

Making Great Leaps Forward: Accounting for Detectability in Herpetological Field Studies

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ABSTRACT.—Detecting individuals of amphibian and reptile species can be a daunting task. Detection can be hindered by various factors such as cryptic behavior, color patterns, or observer experience. These factors complicate the estimation of state variables of interest (e.g., abundance, occupancy, species richness) as well as the vital rates that induce changes in these state variables (e.g., survival probabilities for abundance; extinction probabilities for occupancy). Although ad hoc methods (e.g., counts uncorrected for detection, return rates) typically perform poorly in the face of no detection, they continue to be used extensively in various fields, including herpetology. However, formal approaches that estimate and account for the probability of detection, such as capture-mark-recapture (CMR) methods and distance sampling, are available. In this paper, we present classical approaches and recent advances in methods accounting for detectability that are particularly pertinent for herpetological data sets. Through examples, we illustrate the use of several methods, discuss their performance compared to that of ad hoc methods, and we suggest available software to perform these analyses. The methods we discuss control for imperfect detection and reduce bias in estimates of demographic parameters such as population size, survival, or, at other levels of biological organization, species occurrence. Among these methods, recently developed approaches that no longer require marked or resighted individuals should be particularly of interest to field herpetologists. We hope that our effort will encourage practitioners to implement some of the estimation methods presented herein instead of relying on ad hoc methods that make more limiting assumptions.

Data from field studies on amphibian and reptile populations or communities are typically reported as some form of count statistic reflecting population size, species presence/absence, or species richness. For instance, depending on the objectives and methods, statistics might include the number of Spotted Salamanders (*Ambystoma maculatum*) captured at a pond drift fence per unit of sampling effort (trap night), the total number of lizard species seen during a visual encounter survey in a forest quadrat, or the number of control and treatment sites where Green Frogs (*Rana clamitans*) were heard calling. In other cases, the number of previously marked individuals caught on a later occasion (i.e., a return rate) might be used as a measure of survival for that period. These count indices or return rates are then used in subsequent statistical analyses (e.g., ANOVA, linear regression) to evaluate patterns and test hypotheses of interest. Such approaches assume that

individuals or species are detected perfectly (i.e., the probability of detecting an individual or a species is 1), or that the probability of detection is constant. Such practices have been extensively criticized in the literature, because the assumption of perfect or constant detectability is seldom true (Preston, 1979; Nichols, 1992; Pollock et al., 2002; Williams et al., 2002).

Most field herpetologists will agree that many amphibians and reptiles are difficult to detect in their natural environments. Indeed, many species are nocturnal, have cryptic color patterns, live underground or in murky waters, and may be conspicuous only during certain times of the year or under particular weather conditions. In addition, detectability can depend on the sampling method selected, sampling effort, habitat type, as well as on the visual or aural acuity of the observers, their fatigue, experience, and motivation (Heyer et al., 1994; Bailey et al., 2004a). Thus, evaluating the size of a population of a target species, survival probability, or the total number of species present within a study area requires more sophisticated approaches than simple count-based indices.

In a population study, the expected value of the total number of individuals counted ($C =$ total number of individuals observed, heard,

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captured, etc.) during a sampling period is given by the product of the probability of detection (P) and the true unknown total number of individuals (N) in the population, such that $E(C) = PN$ (Otis et al., 1978; Nichols, 1992; Anderson, 2001; Williams et al., 2002). To illustrate, consider that during the sampling of a forest quadrat an investigator encounters 40 Red-Backed Salamanders (*Plethodon cinereus*). This means that $PN = 40$, or $N = 40/P$. Without any knowledge of the probability of detection, it becomes impossible to estimate N : there are an infinite number of combinations of PN yielding 40 (e.g., 0.1×400 , 0.25×160 , 0.5×80 , 1×40). We know that at least 40 individuals occur in the quadrat (i.e., salamanders detected by the investigator), but all we can conclude about population size is that $N \geq 40$ unless we estimate P . One quickly realizes the magnitude of the problem and potential repercussions on the assessment of population size and trends. Such issues are apparent in the evaluation of global amphibian declines (Houlahan et al., 2000; Alford et al., 2001; Green, 2003; Schmidt, 2004). Imperfect detectability also extends to the estimation of survival, the number of species present at a site, or the number of sites occupied by a species of interest.

In an attempt to mitigate the confounding effects of detectability, investigators have attempted to standardize methods or sampling conditions (Heyer et al., 1994; Pollock et al., 2002; Anderson, 2001, 2003), but it remains difficult to account for, or even identify, all possible factors influencing detection (e.g., observer hearing or visual acuity, animal behavior, weather conditions). Fortunately, a number of statistical approaches have been developed to estimate the probability of detection from single-site population studies to community level studies over large scales. However, these methods are not widely used by the herpetological community, and most herpetological papers from field surveys are still based on some form of count statistic or return rate uncorrected for the probability of detection. Here, we review methods for estimating detection probability that may appeal to a wide audience, ranging from the undergraduate student to the seasoned field researcher conducting herpetological fieldwork.

We begin by introducing model selection and related concepts that are used throughout this paper. The rest of the paper is divided in two major sections. In the first part, we review methods that are used to estimate abundance and some of the vital rates that influence abundance (i.e., survival and movement probabilities) when individuals are captured or resighted. For the second part, we shift our

focus to techniques where individuals are not captured or resighted, often conducted at larger spatial scales where it is either impractical or impossible to individually mark animals. Here, the interest may be to estimate the proportion of sites occupied by a species, abundance, or the probability that a species will go extinct at a site. Throughout this paper, we use real herpetological data sets to illustrate the use and interpretation of these methods. We also provide Appendix 1 detailing existing software that allows practitioners to implement the methods mentioned herein, as well as formally test some of their assumptions.

MODEL SELECTION

In many examples featured in this paper, we use model selection strategies and inference based on the second-order Akaike Information Criterion, or AIC_c (Akaike, 1973; Hurvich and Tsai, 1989; Burnham and Anderson, 2002). This framework consists of specifying, a priori, potential models explaining the process of interest and selecting models that fit the data well with a minimum number of variables (i.e., a trade-off between bias and variance). Among the advantages of this approach, one can directly weigh the evidence in favor of a model, given the set of candidate models, using Akaike weights (w_i) (Burnham and Anderson, 2002). For instance, for a given data set, a model with an Akaike weight of 0.5 has four times the support of a model with an Akaike weight of 0.125 ($0.5/0.125 = 4$): such comparisons are termed "evidence ratios." In cases where several models have similar weight, one can base inferences on the whole set of candidate models, a procedure called model averaging or multimodel inference (Buckland et al., 1997; Burnham and Anderson, 2002). This consists of using the information available (e.g., estimate of a parameter of interest, predicted value) from the whole set of models to compute a mean weighted by the Akaike weight of each model. For more details on the use of the AIC_c and multimodel inference in herpetology, consult Mazerolle (2006).

PART I: ESTIMATING ABUNDANCE AND ASSOCIATED VITAL RATES WHEN INDIVIDUALS ARE CAPTURED OR RESIGHTED

In this section, we present methods to estimate abundance and associated vital rates of a population, while accounting for detectability, when individuals are captured or resighted. We present three classes of capture-mark-recapture (CMR) models: closed-population, open-population, and robust design mod-

els. Closed population models focus on estimating abundance where the target population is sampled over a short time period during which no births, deaths, immigrations, or emigrations occur. In contrast, open population models typically focus on demographic rates such as survival and involve studies over longer time periods where birth, death, immigration, or emigration can occur. The third class, robust design, is a mixture of open and closed population models.

CLOSED POPULATIONS MODELS: ABUNDANCE

Closed population estimators have been developed for different study designs (Otis et al., 1978; Williams et al., 2002). Well-known estimators like the Lincoln-Petersen (Lincoln, 1930) only require two sampling occasions. However, three or more sampling occasions (t) permit more flexible modeling and are highly recommended. Individuals are normally captured, marked and released to be recaptured or resighted on a later occasion. Alternatively, individuals may be removed from the population following initial capture (removal or depletion methods: Otis et al., 1978; White et al., 1982). At the end of the study, one can generate a capture history for each individual with a series of ones and zeros to indicate whether the individual was seen on each occasion. For instance, we see from a history of "101" that the individual was captured on the first and third occasion but not on the second occasion. The combination of these types of data with various closed-population models allows one to estimate population size (N) and capture probabilities (P).

Assumptions.—Assumptions of the closed-population models include the following: (1) No births, deaths, immigration, or emigration during the sampling interval (the closure assumption); (2) All individuals are equally likely to be captured within each sample (equal capture probability) and no animal has probability of capture equal to zero, $P \neq 0$; (3) Marks are not lost or overlooked by the observer, and all marks are recorded correctly.

Numerous models have been developed to relax assumption 2; the most widely applied are those included in program CAPTURE (Appendix 1). However, researchers are in no way limited to these models (Pledger, 2000; White, 2005; Conn et al., 2006). Collectively, closed-population models allow detection (i.e., capture) to vary with time (t), behavioral (or trap) response (b), and heterogeneity (h). Here, heterogeneity implies that capture probabilities vary among individuals in a manner not readily explained by potential individual covariates.

When variation among individuals is associated with factors such as species type, body size class, or sex, stratified analyses can be used (i.e., analysis by groups). If covariates are measured on each individual (e.g., mass, length), one can include the effect of these covariates on capture probability with the conditional likelihood (conditional on individuals observed) models of Huggins (1989, 1991) and Alho (1990). In this specific case, abundance is not itself a parameter in the model but is computed as a derived parameter, based on the estimated capture probability.

Example.—Bailey et al.'s (2004b,c,d) study on terrestrial salamanders compared a variety of population estimation methods. The data were collected over a three-year period at several sites within Great Smoky Mountains National Park, where salamanders of multiple species over 18-mm snout-vent length (SVL) were individually marked using fluorescent elastomer (Bailey et al., 2004b). For illustrative purposes, we analyze a small subset of their data, consisting of two species (*Plethodon serratus* and *Plethodon glutinosus* complex) from one site in 1999. In this example, a CMR study was conducted over four consecutive days, followed immediately by a temporary removal study where the site was visited every other day for eight days (resulting in four removal occasions: captured individuals were held during the eight days, then released, Bailey et al., 2004d). The species were treated as groups in the analysis; hence, abundance was estimated for each species. Including the species in a common analysis allowed us to share information across the species, which provides greater statistical efficiency (i.e., better precision of the estimates).

We used the free software Program MARK 4.2 (Appendix 1) to estimate population size with data collected during the four consecutive visits using four models: M_o (constant capture probability), M_b (behavioural response), M_t (time variation), $M_{species}$ (variation among species). Huggins-Alho conditional closed-capture models were used. We then compared the model-averaged population estimates to estimates from the subsequent removal study. Removal study estimates were obtained with the variable probability removal estimator (M_{bh} , Pollock et al., 1990) of program CAPTURE (Appendix 1). Finally, we report a simple Lincoln-Petersen (two-sample M_t ; Lincoln, 1930) estimate obtained by condensing captures from the mark-recapture study, collectively considering them a single initial sample, then using the removal study as a single "recapture occasion."

Results.—Model selection results from the CMR analyses indicated slightly higher support for a model with species-specific detection

TABLE 1. Model selection results from analysis of mark-recapture closed-population of *Plethodon serratus* and *Plethodon glutinosus* complex at one site in Great Smoky Mountains National Park during 1999.

Model ^a	Number of parameters (<i>K</i>)	AIC_c	ΔAIC_c	Akaike weight (w_i)
$M_{species}$	2	97.74	0.00	0.51
M_o	1	98.19	0.46	0.41
M_t	4	101.47	3.74	0.08

^a Behavioral model (M_t) was fit to the data, but the model did not converge.

probabilities compared to the constant detection model, but there was considerable model selection uncertainty (Table 1). The evidence ratio with the second-ranked model (0.51/0.41 = 1.24) does not give clear evidence that the $M_{species}$ model is the "best" model; thus, all models are included in a model-averaged estimate of population size. The population estimate (for both species combined) from the removal study was lower than either the model-averaged estimate or the Lincoln-Petersen estimate (Table 2), a common finding by Bailey et al. (2004d).

Discussion.—The assumption of equal detection probability across time, space, and individuals is unlikely to hold for most amphibian and reptile species. Modern closed-population models offer researchers a variety of options for relaxing this assumption and combining data to better estimate p (White, 2005; Conn et al., 2006). In the example presented here, there is considerable uncertainty in the factors that contribute to variation in detection probability for a population of terrestrial salamanders consisting of two species. The removal population estimate was somewhat lower than the model-averaged four-occasion CMR estimate or the Lincoln-Petersen estimate, which are both robust to temporal variation. Ignoring heterogeneity leads to underestimates in population size, whereas ignoring model selection uncertainty may also lead to an overstatement of the precision of population estimates (see Table 2).

For further examples of closed mark-recapture population estimation in herpetofaunal populations, see Jung et al. (2000, 2002, 2005), Fogarty and Vilella (2003), Funk et al. (2003), and Nelson et al. (2002). Removal methods have been used by Bruce (1995), Salvidio (1998), Petranka and Murray (2001), and Jung et al. (2002).

Other Approaches Related to Sampling Closed Populations.—Other designs can also account for detectability and estimate abundance, namely double sampling methods with independent or dependent observers. The independent observer method consists of two observers (observers

TABLE 2. Estimates, standard errors, and 95% confidence intervals of terrestrial salamander population size (\hat{N}) from capture-recapture and removal models conducted at one site in Great Smoky Mountains National Park during 1999.

	\hat{N}	SE(\hat{N})	95% CI
Closed-population (model averaged)	74	50.40	(24, 172)
Removal M_{bh}	29	8.76	(24, 68)
Lincoln-Petersen	63	12.61	(38, 87)

1 and 2) counting animals (or objects) independently within a very short time period so that the population can be considered closed (Williams et al., 2002; Moore et al., 2004). To implement this method, we must identify the individuals observed only by observer 1, only by observer 2, and the individuals detected by both observers. The method can be extended to more than two observers and analyzed with the closed models presented above (Nichols et al., 1986). This method could be potentially useful to estimate the number of alligator nests or salamander burrows, where each observer would take the position of each object of interest with a global positioning system (GPS) receiver.

In a dependent observer study, data are recorded differently. Observer 1 indicates to observer 2 each time an animal is sighted, whereas observer 2 notes all animals seen by observer 1 as well as any individual missed by observer 1; observers switch roles halfway through the survey (Cook and Jacobson, 1979; Nichols et al., 2000). Software is also available to analyze such data (Appendix 1). Implementations of this method in herpetology include Jung et al. (2002) and Grant et al. (2005).

Another alternative consists of estimating detectability and abundance from a marked subpopulation (Williams et al., 2002). Here, the idea is to capture, mark, and release individuals during an initial sampling effort and then conduct one or more surveys without physically capturing individuals shortly after initial release (to respect the closure assumption). For instance, one could batch mark (e.g., by immersion in a solution of neutral red dye) tadpoles captured at a pond during a single capture event, release the individuals back into the pond, and then survey the pond a few hours later by snorkeling to record the number of marked individuals resighted. This is a special case of the Lincoln-Petersen estimator. For multiple resighting occasions, a program exists to implement different estimators for such studies (Appendix 1).

OPEN POPULATION MODELS: SURVIVAL ESTIMATION

The Jolly-Seber model is the basic open population capture-recapture model (Jolly, 1965; Seber, 1965). The study design appropriate for using this model consists of capturing, marking, and releasing individuals during three or more time periods t (i.e., capture occasions). Each time period is separated by an interval during which individuals are subject to mortality and during which new individuals may be recruited into the population. The original parameterization of this model allowed for estimation of population size at each time period, as well as recruitment, survival, and detection probabilities. Multiple alternative parameterizations of the Jolly-Seber model have been developed, both to allow for estimation of additional parameters (including, in various cases, recruitment, seniority, population growth rate, and super-population size) and also to allow for improved properties for model estimation (see Discussion below).

A familiar simplified form of the Jolly-Seber model is the "deaths-only" model, known as the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965). Model parameters include apparent survival probabilities (ϕ) and capture probabilities (P). Here, apparent survival refers to the probability that an individual alive at time t survives to time $t + 1$ and does not permanently emigrate out of the study area. In other words, mortality and permanent emigration are confounded in the CJS model (see assumption 2, below).

Assumptions.—Assumptions of the CJS model include the following: (1) Individuals are homogeneous in their survival and detection probabilities; (2) There is no emigration from the study area, or a relaxed form of Assumption (2) is that all emigration is permanent; (3) Samples are instantaneous, and animals are released immediately after sampling; (4) Marks are not lost, and all marks are correctly read.

When ad hoc methods (e.g., return rates) which do not account for detection < 1 are used to estimate survival, they produce only a minimum estimate of survival (for a useful discussion, see Schmidt et al., 2002). These methods produce valid estimates of survival only if assumptions 2 through 4 hold, in addition to the strong assumption that detection probabilities are equal to 1.

Example.—Frequently, in addition to estimating survival probabilities, investigators are interested in answering questions about the factors that influence survival. These may include group variables (e.g., sex, site), environmental variables (e.g., rainfall, human disturbance), or variables at the individual level

TABLE 3. Model selection results from analysis of apparent survival rates (ϕ) of Ornate Box Turtles captured at a drift fence in western Nebraska over a 20-yr period. Note that DcJanMN stands for minimum winter temperature.

Model ^a	Number of parameters (K)	AIC _c	Δ AIC _c	Akaike weight (w_i)
ϕ (Sex · DcJanMN) $P(t)$	15	650.99	0.00	0.51
ϕ (Sex + DcJanMN) $P(t)$	14	651.08	0.09	0.49

^aIn both models an additional variable was used, as in Converse et al. (2005), to avoid biasing results caused by temporary emigration but is omitted from the model names here for brevity. See that paper for more discussion of the variable.

(e.g., size, physiological condition). Lebreton et al. (1992) provided a basic framework for addressing questions of this kind within mark-recapture models.

Converse et al. (2005) presented such an analysis for Ornate Box Turtles (*Terrapene ornata ornata*). The data were collected over a 20-yr period at a drift fence in western Nebraska maintained primarily for a study of Yellow Mud Turtles (*Kinosternon flavescens*; Iverson, 1991). Here, for illustrative purposes, we present an extension of the analysis by Converse et al. (2005), in which we examine whether an important interaction exists between sex and minimum winter temperature (DcJanMN; estimated as the minimum temperature over the months December and January), that is, whether male and female survival are related in substantially different ways to minimum winter temperature.

We used the free software Program MARK 4.2 (Appendix 1) for the analysis. We proposed two models of apparent survival, one with an interaction between sex and DcJanMN— ϕ (Sex · DcJanMN)—and one without— ϕ (Sex + DcJanMN). In both cases, detection probabilities were allowed to vary across sampling year t , designated as $P(t)$. We used model selection procedures implemented directly in Program MARK, to make inference about the biological question of interest (Burnham and Anderson, 2002).

Results.—Model selection results indicated only slightly higher support for the model with an interaction between survival and DcJanMN than for the model without an interaction term (Table 3). In this example, the evidence ratio of Akaike weights ($0.51/0.49 = 1.04$) is not convincing that the model with the interaction term is a definitively better model of apparent survival than the model without. Figure 1

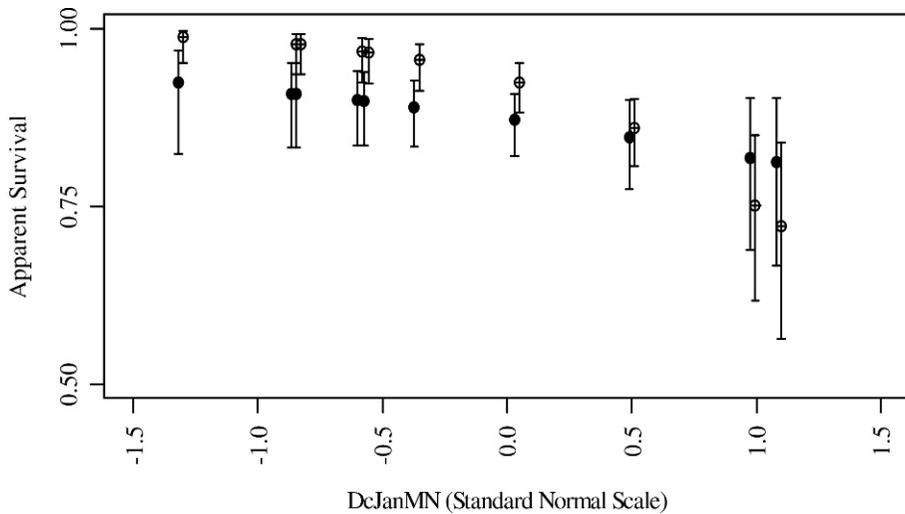


FIG. 1. Apparent survival estimates for male (closed circles) and female (open circles) Ornate Box Turtles as a function of minimum winter temperature, presented on a standard normal scale. Estimates are based on a model of apparent survival with an interaction term between sex and minimum winter temperature (DcJanMN). Predicted survival rates are equal for the two sexes when temperatures are slightly more than 0.5 standard deviations above the mean. However, model selection results indicate that the estimated interaction between sex and DcJanMN is not a strong effect. (Converse et al., 2005).

illustrates the relationship between estimated apparent survival and minimum winter temperature for the model with the interaction term.

Discussion.—Converse et al. (2005) speculated that the observed negative relationship between estimated apparent survival and minimum winter temperature was caused by rapid depletion of lipid reserves caused by higher metabolic rates in warm winters. The results presented here indicate that female survival may be slightly more sensitive than male survival to this effect. However, the evidence for higher sensitivity in females is not strong.

The analysis presented in Converse et al. (2005) also suggested that the data violated assumption 2 (i.e., temporary emigration was occurring). This was diagnosed because estimates of survival dropped substantially in the last time interval (Converse et al., 2005). If indeed temporary emigration was prominent in these data, the phenomenon can be dealt with in several ways, most effectively through design (see Robust Design below).

Alternative parameterizations and extensions of the Jolly-Seber model include the works of Pradel (1996), Pradel et al. (1997), Schwarz and Arnason (1996), and Link and Barker (2005). These models enable the estimation of additional parameters such as abundance, seniority, recruitment, transience, and population growth rate. However, these additional parameters come at the price of more restrictive assump-

tions than the CJS model. Readers should consult the cited sources for more information.

For further examples of applications of the CJS model to estimate survival in herpetofaunal populations, see Woodward et al. (1987), Flatt et al. (1997), Schmidt and Anholt (1999), Hohenweg Peter (2001), Kazmaier et al. (2001), Diller and Wallace (2002), Schmidt et al. (2002), Anholt et al. (2003), Bjorndal et al. (2003), Hokit and Branch (2003), Retallick et al. (2004), Altwegg et al. (2005), Lind et al. (2005), Scherer et al. (2005), and Schmidt et al. (2005).

MULTISTATE POPULATION MODELS AND THE ROBUST DESIGN

In the CJS open population model described above, it is assumed that each animal within a predefined group (e.g., sex class) is subject to the same probabilities of survival and capture. However, in many cases, these assumptions are severely compromised. For example, terrestrial salamanders spend considerable time underground. Pond-breeding amphibians and nesting sea turtles might disperse to other breeding locations or skip breeding altogether. Metamorphs become unavailable for capture, until they become reproductively active and return to breeding sites. Ignoring these issues will often bias estimates of survival. Furthermore, variation in vital rates among these life stages, as well as probabilities of movement or transition between stages, are often of interest for testing

hypotheses about life history or constructing population models.

Multistate mark-recapture models (MSMR, Arnason, 1973; Brownie et al., 1993; Schwarz et al., 1993) allow investigators to account for multiple locations or life stages (see Lebreton and Pradel, 2002; Kendall, 2004). For example, a study of both breeding and nonbreeding amphibians associated with two different ponds might be viewed as consisting of four states (breeders in pond 1, nonbreeders affiliated with pond 1, and the same for pond 2). Under this class of models, parameters consist of survival and capture probabilities for each state and probabilities of transition between states (e.g., from breeder to nonbreeder, or from pond 1 to pond 2). Assumption 1 of the CJS model is modified to assume that within each state there is no undescribed heterogeneity in apparent survival and capture probabilities. Apparent survival under these models means an animal survives and does not permanently emigrate from the collection of monitored states.

In many herpetological studies, temporary emigration from the study area(s) causes complications, violating assumption 2 of the CJS model (see above). For many herpetofaunal populations, it is impractical to reasonably sample intermediate life stages, nonbreeders, or individuals that are skipping a breeding season (Kendall and Bjorkland, 2001; Bailey et al., 2004e; Dutton et al., 2005) or those that disperse temporarily to breeding sites outside the study area (Rivalan et al., 2005). Multistate models can account for these emigrants by defining one or more unobservable states, for which detection probability is zero (see Kendall and Nichols, 2002; Schaub et al., 2004). However, information on unobservable states must be derived indirectly; thus, in most cases some supplemental information (e.g., satellite telemetry) is required to estimate parameters in a robust way (Kendall, 2004). Alternatively, unobservable states such as skipped breeding or temporary emigration can be accounted for indirectly by employing some version of the robust design (e.g., Pollock, 1982; Williams et al., 2002). This framework consists of partitioning each primary sampling period of interest into multiple secondary sampling periods, where it is assumed that the state of the animal is maintained over all secondary samples. We will briefly describe three versions of this design, each with different assumptions about the capture process within a season (primary period), that are pertinent to herpetofaunal populations.

Pollock's Robust Design.—The original version of the robust design (Pollock, 1982) assumes that, for the duration of the sampling effort

within a given primary period, the population of interest is closed to additions and subtractions (i.e., no births, immigrants, deaths, or emigrants). The idea, as applied by Bailey et al. (2004d), is to nest a series of closed population model analyses, one for each primary period, within an open population analysis based on either the CJS or multistate models. The potential advantages are the ability to estimate more parameters of interest, with better precision, and where temporary emigration occurs, the ability to estimate survival with less bias and movement probabilities that are time-specific. Finally, Kendall (1999) showed that this model structure is robust even when certain types of violations of the closure assumption occur within primary periods (e.g., losses such as emigration or death).

Open Robust Design.—The function and modeling advantages of the open robust design (Schwarz and Stobo, 1997; Kendall and Bjorkland, 2001) are similar to those of Pollock's closed robust design. In this case, however, closure within a season is not assumed; hence, modeling of capture probability is not as flexible as with closed models. Instead, animals are assumed to arrive and depart the study area in a staggered fashion during sampling. In other words, arrival and departure times for individuals within a primary period are variable. The assumption of demographic closure still holds (i.e., no births or deaths). We then model arrival, detection, and departure within each season, in addition to between-season parameters. Kendall and Bjorkland (2001) and Dutton et al. (2005) applied this model to nesting sea turtles.

Gateway Robust Design.—Bailey et al. (2004e) developed the gateway robust design for the case of pond-breeding salamanders, where breeders are captured at drift fences as they arrive and depart from a breeding pond. All captured individuals are breeders; therefore, the assumption of a static state described above is satisfied. In this case, however, mortality between entry and exit is permitted and modeled. Church et al. (2007) applied this type of model to the case of a metapopulation based on breeding ponds, where each pond has a breeding and nonbreeding component.

Example.—Table 4 shows estimates of annual survival for adult female Sea Turtles (*Eretmochelys imbricata*) and the probability a nonnester from the previous year nests in the current year for years 1987–1996. These results are for a nesting population of 22–45 females on Long Island, Antigua (Richardson et al., 1999; Kendall and Nichols, 2002). One set of estimates was computed (with program MARK) using multistate models under the open robust design, while the pooled estimates ignore multiple

TABLE 4. Estimates of survival and breeding probabilities for Hawksbill Sea Turtles (*Eretmochelys imbricata*) tagged at Long Island, Antigua, 1987–1996, from a multistate capture-recapture model, either using or ignoring detailed capture histories within a year.

Parameter	Estimate (SE)	
	Open robust design	Pooled within year
Survival	0.95 (0.013)	0.94 (0.015)
Breeding Prob. 1989	0.80 (0.10)	0.80 (0.16)
Breeding Prob. 1990	0.40 (0.08)	0.40 (0.17)
Breeding Prob. 1991	0.60 (0.08)	0.58 (0.14)
Breeding Prob. 1992	0.68 (0.09)	0.66 (0.17)
Breeding Prob. 1993	0.49 (0.08)	0.49 (0.19)
Breeding Prob. 1994	0.46 (0.08)	0.45 (0.17)
Breeding Prob. 1995	0.61 (0.09)	0.59 (0.21)
Breeding Prob. 1996	0.34 (0.08)	0.34 (0.09)

within-year captures and are consistent with the standard CJS model structure presented in the previous section. Notice the great improvement in precision (i.e., SE's) by incorporating within-year information.

Discussion.—Interesting phenomena, such as temporary emigration (sometimes corresponding to nonbreeding) and arrival and departure at a study area, generate problems in classic models, such as the CJS model. Multistate and robust design models are formidable tools to deal with such scenarios and provide a means to investigate these important life history processes. We believe that herpetologists will benefit by including them in their data analysis arsenal. Readers may consult Wood et al. (1998), Blomberg and Shine (2001), Lowe (2003), and Frétey et al. (2004) for applications of some of the models discussed in this section. Several programs are available to implement multistate and robust design models (Appendix 1).

PART II: ESTIMATING SPECIES PRESENCE, ABUNDANCE, AND ASSOCIATED VITAL RATES WHEN INDIVIDUALS ARE NOT CAPTURED OR RESIGHTED

Marking and recapturing individuals over a large collection of sites is logistically difficult. In this section, we focus on the estimation of species presence, abundance, and vital rates when individuals are not necessarily captured or resighted. The first approach we describe deals with estimating the probability of occupancy (i.e., presence) of a given species over a collection of sites. Then, we present techniques to deal with call indices. The last part deals with two methods of estimating abundance, namely point count and distance sampling techniques.

SITE OCCUPANCY MODELS

In some cases, interest shifts from the number of individuals of a given species in a population at a single site to the number of populations of the species within a larger area or collection of sites. For this purpose, one investigates the patterns of species presence across sites. A site is certainly "occupied" if the species is detected at that site, but failure to detect a species during all sampling occasions does not necessarily imply the species is absent (e.g., see Weir et al., 2005). To address such problems, site occupancy models are an appealing tool as they simultaneously estimate the probabilities of detection (P) and occupancy (ψ) (MacKenzie et al., 2002, 2006; Gu and Swihart, 2004). This type of analysis is analogous to closed populations models that estimate the number of individuals, except that in the site occupancy problem, the site is the sampling unit and the total number of sites sampled is known (MacKenzie et al. 2002). Also note that here, P represents the probability of detecting the species at a site conditional on its presence at that site during the survey. Typical data in the site occupancy framework consist of repeated surveys at a collection of sites, such as anuran call surveys conducted at breeding sites, dipnetting for overwintering tadpoles in ponds, or observing lizards in forest quadrats.

We start with cases where one conducts multiple visits (at least two) to a set of sample sites (for guidelines on study design, see MacKenzie et al. 2002, 2006; MacKenzie and Royle, 2005). Here, a visit could consist of a call survey on a given night at a given site. One either detects or does not detect the species during the sampling visit. Thus, following T visits at a set of N sites, we can generate a detection history consisting of ones (detections) and zeros (no detections) for each site.

Assumptions.—Assumptions of site occupancy models are analogous to those for closed populations: (1) The occupancy state of the sites is static during the period over which surveys are conducted. This means that no local extinctions or colonizations occur between the first and last sampling visit. This assumption can be relaxed if movements in or out of the sites are random. (2) The probability of occupancy is the same for all sites. (3) The probability of detecting the species in a survey, given it is present, is the same for all sites. (4) Within each site, detection of the species in each survey is independent of detections during other surveys.

Typically, what constitutes a suitably "closed" period (Assumption 1) depends on the organism in question: for amphibians, this could be a single breeding season or wintering

TABLE 5. Model selection results from site occupancy analysis of Green Frogs at 34 bog ponds in eastern New Brunswick, Canada over five sampling visits during 2000. Models used to estimate occupancy (ψ) and detection (P) included covariates of distance to closest pond (Distpond), air temperature (Airtemp), and search effort (Effort).

Models	Number of parameters (K)	AIC _c	Δ AIC _c	Akaike weight (w_i)
ψ (Distpond) P (Airtemp)	4	141.87	0	0.61
ψ (.) P (Airtemp)	3	142.79	0.92	0.39
ψ (Distpond) P (Effort)	4	161.30	19.43	0.00
ψ (Distpond) P (.)	3	161.88	20.01	0.00
ψ (.) P (Effort)	3	161.93	20.06	0.00
ψ (.) P (.)	2	163.19	21.31	0.00

period. We can relax assumptions 2 and 3 by allowing occupancy and detection to be modeled as functions of covariates. Covariates on occupancy (ψ) have to be constant through time because the occupancy status is constant, or closed, over all surveys. Covariates on P can be either constant or vary through time (i.e., sampling occasions). Sites with no detections are still visited and a value for the covariate(s) is collected, whereas in capture-recapture models, we do not know the value of a covariate for an animal that was never captured (Otis et al., 1978; MacKenzie et al., 2006).

Example.—To illustrate the use of site occupancy models, we analyzed patterns of Green Frog (*Rana clamitans*) occupancy in 34 acidic bog ponds in eastern New Brunswick, Canada, searched on five occasions with visual and call surveys during a single breeding season in 2000 (data adapted from Mazerolle et al., 2005). For simplicity, we considered models with distance to the closest pond as a possible covariate for ψ and air temperature as potentially influencing P . We contrasted these models with models that assume constant occupancy and detection.

The analysis, run in program PRESENCE (Appendix 1), indicated moderate support ($w_i = 0.61$) for the model consisting of an effect of distance to the closest pond on Green Frog occupancy and air temperature on the probability of detection (Table 5). This model was followed closely ($w_i = 0.39$) by the one with constant occupancy probability across all sites, and detectability varying with air temperature (Table 5). Following model-averaging, an estimated $61.6 \pm 10.6\%$ (estimate \pm SE) of sites were occupied by Green Frogs. In contrast, the naive estimate (based on the number of ponds where Green Frogs were detected) indicated that only 52.9% of ponds were occupied, thereby underestimating the probability of

occupancy. Occupancy marginally increased as the distance to neighboring ponds decreased ($Beta_{Distpond}$: -0.893 , 95% CI: -1.982 , 0.197). Green frog detectability increased with temperature ($Beta_{Airtemp}$: 1.307 , 95% CI: 0.634 , 1.980).

Discussion.—Site occupancy analyses are rapidly gaining attention. For some additional examples of their use in herpetology, see Schmidt (2004, 2005), Pellet and Schmidt (2005), and Smith et al. (2006). A number of extensions to the single season model have been developed with a wide array of applications. For instance, Royle and Link (2006) developed models where the species can be wrongly identified as present when it is absent from the site (e.g., for cases where volunteers in a monitoring program have variable experience). We mention other modifications to the classic single season model below.

Applications to Species Richness Estimation.—MacKenzie et al. (2006) suggest using site occupancy analyses to estimate the fraction of a species list present at a site in a single season. This approach shows promise in species-rich regions such as the tropics in cases where a list of the species occurring in the area already exists. In this framework, one records whether each species on the list has been detected during each sampling visit at a single study site. In comparison with the classic site occupancy design, here, the species become the “sites,” and ψ now represents the fraction of species present at the site. In other words, each species has a detection history at this single study site. One can include covariates on detection for each species, such as body size or habitat specialization. In other instances, investigators may wish to estimate species richness at several sites. To address this issue, Dorazio and Royle (2005), Dorazio et al. (2006), and Royle et al. (2007) have developed animal community models by specifying species-specific models of occurrence.

Multiple Season Models.—MacKenzie et al. (2003) have extended the single-season model to multiple seasons using Pollock’s robust design (see multistate population models above): sites are demographically closed during seasons (no colonizations or extinctions) but open between sampling seasons conducted over multiple years. In addition to occupancy and detection probabilities, these models allow the estimation of extinction and colonization parameters, and one quickly realizes their value to draw inferences about metapopulation dynamics over large spatial and temporal scales. Hossack and Corn (2007) have an interesting application of multiseason models to amphibians before and after wildfires.

Models Incorporating Heterogeneity in Detection.—Heterogeneity in detectability introduces

a negative bias (underestimation) of occupancy estimates (Mazerolle, M. J., J. D. Nichols, and J. E. Hines, unpubl. data). When no covariates are available to model heterogeneity in detection probabilities, one can use a modified version of the finite mixtures models (Norris and Pollock, 1996; Pledger, 2000) to classify sites into two or more groups with differing probabilities of detection (MacKenzie et al., 2006: 139; Royle, 2006). Under the premise that heterogeneity in detection is largely caused by abundance (i.e., detectability increases with abundance), Royle and Nichols (2003) developed models to estimate the average number of individuals/site and the detectability of individual animals. In contrast, detectability in classic site occupancy models (above) is conditional on occupancy of at least one individual of the species. Royle (2006) provides a general treatment of models dealing with site-specific heterogeneity in detectability.

CALL INDEX MODELS

Many surveys of vocal anurans consist of calling surveys in which an observer records a calling index. For example, the familiar "Wisconsin index" used by the North American Amphibian Monitoring Program (NAAMP), takes on values 0–3, where zero is equivalent to not detected; one represents discrete, no overlapping calls; two corresponds to discrete, overlapping calls; and three indicates a full chorus (Weir and Mossman, 2005). In this framework, the goal is to estimate the true abundance level, also termed the latent (i.e., unobserved) abundance index. Conceptually, this is the maximum index value that could be observed in a very large number of visits at a given site.

The aim of call index models is to estimate the latent abundance index (Royle, 2004a; Royle and Link, 2005). We either try to estimate its value at specific sites, its distribution among "replicate" sites, or the manner in which covariates influence the latent abundance index and detection. In other words, we strive to describe the proportion of sites occupied by populations capable of generating index values of 0, 1, 2, and 3 at the sites.

Assumptions.—Call index models share the assumptions of classic single-season occupancy models (Assumptions 1–4). The data for a site consist of the index histories defined over the total number of visits (i.e., abundance index at each visit).

Implementation.—An important issue with call index models is that the latent abundance index at a site may not be observed over the sampling visits because of sampling error. As a result, one must estimate the probabilities of correctly

observing the true abundance class during a sample visit, as well as the probability of misclassifying a site in the wrong abundance classes. The reader is directed to Royle and Link (2005) for technical details of this approach. Call index models including the effects of covariates on detectability can be implemented in programming software such as R (Appendix 1), using a routine supplied on the web by Royle and Link (2005). To our knowledge, this model has not yet been used for analyzing herpetological data with the exception of Royle and Link (2005).

POINT COUNT MODELS

Point count models deal with situations where individual counts are obtained at a collection of sites, but individuals are not or cannot be marked. In such a framework, Royle (2004b) developed a model to estimate average abundance at the sites, as well as a probability of detection of the species. The simplest model produces two parameters: the probability of detecting individuals and the mean abundance across sites. Abundance is modeled either as a Poisson or negative binomial distribution, two discrete distributions commonly used to model counts of individuals (Royle, 2004b). For instance, a study amenable to such analyses could consist of counting the number of Timber Rattlesnakes (*Crotalus horridus*) observed in rocky outcrops at a collection of sites visited on two or more occasions during the snake season of activity.

Assumptions.—In this framework, one visits a collection of sites for two or more sampling visits during which we assume the following: (1) There is no change in abundance at the site between the first and last visit; (2) Detection is constant across sites; (3) Detections within each site are independent across visits; (4) Abundance follows the distribution specified in the model. Models with added flexibility and realism can be built by including covariates (e.g., habitat type) on abundance.

Example.—In this example, we compare the abundance of ranid frogs in 12 bog and 12 upland ponds of eastern New Brunswick, Canada. Data originate from minnow traps set for three consecutive days during July 1999 to capture tadpoles, juveniles, and adults (MJM, unpubl. data). Traps were checked every day for their contents, yielding a count of individuals in each pond, and captured animals were released. We considered models with ranid frog abundance following either a Poisson or a negative binomial distribution. Models included pond type (bog vs. upland) as a covariate on abundance, and effort (number of traps/pond)

TABLE 6. Model selection results from point count analysis of ranid frogs captured at 12 bog ponds and 12 upland ponds in eastern New Brunswick, Canada, with minnow traps set over three consecutive days in July 2002. Models used to estimate abundance (λ) and individual detection (P) included covariates of pond type (Type), and trapping effort (Effort). Note that only the models fitting abundance to a Poisson distribution are shown, as the models with a negative binomial component had convergence problems.

Models	Number of parameters (K)	AIC _c	Δ AIC _c	Akaike weight (w_i)
$\lambda(\text{Type}) P(\text{Effort})$	4	237.02	0	0.97
$\lambda(\text{Type}) P(\cdot)$	3	244.20	7.18	0.03
$\lambda(\cdot) P(\text{Effort})$	3	326.86	89.84	0
$\lambda(\cdot) P(\cdot)$	2	331.84	94.82	0

as a covariate potentially influencing individual detectability. We contrasted these models with simpler forms consisting of constant abundance and/or detectability.

Models fitting ranid frog abundance to a negative binomial distribution did not produce consistent estimates, because of numerical difficulties with the model for this data. Thus, we only report on models fitting abundance to a Poisson distribution. The model consisting of abundance depending on the pond type and detectability varying with effort ranked highest, having 49 times more support (evidence ratio = 0.97 : 0.03) than its closest competitor (Table 6). In conditions where a model has an Akaike weight > 0.90, it is appropriate to base inference on this single "best" model (Burnham and Anderson, 2002). The leading model revealed that ranid frog abundance was considerably lower in bog ponds than upland ponds ($Beta_{\text{Type}}$: -3.23, 95% CI: -4.25, -2.21), whereas detectability increased with trap effort ($Beta_{\text{Effort}}$: 0.40, 95% CI: 0.15, 0.64). Mean abundance at bog and upland ponds was 0.5 and 11.8 individuals per pond, respectively. This is not surprising given the acidic nature of the bog ponds which can limit frog use (mean pH \pm SD: 3.67 \pm 0.27). Thus, overall pond occupancy could be estimated at 100% for upland ($1 - e^{-11.8} = 1$) and 39% for bog ponds (i.e., $1 - e^{-0.5} = 0.39$).

Discussion.—Point count models have been used primarily in ornithological contexts (Kéry et al., 2005; Royle et al., 2005). Dodd and Dorazio (2004) and McKenny et al. (2006) applied this approach with amphibians, but otherwise, we know of no other published examples with herpetological data sets. Program PRESENCE (Appendix 1) can implement point count models with covariates fitting abundance to a Poisson distribution, but for

more flexibility such as fitting models with negative binomial abundance, one can use R (Appendix 1) with available code (see Kéry et al., 2005).

DISTANCE SAMPLING: ESTIMATING ABUNDANCE FROM LINE OR POINT TRANSECTS

A class of models has been developed for situations where the goal is to estimate density using line or point transects after accounting for detectability (Buckland et al. 1993, 2001, 2004). In a line transect, the observer travels along a line, records all detected individuals on one or both sides to some specified width, and measures the perpendicular distance of each to the center line. In contrast, with the point transect technique, the observer remains at a point, records all individuals detected around that point, and measures the distance of each from the point. In both point and line transects, we estimate detectability from a detection function, $g(x)$, which is dependent on the distance to the line or point. Essentially, this function rests on the premise that detectability on the line or point is one, and decreases with distance from the line or point (i.e., animals further from the line are less likely to be detected).

Assumptions.—The main assumptions of distance sampling models include the following: (1) All individuals on the line are observed (detectability at distance 0 = 1, i.e., all individuals along the line are detected). (2) Individuals are detected at their initial position. A relaxed form of this assumption is that any predetection movement is random with respect to the line. (3) Distances are measured accurately.

A new class of distance models has emerged to deal with cases where the assumption of perfect detection at distance zero cannot be met (Buckland et al., 2004). To respect assumption 2, animals must be detected before they attempt any evasive movement (i.e., before being flushed from their initial position), otherwise, this will introduce problems at the analysis stage. For the third assumption, distance can either be recorded on a continuous scale or grouped into intervals (4–8 distance intervals are recommended), depending on the organism.

Implementation.—Some elements of sampling design are worth mentioning to successfully implement distance sampling methods. First, the number of detections is a key component. Buckland et al. (2001) suggest, as a minimum, a total of 60–80 detections from 10–20 replicate transects or points to reliably estimate the detection function and density within a study area. Second, line or point transects should be placed randomly, to ensure plots are representative of the study area. Specifically, placement

should not be along roads, trails, or fence lines, as one cannot assume that patterns along these are the same as in other areas (Buckland et al., 2001). Finally, when it is impossible to measure perpendicular distance (e.g., an animal is seen ahead in the transect instead of on a side), the observer can measure the distance to the animal (r) and sighting angle (θ) to calculate the perpendicular distance as $r \sin(\theta)$. Alternatively, one can place a flag where each individual was observed and return later to measure the perpendicular distance.

Although not very widespread in the herpetological literature, distance sampling methods have been used with Desert Tortoise (*Gopherus agassizii*) (Anderson et al., 2001; Freilich et al., 2005), *Eleutherodactylus* frogs (Funk et al., 2003), and forest lizards and snakes (Rodda and Campbell, 2002). This technique could be potentially useful to estimate abundance of species that are easily observed such as snakes in desert shrub habitat or salamanders at a breeding pond during a nocturnal survey.

MISCONCEPTIONS ABOUT METHODS ACCOUNTING FOR DETECTABILITY

Throughout this paper, we reviewed some of the major approaches to simultaneously estimating and accounting for the probability of detection in herpetological studies. Based on their limited use in the body of herpetological literature, we recognize that many investigators put their trust in ad hoc methods using raw data uncorrected for detectability (e.g., raw counts, trap rates, return rates) and are reticent to adopt a mark-recapture framework perhaps in part due to misconceptions, some of which we address here.

Unrealistic Assumptions.—One common criticism of capture-recapture methods is that there are a number of rigid assumptions made in order to validly use these models. We have noted the important assumptions earlier for each of the model types we presented. Violations of some of these assumptions may lead to biases in the estimates of interest such as abundance, survival, or occupancy (Nichols et al., 1982, 1984; Pollock et al., 1990; Royle, 2006). However, when choosing *ad hoc* methods over techniques that account for probabilities of detection, practitioners (tacitly) make a number of even stronger assumptions. These typically include expectations of constant probabilities of detection across time, sites, or habitats or even detection probabilities of one! Yet, these assumptions are rarely tested for their validity or even acknowledged (Anderson, 2001; Pollock et al., 2002; Williams et al., 2002; White, 2005).

Previous work on a variety of taxa, including reptiles and amphibians, provides strong evidence that assumptions of constant p rarely hold in field settings. For example, when detection probability is estimated using real field data, models with constant probability of detection are rarely supported (see examples herein). The bottom line is that ad hoc methods should not be preferred over techniques that estimate probabilities of detection (Pollock et al., 1990; Nichols and Pollock, 1983; MacKenzie et al., 2002): even when assumptions are violated, formal estimation methods typically yield estimators with smaller biases than those based on ad hoc methods.

Methods Are Too Expensive.—Mark-recapture methods (e.g., estimating survival, abundance) can sometimes require impressive amounts of resources (time, personnel, labor, funds) and that is frequently viewed as their most important drawback. The first response to this criticism is that it is not universally true and depends on several factors such as the behavior of the target species (ease of capture), population size, capture techniques, marking techniques, habitat type, accessibility, and overall goal (short-term vs. long-term study). But if expense is an issue, a shift of state variable from abundance to occupancy, for example, can render even a geographically extensive study affordable. A second response is that the alternatives to a well-designed study are weak inferences and conclusions that are not defensible. If nontrivial field effort is to be expended in an investigation, then we should capitalize on that investment by using good study design and analytical methods.

Proper planning is essential regarding the objectives, target species, sampling technique, and particularly, sampling intensity (Williams et al., 2002; MacKenzie and Royle, 2005; MacKenzie et al., 2006). However, even with the best intentions, a scarcity of captures hinders one's ability to conduct many analyses. In such situations, MacKenzie et al. (2005) and Bowden et al. (2003) have discussed the possibility of borrowing information from other times, locations and even species as a means of developing reasonable inferences when sampling rare or elusive species. Pilot studies allow investigators to assess the feasibility of a study, especially concerning the encounter success (i.e., sample size) and permit readjustment of sampling protocols as necessary. A sound study design can alleviate many problems potentially encountered at the analysis stage (e.g., too few captures, continuous sampling effort instead of discrete sampling occasions, violation of closure assumption).

Detectability Is a Trait of Species.—Detectability is not a trait of a species. Because detectability is influenced by many factors (see introduction), it is possible to obtain different estimates of detectability for the same species across studies. For instance, Schmidt (2005) and Pellet and Schmidt (2005) used site occupancy models on different call survey data of Natterjack Toads (*Bufo calamita*) to estimate mean detectability as 27.3% and 44.2%, respectively. Thus, detectability needs to be estimated in each study to obtain the parameters of interest (e.g., abundance, survival, occupancy).

CONCLUSION

In the last decade, there has been extensive development in field and analytical methods accounting for detectability, and, as a result, new applications have surfaced. In the context of the spatial distribution of animals at landscape scales, the appearance of models adapted to call indices or raw counts of individuals at a collection of sites visited repeatedly have brought more flexibility in the estimation of abundance, because they do not require marked individuals (Royle, 2004b; Royle and Link, 2005).

The methods we covered herein allow investigators to control for variable and imperfect detectability and estimate demographic parameters with less bias than ad hoc methods. These parameters include survival, recruitment, or, at larger scales, parameters such as extinction and colonization used in metapopulations dynamics. Unbiased parameter estimation is vital in assessing the state of populations (e.g., amphibian declines, see Schmidt, 2004; Pellet and Schmidt, 2005), predicting population viability, and properly managing natural resources.

We encourage herpetologists to adopt methods that account for detectability. It is our hope that the methods and sampling designs presented in this paper will inspire researchers to adopt them and, at the very least, will expose herpetologists to these improved statistical methods. With these tools in hand, herpetologists can make great leaps forward, by providing incentive (i.e., accurate estimates of abundance, survival, occupancy) for the conservation of amphibian and reptile populations.

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APPENDIX 1. Freely downloadable software to conduct analyses presented in this paper.

Analysis type	Software	Utility	Interface*	Reference	Site†	
Multipurpose	MARK	Wide range of models	Win	White and Burnham, 1999	WHIT	
	SURVIV	Versatile language	DOS	White, 1983	PWRC	
Open pops	R	Versatile language	DOS-like	Ihaka and Gentleman, 1996	CRAN	
	JOLLY, JOLLYAGE	Jolly-Seber	DOS	Pollock et al., 1990	PWRC	
	RELEASE	CJS/assumptions	DOS	Burnham et al., 1987	PWRC	
	U-CARE	Model assumptions	Win	Burnham et al., 2005	CNRS	
Closed pops	CAPTURE	Abundance	DOS	Choquet et al., 1992	PWRC	
	CLOSTEST	Closure assumption	Win	Rexstad and Burnham, 2005	CLOS	
Multistate/robust design	DOBSERV	Double observer	Win	Stanley and Richards, 2000	PWRC	
	PRESENCE	Site occupancy	Win	Nichols et al., 2006	PWRC	
	NOREMARK	Marking on first visit	DOS	Mackenzie et al., 2006	WHIT	
	M-SURGE	Single or multistate	Win	White, 1996	CNRS	
	MSSURVIV	Multistate	DOS	Choquet et al., 2004	PWRC	
	ORDSURVIV	open robust design	Win/DOS	Hines, 1994	PWRC	
	RDSURVIV	robust design	DOS	Kendall and Bjorkland, 2001	PWRC	
	MSSRYRD	multistate/robust design	Win	Kendall et al., 1997	PWRC	
	Distance Sampling	Distance	Abundance from line or point transects	Win	Kendall et al., 1997	PWRC
			Abundance from line or point transects	Win	Buckland et al., 2001	PWRC

*DOS or Windows

†PWRC: <http://www.mbr-pwrc.usgs.gov/software.html>CLOS: <http://www.fort.usgs.gov/products/software/ClosTest/ClosTest.asp>CNRS: http://ftp.cefe.cnrs.fr/biom/Soft-CR/Last_Update/CRAN: <http://cran.r-project.org>WHIT: <http://www.warnercnr.colostate.edu/~gwhite/software.htm>