Capture–recapture sampling designs

Mark Lindberg & Eric Rexstad

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Abdel H. El-Shaarawi and Walter W. Piegorsch

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Changes in the abundance of animal populations are governed by four parameters often referred to by the BIDE acronym: births, deaths, immigration and emigration. If all these parameters were known for a population, we would understand the rate of change (λ) for a population and which one of these parameters was the most important determinate of population change. The rate of change for a population could also be determined if abundance were known (censused) in successive time periods [16].

Information about BIDE, **abundance**, and **density** (abundance per unit area) is essential for ecologists and biologists studying animal populations. These parameters are the currency for studies of life-history theory [58], quantitative **population ecology** [46], and evolutionary ecology [13]. Biologists require accurate information about abundance and BIDE to make sound management decisions for species conservation [50]. Given the essential importance of these parameters, it is not surprising that a dedicated branch of **environmetrics**, capture–recapture (CR), has evolved for the design and analysis of **population dynamics** of animals [3, 26, 40, 43, 55, 63].

Although all animal populations are finite, they are often numerous, elusive and widely distributed. Therefore, most animal populations are almost impossible to enumerate (census) and specific sampling designs must be used to estimate population parameters. Although some principles of survey sampling [52] apply to CR designs (e.g. random sampling; *see* **Sampling, environmental**), CR designs are characterized by several unique features. Perhaps the most apparent deviation from traditional approaches to sampling is that animals are sampled multiple times. As the CR name implies, animals are initially captured and typically marked for identification in subsequent sampling events (recapture). These sampling events are referred to as sampling occasions and occasions are separated by intervals. Marked animals may enter the sample during the initial capture occasion or during subsequent occasions [42, 44]. The number of occasions, the duration of the occasion and the length of the intervals between occasions depend on the parameters of interest and the models that will be used for estimation.

Animals may be marked with batch marks (groups of animals receive the same marks) or marks that allow the animal to be individually identified. Most designs discussed in this entry require that animals are marked with individually identifiable marks. Physical markers such as legbands and neckbands for birds or ear tags and passive integrated transponders (PIT) tags for mammals may be applied to the animal [33]. For some species, more non-evasive marks such as pelage characteristics [20, 25] or deoxyribonucleic acid (DNA) code [32] may be used (*see* **Biomarkers**). These types of mark may be useful if animals are difficult to handle or if there are concerns about the potential effects of markers on sampling [31, 33].

The recapture occasion(s), following initial capture, is more generally described as an encounter occasion (*see* **Encountered data**), because encounter may be a live recapture [43], a recovery of a dead individual [3], a sighting of a marked animal [18], or a sampling of an animal part, e.g. hair [32] that can subsequently be associated with an individual. The appropriate form of encounter is often determined by the sampling design and the natural history of the species under study. For example, birds may easily be captured during a wing molt when some birds are flightless, but recapture may be difficult after marked birds regain flight, and recoveries or sightings are the only reasonable form of encounter [27]. Again, the sampling design is still characterized by an initial capture following by a series of re-encounters, which we refer to as recaptures.

Our objective is to introduce the various CR sampling designs that are used to estimate parameters for animal populations. Although CR approaches have been used since the 1700s, when they were first used to estimate the abundance of humans [55], most literature has focused on data analysis [26, 43]. We will cover designs that are used to estimate demographic parameters (births and deaths), geographic parameters (immigration and emigration), and abundance or density. For each design, we will emphasize assumptions, identifiable parameters and decisions about the number of occasions and the interval lengths.

Survey of CR Designs

General Assumptions

Although we will discuss the specific assumptions of each suite of CR models and the implications of those assumptions for study design, we first present some general assumptions for the entire set of CR designs [26, 43].

For all designs, a sample is obtained by being able to uniquely identify members of the population of interest, either by the placement of a mark or through passive collection techniques. This process has one important assumption:

Assumption 1 Parameters and processes estimated for the marked population can be applied to the unmarked population of interest.

This assumption, that the sample is representative of the population, is common to all statistical analysis. For CR studies where animals must be captured to be marked, this assumption may be particularly important. Certain trapping techniques may target individuals of different sexes, ages or physiological conditions [59, 61]. Unlike several other assumptions where assumption departures can be diagnosed and parameter estimates can be corrected for violations, violation of this assumption is difficult to detect and may be impossible to correct.

After capture, many different types of marker can be used. In addition to the assumptions inherent to the marking process, several assumptions about the markers must also be made.

Assumption 2 Markers do not affect the behavior or fate of the marked individuals.

If markers affect the behavior of the individual, then Assumption 1 is also violated because marked animals are not representative of the unmarked population of interest. Marker effects may be as obvious as a mortality caused by improper attachment of a radio transmitter [14] or increased depredation of nests discovered (marked) by the biologist [49], but subtle effects such as lower probability of pair formation must also be considered. One additional, general, assumption associated with the marking process is:

Assumption 3 Markers are not lost.

Assumptions 2 and 3 are important, but violations can often be accommodated. For example, closed models can be designed to reflect behavioral responses to capture and marking (trap-happy or trap-shy response). Marker loss creates negative bias in survival estimates and positive bias in abundance estimates, but loss rates can be estimated, if double marking techniques are used, and parameter estimates can be adjusted for bias [37]. However, analysis is much more elegant and parameter estimates are more precise if these assumptions are met.

The last set of general assumptions applies to the recapture process.

Assumption 4 Every marked animal alive in the population at time i has the same probability of capture.

Assumption 5 The fate of each marked animal is independent of the fate of other marked animals.

Assumption 6 Resampling is instantaneous; that is, birth, death, immigration and emigration do not occur during the resampling process.

These assumptions are sometimes collectively called independence of fates and identity of rates among individuals [26]. The first of these assumptions can be relaxed by defining several populations or by designing models with different capture probabilities for each member of the population. The effects of violating Assumption 5 (lack of independence) and Assumption 4 (heterogeneity) are collectively named overdispersion (*see* **Dispersion parameter**). Overdispersion produces an underestimate of variance for the population parameters, may affect model selection procedures, and (some have suggested) may bias parameter estimates; however, there is little evidence to support the last suggestion [1].

Instantaneous sampling is one of the most commonly violated assumptions, because we believe that some biologists fail to understand sampling designs. Instantaneous sounds highly restrictive, but this assumption is met if no births, deaths, immigration or emigration occur during the recapture occasion. Violation of this assumption results in heterogeneity; all members of the marked population do not have the same survival probability over the sampling occasions. For example, an individual seen on the first day of a three month sampling occasion and not seen during the rest of the sampling period must survive for three months longer than an individual seen on the last day of the sampling period [56]. Heterogeneity and overdispersion in general (heterogeneity and interdependence among marked individuals) like other assumptions can be diagnosed and corrected [67]. All samples will have some level of heterogeneity, unless you only mark one individual.

Violation of most assumptions is generally not deleterious, unless all of your markers fall off or if you kill every animal that you trap. However, adhering to model assumptions makes analysis much more straightforward, and understanding these assumptions will generally lead to more efficient data collection.

Known Fate Designs

The known fate designs have been used extensively in environmental and medical studies [12, 64]. As the name implies, these designs are used in settings where the fates of marked individuals are known past marking. For example, in medical applications patients are identifiable (marked) by name and perhaps social security number. After an initial hospital visit (capture) the fate of the patients may be monitored at prescribed intervals and the fate at each recapture occasion is recorded with certainty [62].

In environmental studies, known fate designs are most often applied to studies of animals marked with radio transmitters [5]. However, these designs are also commonly applied to studies of bird nests or young animals that are immobile and therefore have known fates [30, 49]. In each case, the investigator assumes that marked individuals are detected with a probability of 1.0 at each sampling occasion (but see [44]). Because detection probability is a known parameter, known fate designs are typically used to estimate only one parameter, true survival probability. True survival probability is the probability that an animal alive at occasion i survives between occasion i and occasion $i + 1$. We will describe the difference between true and apparent survival probability when we discuss *Cormark–Jolly–Seber (CJS) designs* [8].

Occasions for known fate designs are usually short, relative to the life-history of the study animal, because the location and fate of marked individuals are readily obtained. Therefore, the general assumption of instantaneous sampling is probably rarely violated; BIDE generally do not occur during sampling occasions. Intervals between occasions should be sufficient to allow forces of mortality to act, if the investigator is interested in estimating survival probability. At least one recapture occasion must be included in the design. As with most CR designs, marked individuals that enter the sample up to the penultimate recapture occasion can be used in the analysis. In known fate designs, this delayed entry is often called staggered entry [42].

The number of marked animals used in known fate designs is often lower than in other designs, particularly when radio transmitters are used as a marker, because transmitters are frequently more expensive than other marker types [64]. Despite relatively smaller samples of marked individuals, the precision of survival probability estimates may still be high with known fate designs because nuisance parameters such as detection probability are not estimated. Nonetheless, sampling variation is still present in estimates of true survival probability. Marked individuals are only a sample of the population of interest. In fact, a small sample (say 20) of individuals marked with transmitters may produce precise estimates of survival probability, but these estimates may be difficult to apply to the population of interest because the marked population represents only a small segment of the larger population. Therefore, we encourage scientists to consider carefully the desired scope of application when they are designing capture and marking procedures and identifying a sampling frame.

The sample size is also determined by the number of occasions included in the study. For long-term studies with high mortality, the sample of marked individuals should be augmented for the later occasions, because mortality will reduce the sample of marked animals and may lead to poor precision of the later survival probability estimates [5].

Scientists who use known fate models must be particularly sensitive about the potential impacts of markers on the fates of animals [33]. Several studies have demonstrated a negative impact of radio transmitters on the survival of the marked animals [15, 51]. Recaptures of marked individuals may also attract predators [49].

One additional assumption of known fate designs is that the censoring of marked individuals is independent of their fates [5]. Animals are removed from the sample if the fates of marked animals cannot be determined at a sampling occasion (right censored). If censoring is related to the fate of the marked animal, estimates of survival probability may be biased. If, for example, all censored transmitters are destroyed by the predator responsible for killing the marked bird, then survival estimates will be positively biased because estimates of survival probability will be based only on the animals with functioning transmitters. Frequent monitoring will aid in determining the fate of marked individuals and will therefore minimize the probability of violating this assumption.

Known fate designs have been generalized to account for cases where marked animals may be right censored because they emigrate from the sampling area [45]. This approach combines known fate and CJS designs. We will consider the advantages of combined designs in another section.

CJS Models

This family is probably the most commonly known of the CR sampling designs. The analytical techniques associated with this design were simultaneously and independently derived by Jolly [19] and Seber [53]. Estimable parameters from this basic design (an *unconditional Jolly–Seber design*) include apparent survival (ϕ), abundance (N) and births (B). When conditioning on the number of marked animals released, such that there is no attempt to model probability of first capture of unmarked individuals in the population, this conditional Jolly–Seber parameterization results in the ability to estimate apparent survival only (CJS model). Apparent survival probability is the probability that an animal alive at time i is still alive at time $i+1$, given that the animal has not permanently emigrated from the population. This conditional survival probability therefore differs from the true survival probability described under the known fate and band recovery model, because mortality and permanent emigration cannot be distinguished with this sampling design. We subsequently describe multistate models and combined models that can be used to separately and simultaneously estimate true survival probability and permanent and temporary emigration.

The theory and analysis approaches of CJS models are thoroughly described in [7], [25], [42] and [55]. We will examine the design elements of this CJS sampling scheme in our section on band-recovery models, but none of these publications develop design features in detail.

Bias in estimates of survival probability [11] is likely to be of minimal concern to an investigator employing unconditional Jolly–Seber designs; however, bias is likely to be negative in estimates of population size in the face of heterogeneity in capture probabilities [42]. A detailed set of simulations is presented in [42], in which the authors demonstrate the effect of population size, apparent survival rates, and capture probability upon coefficients of variation in the biologically relevant parameters under an unconditional Jolly–Seber design. From this discussion, and equations contained therein, an investigator can derive the precision likely to be obtained in the estimates of interest from a field study. The most salient feature to consider when using the unconditional Jolly–Seber design for parameter estimation is the concept of error propagation. Estimates of recruitment are obtained as functions of estimates of population size and apparent survival. Consequently, the precision of recruitment estimates will, by definition, be lower than the component estimates.

Closed Models

The motivation for closed model sampling of populations is the estimation of population size or population abundance. This parameter is denoted by N:

$$N = \frac{c}{p} \tag{1}$$

where c is the number of individuals detected and p is the probability of an individual being detected [35]. From this identity it is clear that abundance estimation is predicated exclusively on the ability to estimate this nuisance parameter p.

The assumptions associated with closed population models, in addition to those to described in our section on general assumptions, include an assumption that during the entire period during which sampling is conducted the population is both demographically and geographically closed [21, 40]. In other words, no individuals are allowed to be added to or subtracted from the population of interest.

In addition to this stringency of the closure assumption, a by-product of using closed designs is a relaxation of the general assumption of equal probabilities of capture of all individuals in our population at every sampling occasion. This assumption need not be strictly adhered to in closed population models, fundamentally because of the work of Burnham and Overton [6]. Models developed by these authors incorporate explicit estimation, and the recognition of individual heterogeneity (differences in capture probability among individuals) due to any of a host of factors is allowed to exist in their heterogeneous model.

The sampling considerations associated with closed designs include adherence to the closure assumption. Operationally this may be brought to bear by keeping the sampling intervals, the length of time that passes between sampling occasions, brief. This is intended to ensure that population size, the number of individuals in a population, will not change during the entire duration of the experiment. In addition to that, the sampling occasions should be as close to instantaneous as possible. If the closure assumption is violated in a closed sampling design, an investigator can use the unconditional Jolly–Seber analysis technique to produce the estimates of the parameter of the interests, namely abundance [42].

Issues associated with the specific mechanics of conducting a closed CR sampling study can be found in [63]. This report gives a detailed treatment of the subjects of laying out sampling plots, the size of sampling plots and the frequency of sampling of occasions. Sample sizes emanating from these types of design are a complex product of the number of traps, the number of occasions, the density of individuals and the density of traps. In addition to considerations presented in [63], detailed analytical solutions to sample size considerations necessary for a special case of closed population models known as the Lincoln–Peterson estimators are given in [48]. The reader who is interested in obtaining a first approximation to sampling intensity and sample sizes necessary to achieve desired levels of precision, is encouraged to consult [48] for a detailed explanation of their analytical solutions.

A novel design derived from the classical Lincoln–Petersen method for estimating abundance was put forward in [65]. This design differs from that discussed previously, in that recapture events take place visually, hence no marks are introduced into the population subsequent to the initial sampling event. This design can be employed in conjunction with telemetry studies of big game. A simulation study and associated software [66] offer the opportunity for investigators to explore design issues prior to initiation of field efforts.

Band Recovery or Exploitation Models

Banding models are extensions of the known fate models discussed previously. They are differentiated by two mechanistic distinctions. Known fate designs begin tracking the marked individuals immediately after application of the marks, whereas there is a passage of time between marking and resighting in banding models. This is because banding models employ the services of surrogate samplers, namely hunters, trappers or fisherman, to detect marks which can only be done (legally) during the harvest season. The classical reference for the description of banding models is [3], a revision of an original handbook published in 1975. Original work in this area was put forward in [54].

The traditional application of banding model designs is for exploited waterfowl populations. The life history characteristics of these species facilitate marking of individuals during the flightless period (molting) that occurs in late summer. Hunting seasons begin in the fall, approximately three months after the marking period. As we will see, there are numerous extensions and modifications to this basic sampling design that are used by countless employees of state and Federal natural resource management agencies.

The parameters associated with a banding design are true survival probability S, most often characterized on an annual basis (from marking occasion to marking occasion), and a nuisance parameter (denoted as f or r), defined as the probability of a marked animal being shot and recovered during the sampling period (e.g. hunting season). Hence, the survival probability estimated from banding models differs from that estimated with CJS models (see above) because the survival probability is true, rather than apparent. In the case of waterfowl that move throughout the continent in the course of a year, the marking location can be thousands of kilometers from the location where the individual was sampled by a hunter. Investigators contemplating the use of banding designs should recognize the geographical element of the sampling design.

These designs have also been employed in studies of fish populations sampled by anglers [69]. In this context, the geographical issue is resolved by having a closed volume of **lake** from which the marked population of fish is unable to disperse.

A nuance of this sampling design (temporal and possibly spatial segregation of marking and resighting occasions) is that mortality is assumed not to occur between the time of the application of the mark and the initiation of the exploitation season. Hence, all marks applied in the population are still viable at the beginning of exploitation.

In designing a banding study, the investigator has a number of points of intervention when implementing the study. Obviously, the number of marks and the number of deployments of marks are at the investigator's discretion. The number of periods (years) over which resighting/exploitation can occur can exceed the number of periods of mark application. By doing so, the detections of animals can be prolonged, and precision in survival rates can be enhanced. The cost of this is that survival and recovery rates cannot be separately estimated in the years following the termination of marking. However, the resighting/exploitation aspect of sampling can be less stringently influenced by the investigator, because the sampling is conducted by the hunting public. The nuisance parameter f or r is also defined by the probability that a hunter who retrieves a marked individual will report it to the authorities. Mathematically, the definition of recovery rate [3] is

$$f = H\lambda \tag{2}$$

where H is the harvest rate exerted by hunters and λ is the reporting rate. This reporting rate can be estimated [34], and can be influenced by solicitation by natural resource agency personnel. This is one manner in which an investigator can increase the sample size; and solicitation efforts do not induce bias in the estimate of survival rate. Although applications of marks are assumed to occur instantaneously, this assumption cannot be met. The effect of violation of this assumption is found to be minor [56].

An extensive numerical investigation of sample size calculations can be found in [68]. The investigator can explore the assessment of maximizing the precision of a single survival estimate, or maximizing the mean precision over a series of estimates.

Multistate Designs

The multistate models and designs are a generalization of the CJS approach, which are used to estimate geographical parameters [4]. Like CJS designs, capture probabilities and apparent survival probabilities are estimated. In special cases, where multistate designs include sampling of all possible 'states', true survival probability may be estimated. However, the unique feature of multistate designs is that multiple states are sampled and movements or transitions among these states are estimated. State definitions may include physiological or behavioral states, such as weight classes [36] or breeding and non-breeding states [10], geographical states [28, 57], and possibly combinations of states [39]; e.g. breeding and nonbreeding individuals in areas A and B. Individuals in each defined state must be sampled, at least three sampling occasions must be used, and occasions should be separated by an adequate amount of time to allow both deaths and movements among states to occur.

Capture and survival probabilities are defined by time- and state-specific characteristics; P_i^a is the probability that an individual in state a is captured at time i, and S_i^a is the probability that an individual in state a at time i survives between time i and time $i+1$, and exists in any state. In addition to the general CJS assumptions, these designs require the additional assumption that survival probability depends on the state at time i not the state at time $i+1$ [4]. This assumption may be violated if movements between states occur at the start of the interval between time i and time $i+1$. The effect of the violation of this assumption on the estimates produced from this design has been examined [17].

The new parameter estimated with multistate models is movement probability Ψ_i^{ab}, the conditional probability that an individual in state a at time $i-1$ is in state b at time i, given that it survives between time $i-1$ and time i. An individual may also remain in the same state between time $i-1$ and i (e.g. remain in state a, Ψ_i^{aa}). Movement probabilities are derived parameters resulting from the decomposition of transition probabilities ϕ^a, the product of movement and survival probability. This decomposition is valid, if the assumption about survival probability depending on the state at time i not the state at time $i+1$ is met [4].

The multistate models are data hungry and we encourage investigators to carefully consider their design prior to collecting any data. Using the simulation module in program MARK [67] may be a particularly productive exercise for design considerations. We encourage investigators to consider two particular aspects of design. First, if you expect that movement probabilities are low, then detection probabilities must be high to detect movements among states [57]. Distinguishing between no movement and low probabilities of movement will be challenging when detection probability is low and detected movements will be estimated with poor precision, because few moving individuals will be included in the sample. This is analogous to studying survival probability in a species with low mortality. If there is no mortality, then estimates of survival probability are undefined. Second, investigators must consider the number of states. Obviously, with more states, more potential movements must be sampled. However, more states also means additional capture and survival probability parameters. For example, with two states (*a* and *b*) and three time periods there are twelve identifiable parameters: S_1^a, S_2^a, S_1^b, S_2^b, p_2^a, p_3^a, p_2^b, p_3^b, ψ_2^{ab}, ψ_3^{ab}, ψ_2^{ba}, and ψ_3^{ba}, Only one movement probability is shown (e.g. ψ_2^{ab}) because the other parameter (e.g. ψ_2^{aa}) is obtained by subtraction ($\psi_2^{aa} + \psi_2^{ab} = 1.0$). With three states and three time periods the number of identifiable parameters doubles to 24. In comparison, the number of identifiable parameters in a design with two states and one additional sampling occasion (four total) is 18.

States may be combined after data collection and prior to analysis or as a constrained model in the analysis framework, if the data indicate that the more complex model would not be supported. We do not know of any ‘poststratification’ penalty for this approach, such as increased sampling variance. Nonetheless, combining states after data collection is inefficient and indicates that additional design effort is warranted.

Multistate designs have greatly increased the potential for quantitative studies of life-history theory, evolutionary ecology and geographical components of **population dynamics** [38, 39]. Their application is not limited to these areas, but we think these areas have been quantitatively neglected. However, data-based modeling requires sound data. These data hungry models will require careful design to produce meaningful estimates.

Combined Designs

An exciting and relatively new area of CR studies is a design that results from a combination of approaches that we have discussed. These combined designs offer two main benefits. First, additional data from separate designs may increase the precision of parameter estimates [2]. Second, combinations of designs may help identify new parameters [8, 29, 38].

The oldest combined design is the robust design model that combines a closed population and the CJS design [41]. This design, which includes a closed secondary sampling occasion within an open primary sampling occasion, was originally formulated to estimate parameters with higher precision and allow greater flexibility for modeling the sources of variation in capture probability. Recently, the robust design was generalized and used to estimate new parameters, notably completely random and Markovian temporary emigration [22, 23, 24, 38]. Thus, this combined design produces both the benefits discussed above.

Other combined designs include combinations of band-recovery and CJS designs [8]; robust design, CJS and band-recovery designs [29]; and designs which includes encounters of individuals outside the normal sampling framework [2]. All these designs allow identification of new parameters; the Barker designs are particularly useful for increasing the precision of parameter estimate. Perhaps, the designs we previously discussed can be considered simplifications of these more general combined designs. We anticipate that additional designs will be combined in the future.

Summary

You may have read this entry hoping that we would provide specific details about the number of animals that should be marked or guidelines for specific capture probabilities. When available, we have referred to material that offers some insights about these features of designs. However, given the range of information we have covered, this review was necessarily broad. Furthermore, recommendations for design features such as sample sizes require knowledge about the desired level of precision and possibly information about logistical or financial constraints. Therefore, detailed design advice is difficult to provide without additional information. We recommend that you use this review as a coarse level filter to decide which CR design is appropriate for your interest (Figure 1). After making this decision, we strongly urge you to investigate simulation modules that are components of various analysis software (e.g. the programs RELEASE and MARK [67]). Simulations can allow you to specify a range of scenarios and explore the details of a specific analysis (*see* **Simulation and Monte Carlo methods**).

Although parameter estimation is the primary goal of CR designs and analysis, this goal cannot

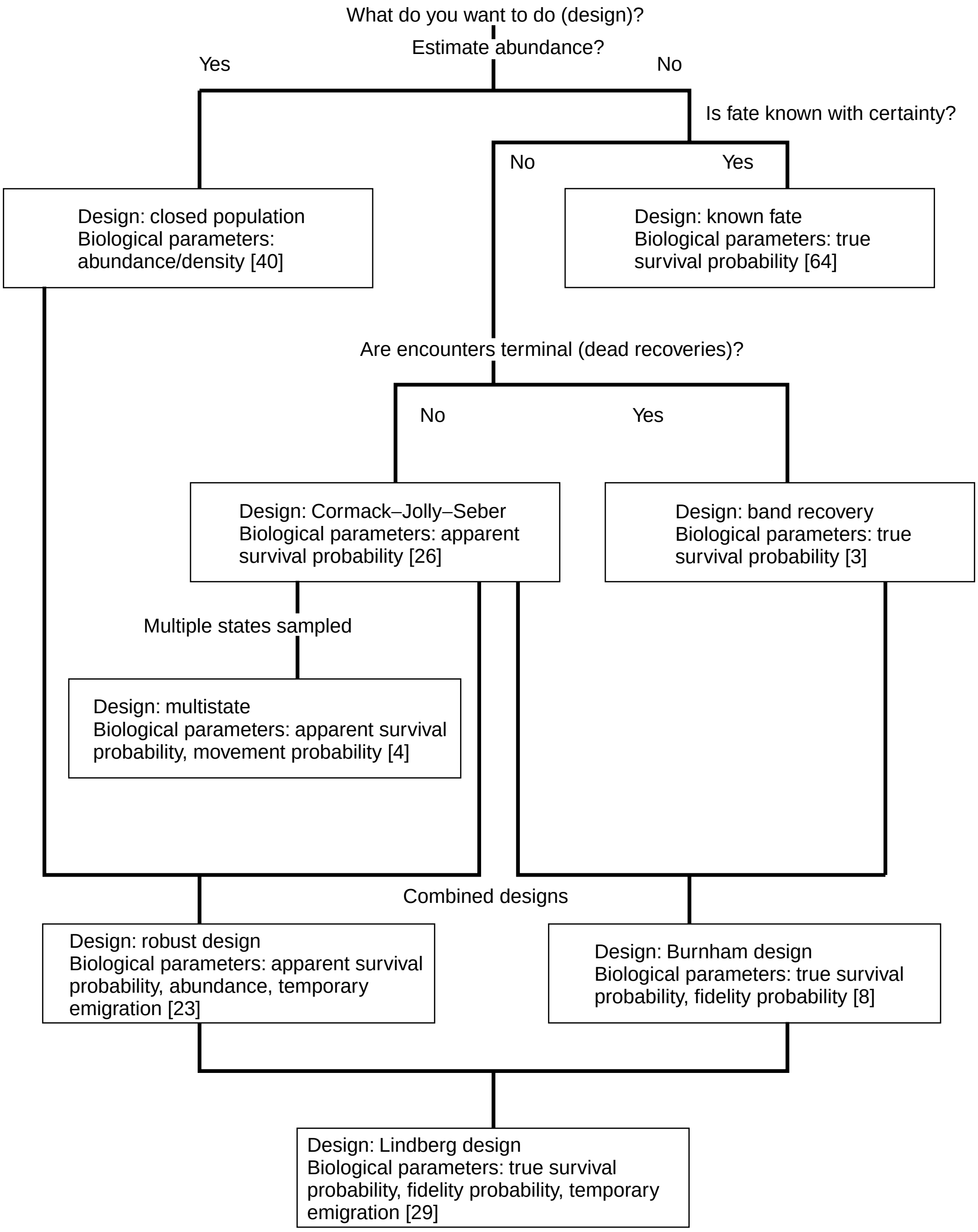

Figure 1 Stylized decision tree differentiating study designs described in this entry

be accomplished without designating and selecting from among competing models that are used for estimation [9]. A component of the design and simulation phase of the study should therefore include a priori designation of competing models and an evaluation of model selection uncertainty (*see* **Model uncertainty**).

CR designs and the associated modeling and estimation theory are well-founded principles for the study of animal populations. Inferences from

CR studies are data-based, and the inference quality (scope and strength) is therefore determined by the data collected. In this setting, the design phase of the study is essential for valid inferences. Problems with data quality cannot be resolved during analysis and these problems generally reflect poor design.

We anticipate that the use of CR designs and analysis will become more common because the need for rigorous information on a variety of species and issues seems virtually endless. We expect to see increased use of known fate designs as marking technology advances. We also think that these designs will be particularly useful in **biomonitoring** programs [47, 60], which have been identified as a major directive of a number of resource management agencies.

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(*See also* **Capture–recapture methods**; **Survival analysis**)

MARK LINDBERG & ERIC REXSTAD