIC value is a better approximation of the underlying biological processes than other models with higher values (Barnett et al. 2010). Unfortunately, model selection based on DIC sometimes works poorly with Bayesian models because of challenges in counting the effective number of parameters in hierarchical models with random effects (Millar 2009; Barker and Link 2015). Hooten and Hobbs (2015) reviewed alternatives for Bayesian model selection, and recommend the Watanabe-Akaike Information Criterion (WAIC) as an alternative for model selection with hierarchical models, Bayes factors for conducting Bayesian model averaging, and model-based methods such as stochastic search variable selection for an integrated approach to model fitting and selection.

In a MLE analysis, parameter estimates can be taken from the minimum AIC model as the most parsimonious model that contains the variables of interest, or by model averaging across the candidate models via multimodel

inference. One potential disadvantage of MLE methods is that the 95% confidence intervals (CI) of the parameter estimates are based upon asymptotic assumptions which may be not be appropriate for small datasets. If a parameter is not included in the likelihood, it cannot be modeled but must be calculated as a derived parameter once a model has been fit. For example, abundance is treated as a derived parameter in some closed population models, and is calculated as the number of uniquely marked individuals plus an estimate of the number never caught: $\hat{N} = M_{t+1} + \hat{f}_0$. Derived parameters can also include real parameters that are projected to a different time period or combined in a function. For example, expected longevity might be extrapolated from apparent survival: $\hat{L} = -1/\ln\hat{\phi}$. In an MLE framework, confidence intervals for derived parameters must be calculated analytically with the delta method, or numerically with bootstrapping methods (Powell 2007; Cooch and White 2018).

In a Bayesian model, estimates of variance and 95% credible intervals (CRI) for parameter estimates are taken directly from the posterior distributions after the model has converged. The CRI from the posterior distribution are exact for any arbitrary sample, which may be an advantage if sample sizes are small (Gardner et al. 2010). Moreover, posterior distributions can be calculated for any real or derived parameter, and use of the delta method or bootstrapping are not required. One drawback for Bayesian models is that computational times to reach convergence can be considerably longer than MLE methods, potentially restricting the number of alternative models that can be tested. Implementation of Bayesian models also requires programming expertise with specialist software, but available textbooks with sample code provide a useful starting point (Kéry and Schaub 2012; Royle et al. 2014).

7.22 Software Tools

A growing number of software tools are available for analyses of mark-recapture data for marked individuals with imperfect detection (Mazerolle 2015). Two widely used software packages with a wide range of alternative models and extensive documentation include Programs `MARK` (White and Burnham 1999; Cooch and White 2018), and `E-SURGE` (Choquet et al. 2009a; Choquet and Gimenez 2012). The `U-CARE` software provides tools for assessing GOF tests for CJS, multistate, and other models (Choquet et al. 2009a). The `R` software environment offers a suite of specialized packages for mark-recapture analyses including: the `R2ucare` package for GOF tests (Gimenez et al. 2017), the `RMark` package as an interface to `Mark` (Cooch and White 2018: Appendix C), the

marked package for fitting basic mark-recapture models with MLE or Bayesian MCMC methods (Laake et al. 2013), the secr package for spatially explicit capture-recapture models (Efford 2017), and the multimark package for modeling encounters of individuals identified by natural marks (McClintock 2015). The unmarked package offers a range of hierarchical models for unmarked individuals, including distance sampling, occupancy models, and count-based models (Fiske and Chandler 2011). Bayesian mark-recapture models can be run from an R environment with the R2WinBUGS package as an interface to WinBUGS or OpenBUGS, or with the rjags or R2jags packages as an interface to JAGS (Kéry and Schaub 2012; Royle et al. 2014). Many of these software tools are open-source programs available as free downloads, and have online support from dedicated communities, including the phidot forum, or the unmarked forum at Google Groups.

7.23 Online Exercises

Creating the encounter histories for marked individuals is a necessary first step for any mark-recapture analysis. Exercise 1 is an example of an R script for a songbird dataset that shows the steps for converting a vertical file with captures on different occasions into a horizontal encounter history with ones and zeros for detection and nondetection events. Another common input format for mark-recapture analyses is the m-array. Exercise 2 is an R script that can be used to summarize encounter histories into a standard m-array for input to different software packages. Last, Exercise 3 provides an example of a basic CJS analysis for a classic dataset on European Dippers (*Cinclus cinclus*) using the RMark software package as an interface to Program MARK.

7.24 Future Directions

Many questions in population biology, evolutionary ecology, and wildlife management require robust estimates of demographic parameters and their variance. Mark-recapture analyses based on live encounter data are often cost effective, and provide estimates of apparent survival and other parameters that are unbiased with good precision. Fundamental models such as the CJS, Jolly–Seber, and multistate models will remain important as stand-alone tools and as building blocks for more complex models. Mark-recapture methods are an area of active research among quantitative ecologists and major advances continue to be made in five areas. One area has been development of new models that relax the assumptions of standard mark-recapture models, such as multistate models that allow for unobservable or uncertain states. A second area has been integration of live encounter data with other sources of auxiliary data, such as movement data in spatial CJS models, dead recovery data in joint models, or population counts and fecundity data in integrated population models. Third, tests for model fit and corrections for overdispersion are standard procedures for fundamental models like the CJS and multistate models. GOF tests have not yet been developed for multistate models with unobservable states, integrated population models, and other complex models but remain an area of active research. Fourth, continuing development of new software tools with comprehensive documentation has led to widespread adoption of mark-recapture methods, including hierarchical models in a Bayesian framework which provide flexibility for model design. Last, open data and open source software are quickly becoming the new standards for ecological research. Archiving of long-term datasets will facilitate retrospective analyses of existing datasets as new statistical tools become available, and will provide the necessary baseline for understanding future patterns of ecological change. Documentation of software code will allow the next generation of ecologists to continue to use mark-recapture models to tackle the most challenging questions in population biology.

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