

# 27. ESTIMATING ABUNDANCE

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## 1. Introduction

Fundamental to much of applied ecology, including species management and conservation, is the ability to reliably estimate population size, or *abundance*. This is particularly true for reptiles given growing evidence of declines globally (Gibbons et al. 2000, Reading et al. 2010) and high levels of data deficiency (Böhm et al. 2013). The major challenge arises because rarely are all the individuals in a population encountered during a survey, and that the resulting *counts*, i.e. the number of individuals encountered,  $n$ , represents only some fraction of the true abundance,  $N$ . Although the distinction between counts and true abundance is an important one, the two are intuitively related and, by repeatedly sampling and marking individuals in a population, capture-recapture methods provide a formalization of this relationship and a framework for estimating true population size.

In this chapter, we provide a non-technical overview of ‘closed population capture-recapture’ models, a class of well established models that are widely applied in ecology (Borchers et al. 2002, Williams et al. 2001), and regularly adopted for studies of reptiles (Mazerolle et al. 2007), to estimate abundance from counts of marked individuals while accounting for imperfect detection. We first describe some classic closed population models for estimating abundance (Otis et al., 1978), then consider some recent extensions that provide a spatial context for the estimation of abundance, and therefore density,  $D$  (spatial or spatially-explicit capture-recapture: Efford 2004, Royle et al. 2014), and finally provide an example of estimating abundance and density of reptiles using an artificial cover object survey of slow worms, *Anguis fragilis*.

## 2. Closed Population Capture-Recapture

### 2.1. Sampling a population

The primary objective in a closed population capture-recapture study is to estimate the abundance of a population of interest. The population of  $N$  individuals is subjected to repeated sampling for a specified number of occasions, say  $K$ , where, in the first sampling occasion, all captured individuals are marked and released, and then at each subsequent sampling occasion the detection of marked

individuals is recorded and unmarked individuals are marked. Identifying a focal population, the spatial extent of the population is implicitly defined and the method of capture depends on the species in question and available resources. For reptiles, survey methods that allow individuals to be captured and marked include, for example, visual searches within a defined area (Zylstra et al. 2010), cage traps (Tyrrell et al. 2009, Christy et al. 2010) or pitfall traps, and the use of artificial cover objects (ACO, Grant et al. 1992) (see also Chapter X). Once captured, individuals can be uniquely identified using either natural markings that can be used to determine individual identity (Sacchi et al. 2010), using tags or markings (Grant & Doherty 2007) or physical marking such as toe clipping (Paulissen & Meyer 2000) (see also Chapter X).

Such repeated sampling results in individual encounter histories that, for each of the  $i = 1, \dots, n$  individuals encountered, describes whether or not individuals were detected in each of the  $K$  occasions. For example, in a  $K = 4$  occasion capture-recapture study, an individual with an encounter  $y_i = (0101)$  was encountered  $y_i = 2$  times; first in occasion 2, and then again in occasion 4, and was not encountered in occasions one or three. In Table 1 we provide an example of encounter history data for a  $K = 4$  occasion capture-recapture study during which  $n = 8$  individuals were captured.

Table 1: An example of an encounter history for a  $K = 4$  occasion capture-recapture study during which  $n = 8$  individuals were detected.

Individual	Occasion				y
	1	2	3	4	
1	0	1	0	1	2
2	1	0	0	1	2
3	0	1	1	1	3
4	1	1	0	0	2
5	1	0	0	1	2
6	0	0	1	1	2
7	0	0	1	0	1
n=8	1	0	0	1	2

Estimating abundance using encounter history data collected using the general sampling scheme we have described above is basically the process of estimating how many individuals were *missed*, i.e., how many individuals have encounter history  $y_i = 0$ . The ability to do so requires that the following basic assumptions are met:

1. the population is closed to demographic processes and to movement
2. individual marks can be identified unambiguously and are not lost
3. individuals are equally likely to be captured

A ‘closed’ population is one that experiences no additions or subtractions for the duration of the study, and whose size is therefore assumed to be fixed during

sampling. Defining a sampling period over which the assumption of closure can be satisfied means that an individual detected at least once during the study was present for the entire study, and therefore, failure to detect that individual in any occasion was due to imperfect detection. This highlights the importance of the second assumption – that individuals are identified unambiguously – because misidentification would lead to erroneous encounter histories that don’t reflect the true process of encountering individuals. The third assumption is less important as we will see later, but satisfying this assumption means that we can employ the simplest formulation of a capture-recapture model, model  $M_0$ .

## 2.2. Estimating abundance using model $M_0$

Under model  $M_0$ , the encounter probability for each individual,  $p_i$ , is assumed to be the same for all individuals in the population, i.e.,  $p_i = p$ . Then, whether or not we encounter an individual  $i = 1, 2, \dots, N$  during sampling occasion  $k$ ,  $y_{ik}$ , is a Bernoulli trial (a “coin flip”) with constant probability  $p$ , which we can write formally as:

$$y_{ik} \sim \text{Bernoulli}(p).$$

i.e., there are no individual or temporal covariates that affect  $p$ . The basic idea of all closed population capture-recapture methods is that the pattern of detections in the encounter histories of individuals observed at least once provides information about individual detectability, or detection probability,  $p$ , which in turn, can be used to estimate the number of individuals *not* encountered. The underlying concept can be understood by recognizing that the observed number of individuals  $n$  is related to the total population size  $N$  by the expression:

$$E(n) = N\tilde{p}$$

where  $E()$  denotes statistical expectation and  $\tilde{p}$  is the probability that an individual is captured *at all* during the study. In a study of  $K$  survey occasions  $\tilde{p}$  is directly related to the basic parameter  $p$  by the formula

$$\tilde{p} = 1 - (1 - p)^K$$

This expression applies to model  $M_0$  but the expression relating  $p$  to  $\tilde{p}$  is different depending on the specific capture-recapture being considered. In general the parameter  $p$  can be estimated from the observed encounter histories and, in turn, this is used to estimate  $\tilde{p}$  and then finally we estimate  $N$  by  $\hat{N} = n/\tilde{p}$ .

This estimator is typically called the ‘conditional estimator’ of  $N$  because it is derived from an expression for the probability of the encounter history conditioned on the event that an individual is encountered at all (i.e., at least once). The conditional probability of encounter derives from a straightforward application of the law of total probability. The conditional estimator of population size  $N$  has only one canonical estimated parameter, that being  $p$ , and  $N$  is a derived parameter. An alternative framework for inference about  $N$  is based on the ‘full likelihood’ in which  $N$  appears explicitly in the likelihood. The two approaches are both widely used in all contexts, and there is little practical difference.

### 2.3. Variation in $p$ : beyond $M_0$

The assumption of equal capture probability is a rather restricting one and there are many situations under which the capture probabilities would be expected to vary. For these situations, model  $M_0$  is not appropriate although and Otis et al. (1978) described a family of models that can be used to deal with most sources of variation in individual encounter probabilities:

$M_0$  Capture probability is the same for all individuals (Section 2.2)

$M_t$  Capture probability is the same for all individuals, but varies between sampling occasions (time) (note that below we use  $k$  for the time index in our development).

$M_b$  Capture probabilities vary depending on whether or not individuals have been captured previously (behavioral response).

$M_h$  Capture probabilities vary among individuals (individual heterogeneity).

Variations of these different models exist. For example, the usual application of model  $M_t$  involves occasion-specific parameters  $p_k$ , but we can also consider systematic variation in detection probability that results from explicit covariates. For example, we could model seasonal variation in  $p_k$  using a quadratic polynomial in Julian day,  $J_k$ , such as:

$$\text{logit}(p_k) = \alpha_0 + \alpha_1 J_k + \alpha_2 J_k^2$$

and estimate the parameters  $\alpha_0$ ,  $\alpha_1$  and  $\alpha_2$  instead of fully occasion specific parameters  $p_k$ . The behavioral response model is usually parameterized as a permanent change in  $p$  for individuals subsequent to their initial capture (i.e.  $p_{pre}$  and  $p_{post}$ , for capture probability *prior to* and *after* first capture respectively). This could be the result of ‘trap happiness’ due to having baited traps (uncommon in reptile studies) or it could be the result of ‘trap shyness’ due to aversion to handling. Sometimes a transient or ephemeral behavioral response may be sensible (Yang and Chao 2005). Under this type of model the response to initial capture only lasts for a brief period after initial capture.

Model  $M_h$  has been an important model in capture-recapture because it has long been recognized that the existence of individual heterogeneity in capture probability will lead to under-estimation of  $N$  when it is not accounted for. Thus much attention has been focused on developing more flexible classes of model  $M_h$ . Thus, model  $M_h$ , has many different variations. Norris and Pollock (1996) formulated the model in terms of a finite mixture or latent class model in which each individual in the population belongs to a finite (and small) number of classes represented by distinct values of  $p$  (see also Pledger 2000). Dorazio and Royle (2003) considered continuous mixtures such as the beta-binomial and logit-normal models (see also Coull and Agresti 1999).

## 2.4. Removal Sampling

Removal sampling is unlike other capture-“recapture” methods in the sense that individuals are captured only once but then removed from the population and, hence, not available to be recaptured. The idea of removal sampling is that by repeatedly removing individuals, we should realize a decrease in catch frequency, and this realized decrease is informative about detection probability which can then be used to obtain an estimate of the population size  $N$  as it was *prior* to the initiation of the sampling activity. Intuitively, we expect to capture  $p \times N$  individuals during a single sample and, if we remove those individuals, we should expect to capture  $p \times (N - p \times N) = p(1 - p)N$  individuals in the 2nd bout of removal sampling. Note that the ratio of these two removal counts is  $1 - p$  which produces a direct estimate of  $p$  from which  $N$  can be estimated by a suitable algebraic function of the counts.

In practice, removal sampling is done using ‘temporary’ removals in which an area is searched and individuals are temporarily housed in a bucket or cage during successive passes (Garden et al. 2007). At the end of the study they would normally be released to where they were initially captured. Of course earlier applications of removal sampling to fisheries involved permanent removal, typically harvest, but that is not practical in most studies of reptiles.

## 2.5. Hierarchical capture-recapture models

Closed population models are usually described in the context of sampling a single closed population. However, in practice, it is almost always the case that multiple populations of individuals are sampled. For example, small mammal trapping studies might involve a number of live trapping grids, or reptile and amphibian studies might involve a number of distinct cover board arrays. In such cases we can think of the distinct populations being sampled by each array as spatial strata, with potentially stratum specific parameters such as  $p_g$ ,  $N_g$  ( $g$  for ‘grid’) which could be estimated by applying closed population models to data collected from each stratum. However, analyzing the data from these stratified populations “one-at-a-time” can be statistically inefficient (Converse and Royle 2012). Instead, there can be distinct advantages to combining all of the data into a single capture-recapture model but tying the different models together by imposing model structure on the detection probability or abundance parameters using a hierarchical modeling framework. For example, a simple model allowing for variation in population size among a collection of  $g = 1, 2, \dots, G$  trap arrays is  $N_g \sim \text{Poisson}(\lambda)$ . This model allows each population to have it’s own ‘size’ but builds in a weak stochastic dependence between the populations, so that all of the data are used to estimate the shared parameter  $\lambda$ . The end result is more precision to estimate the population-specific parameters by combining the information from all of the distinct populations. See Royle (2004), Dorazio et al. (2005) and Royle, Converse and Link (2012).

## 2.5 Individual covariate models and distance sampling

Model  $M_h$  is the standard closed population model when *unexplained* individual heterogeneity in capture-probability exists. However an important related class of models are models in which individual heterogeneity can be explained by explicit individual covariates. These are often called “individual covariate models” but, in keeping with the classical nomenclature on closed population models, Kéry and Schaub (2012) referred to these models as “model  $M_x$ ”, the  $x$  representing some explicit covariate (of course multiple covariates are allowed). Classical examples of covariates influencing detection probability are type of animal (juvenile/adult or male/female), a continuous covariate such as body mass, or a discrete covariate such as group or cluster size. For example, in models of aerial survey data, it is natural to model the detection probability of a group as a function of the observation-level individual covariate, “group size” (Royle 2009, Langtimm et al. 2011).

The basic encounter model for model  $M_x$  is the same as our other closed models, the Bernoulli encounter model:

$$y_i \sim \text{Bernoulli}(p_i).$$

To model the covariate, we use a logit model for encounter probability of the form:

$$\text{logit}(p_i) = \alpha_0 + \alpha_1 x_i \quad (1)$$

where  $x_i$  is the covariate value for individual  $i$  and the parameters  $\alpha_0$  and  $\alpha_1$  are the parameters to be estimated.

Traditionally, estimation of  $N$  in model  $M_x$  is achieved using methods based on ideas of unequal probability sampling (i.e., Horvitz-Thompson estimation). This idea was developed independently by Huggins (1989) and Alho (1990). The estimator of  $N$  is given as a derived parameter:

$$\hat{N} = \sum_{i=1}^n \frac{1}{\tilde{p}_i}$$

where  $\tilde{p}_i$  is the probability that individual  $i$  appeared in the sample. This is related to the more fundamental parameters  $\alpha$  in the model for detection probability according to:

$$\tilde{p}_i = 1 - (1 - p_i)^K$$

where  $p_i$  is a function of parameters  $\alpha_0$  and  $\alpha_1$ . In practice, parameters are estimated from the conditional-likelihood of the observed encounter histories.

An alternative formulation of model  $M_x$  is the “full likelihood” which requires that we put a model on the individual covariate  $x$  allowing for the sample not only of the encounter histories but also of the covariate to be extrapolated to the population. For example, if we have a continuous trait measured on each individual, then we might assume that  $x$  has a normal distribution:

$$x_i \sim \text{Normal}(\mu, \sigma^2)$$

If the covariate was group size then, naturally, some discrete probability mass function would be needed. Inference for individual covariate models from the standpoint of the full likelihood is discussed widely, including in Royle (2009), Kéry and Schaub (2012).

Individual covariate models are important in practice for the simple reason that heterogeneity exists in almost every capture-recapture study due to the spatial organization of traps and of individuals in the population (see next section). Thus, they were adopted historically to account for spatial structure in capture-recapture (Boulanger and McLellan 2001, Karanth and Nichols 1998). For this purpose an individual covariate is created which describes *where* the individual is located in relation to the trapping array. This approach leads naturally to more recent spatial capture-recapture models described in the next section.

### 3. Spatial Capture-Recapture

One of the main deficiencies with classical closed population models is that they do not permit direct estimation of animal *density* because, in almost all practical field applications, it is not possible to precisely define the area sampled by a set of trapping devices. This is because individuals being captured move about space and can be captured without the biologists knowing from whence those individuals originated or how much space they are using. Newly developed *spatial capture-recapture* (SCR) models (also called spatially-explicit capture-recapture, SECR) provide a technical framework for dealing with this problem (Efford 2004, Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2014). These models follow logically on from model  $M_x$ , where  $x$  is the activity center of the individual as we will see below.

The sampling scheme for a *spatial* capture-recapture analysis is the same as described above, i.e., there is a population of  $N$  individuals, but now we consider each individual having an activity center that has  $X$  and  $Y$  coordinates ( $\mathbf{s}_i = [s_{i,X}, s_{i,Y}]$ ). Now the goal is to estimate the number of individuals (or activity centers) within a region of interest which we refer to as a *state-space*, or  $\mathcal{S}$ , which is to say we wish to estimate density:  $D = N/||\mathcal{S}||$ , where  $||\mathcal{S}||$  is the area of  $\mathcal{S}$ . We assume that these activity centers are distributed uniformly throughout across space:

$$\mathbf{s}_i \sim \text{Uniform}(\mathcal{S}).$$

As before, the population is subjected to sampling using some trapping devices (for convenience, we will refer to these as ‘traps’). However, we explicitly acknowledge both how many traps there are:  $j = 1, \dots, J$  traps, and the locations of each of the traps, which we denote as  $x_j$ . The acknowledgement of the spatial structure of the traps means observations can be spatially indexed so encounter histories describe *who* ( $i$ ), *when* ( $k$ ), and importantly, *where* ( $j$ ) individuals were located, i.e.,  $y_{i,j,k}$ . Typically, these observations are assumed to be binomially distributed with sample size  $K$  (the number of sampling occasions):

$$y_{i,j} \sim \text{Binomial}(K, p_{i,j}),$$

where  $p_{i,j}$  is the probability of encountering individual  $i$  in trap  $j$ , which depends on the distance between the trap location ( $x_j$ ) and the individual's activity center ( $s_i$ ) as follows:

$$p_{i,j} = p_0 \times e^{-(1/2\sigma^2)d(x_j,s_i)^2}. \quad (2)$$

This is referred to as the half-normal or ‘bivariate normal’ encounter model where  $\text{logit}(p_0) = \alpha_0$  is the baseline encounter probability, which is the probability of encountering an individual at its activity center, the parameter  $\sigma$  describes the rate at which detection probability declines as a function of distance, and  $d(x_j, s_i)$  is the Euclidean distance between trap  $j$  and the activity center of individual  $i$ . In a spatial capture-recapture analysis, the parameters to be estimated are  $\alpha_0$  and  $\sigma$  in addition to population size  $N$ . As in model  $M_h$ , the additional parameter  $\sigma$  accommodates individual heterogeneity in  $p$  but, unlike model  $M_h$ , the parameter represents an explicit source of heterogeneity, that due to distance between individual activity or home range centers and trap locations.

SCR models address the density estimation problem directly by parameterizing the model directly in terms of individual activity centers  $s_i$  and prescribing the state-space  $\mathcal{S}$ . The inference problem then reduces to estimating the number of such activity centers in the well-defined area  $\mathcal{S}$ , i.e., density. Density,  $D$ , is simply a transformation of  $N$ :  $D = N/\text{Area}(\mathcal{S})$ .

## 4. Software

Non-spatial closed population capture-recapture models can be fit using both classical (frequentist) and Bayesian methods, and here we outline some of the common software options and material sources for doing so.

By far the most widely used software for fitting such models is the Windows-based program **MARK** (White & Burnham 1999), a free, user friendly and extremely well-documented application for fitting most of the standard closed population models using maximum likelihood ([www.phidot.org/software/mark/](http://www.phidot.org/software/mark/)). In an effort to facilitate easier model development, increased reproducibility and to allow for a more organized and automated work flow, Laake & Rexstad (2008) developed the **R** package **RMark**, an interface between **R** and **MARK** that can be used to construct input files and extract output that can be manipulated in the **R** environment ([www.phidot.org/software/mark/rmark/](http://www.phidot.org/software/mark/rmark/)). The **R** package **unmarked** (Fiske & Chandler 2011) can also be used to fit hierarchical versions of some standard closed population capture-recapture models using maximum likelihood (see Kéry and Royle 2015, ch. 7). In addition to detailed documentation, both **MARK** ([www.phidot.org/forum/index.php](http://www.phidot.org/forum/index.php)) and **unmarked** (<https://groups.google.com/forum/#!forum/unmarked>) have supporting web based forums.

Spatial capture-recapture models cannot (yet) be implemented in **MARK**, and, although a windows-based spatial equivalent exists (**DENSITY**: Efford, et al. 2004), it is no longer in development and likelihood analysis of SCR models is typically conducted using the **R** package **secr** (Efford 2011). **secr** implements



a wide variety of spatial capture-recapture methods, including spatial version of the models described above and in Otis et al. (1978), all within the **R** environment (**secr** forum can be found here: <https://groups.google.com/forum/#!forum/secrgroup>)

Often situations arise when an analysis requires a ‘non-standard’ approach (e.g. an integrated population model: Shaub & Abadi 2011, demographic metapopulation models: Sutherland et al. 2014, models for transience and dispersal: Royle et al. *In review*). In these cases, available likelihood-based methods cannot be used and instead a Bayesian analysis is preferred. Bayesian methods, specifically the use of Markov Chain Monte Carlo (MCMC) using the BUGS language, offer a great deal of flexibility and modeling freedom (Kéry and Schaub 2013).

Bayesian analysis of capture-recapture models is done using a method related to classical “data augmentation” from the statistics literature (e.g., Tanner & Wong, 1987). This is a general concept in statistics but, in the context of capture-recapture models, where  $N$  is unknown, it has a consistent implementation across classes of capture-recapture models and one that is really convenient from the standpoint of doing MCMC (Royle et al. 2007; Royle & Dorazio 2012). Chapter 6 of Kéry & Schaub (2011) provide an accessible and complementary development of Bayesian analysis of non-spatial closed population models. The tremendous benefit of formulating SCR models in the BUGS language is that it is relatively trivial to extend from the non-spatial model to the formulation on the closed population model. In their book, Royle et al. (2014) provide a thorough treatment of SCR and Bayesian methods for analyzing a SCR models which has an associated forum (<https://groups.google.com/forum/#!forum/spatialcapturecapture>).

## 5. Slow worm example

We provide an example here using a study of the slow worm (*Anguis fragilis*) conducted in Mueterschwanderberg, canton Nidwalden, Switzerland (Meier 2012, thesis). A more detailed SCR analysis of the data from that study is given by Meier et al. (in prep). Here we analyze a portion of the data from one of the artificial cover object arrays which used 23 cover objects (Fig. 1). This ACO array was operated over 59 days and it produced encounter histories on 44 unique individuals, 23 captured once, 4 capture twice, 4 thrice, 5 four times, 3 five times, 1 six times and 4 seven times.

An immediately obvious ‘feature’ of this ACO array is the irregular and uneven distribution of cover objects. While we may apply capture-recapture models to the data from this study to estimate population size  $N$ , it is clear that the irregular ACO array should be a hinderance to a clear interpretation of this estimate because there is no obvious way to compute a sample area for this grid. Moreover, the spatial heterogeneity in trap density is almost certain to induce heterogeneity in detection probability of individuals depending on the location of individuals relative to traps. While we can use model  $M_h$  to account for some heterogeneity, that model is not an explicit model of heterogeneity due to spatial proximity of individuals to traps. Nevertheless, we fit both models  $M_0$  and  $M_h$  to these data in order to see how they compare. We will also fit

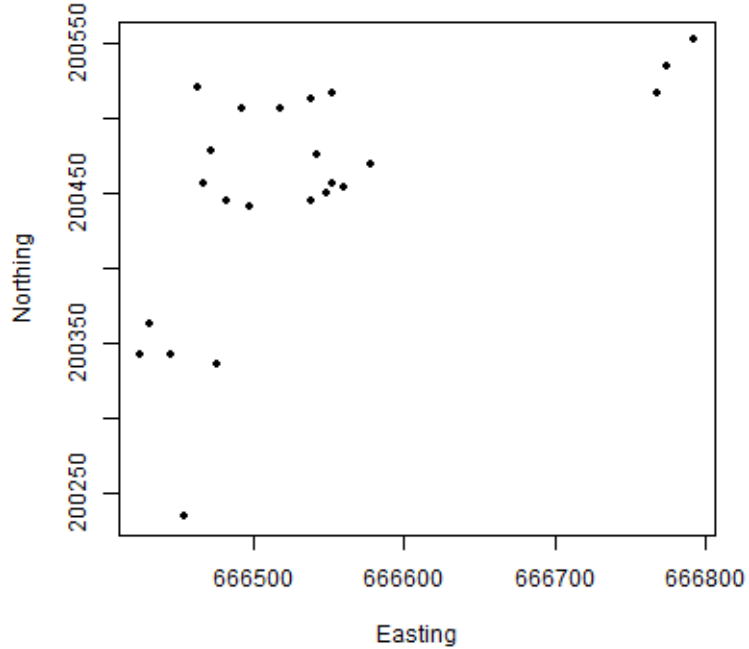


Figure 1: Artificial cover object (ACO) array from the slow worm study of Meier (2012). Sampling from this array over 59 days produced encounter histories of 44 individuals.

the SCR model to see how we can convert an estimate of  $N$  to density.

We fit the logit-normal variety of model  $M_h$  (Coull and Agresti 1999, Dorazio and Royle 2003) which assumes that the logit-transformation of individual detection probability  $p_i$  has a normal distribution with variance  $\theta^2$ :

$$\text{logit}(p_i) \sim \text{Normal}(\mu, \theta^2).$$

Therefore this model has 3 parameters ( $N$ ,  $\mu$  and  $\theta$ ). The additional parameter  $\theta$  accommodates over-dispersion or individual heterogeneity in  $p$ . For the analysis of the SCR model we defined the state-space by creating the minimum area rectangle around the trap array and then buffering that by 40 meters, creating a state-space having an area of 10.64 ha (Figure 1). The summary results from fitting these 3 models to the slow worm data are given in Table 2. We note that AIC is *not* comparable between SCR and ordinary closed models because the models are fitted to different data sets: SCR models use the individual, trap and occasion-specific encounter data whereas ordinary capture-recapture models aggregate over all traps to produce a simpler reduced-information individual

by occasion-specific encounter history. A key point of this comparison is that the estimates of  $n_0$  (the number of uncaptured individuals), and hence of  $N$ , are radically different. Model  $M_h$  and the SCR model both accommodate heterogeneity in encounter probability which is indicated in these data ( $\theta = 1.114$  under the logit-normal model  $M_h$ , which is favored strongly over model  $M_0$  by AIC). Thus, the estimated  $N$  is increased substantially in comparison to model  $M_0$ . In addition, the SCR model produces an estimate of  $N$  that applies to a specific, well-defined region (the state-space) having an area of 10.64 ha. Thus we can compute directly an estimate of the *density* of slow worms, which comes out to 14.68 slow worms/ha.

Table 2: The results of fitting models  $M_0$  and  $M_h$  and an ordinary SCR model to the slow worm data. Model  $M_h$  has one extra parameter compared to model  $M_0$ , the individual heterogeneity parameter  $\theta$ . The SCR model has one additional parameter,  $\sigma$ , the scale parameter of the encounter probability model relating individual  $p$  to distance between individual activity center and trap location.

Model	$p_0$	$n_0$	extra parameter	N	D(/ha)	AIC
$M_0$	0.0396	3.97		47.97		-73.42
$M_h$	0.0149	30.88	1.114	74.88		-89.21
SCR	0.0501	112.14	21.005	156.14	14.68	320.39

## 6. Summary

Capture-recapture methods have been the standard for estimating population size and density for many decades and provide a framework for sampling populations and estimating key parameters, namely population size or abundance. However, we have also argued that capture-recapture is inherently spatial because of the way we typically conduct sampling (e.g. artificial cover objects, pitfall or cage traps etc...), and yet traditionally this has almost never been addressed in the application of capture-recapture methods. These non-spatial methods have a number of deficiencies that would appear to limit their usefulness in practice (but, strangely, have not). For example, they do not allow the direct estimation of density, they do not account for the spatial organization of trapping arrays, or of individuals within the population being studied. Moreover, despite capture-recapture studies often involving explicit questions about spatial ecology, space is largely ignored, opting instead for a “fishbowl” view of systems.

We demonstrated that the source of heterogeneity that is likely to be an issue in almost all CR studies, i.e., spatial distribution of individuals relative to traps, can be addressed using spatial extensions of capture-recapture models, namely “spatial capture-recapture”. The obvious benefit of SCR is that the spatial region for which abundance is estimated is explicitly defined and that *absolute* density can be computed directly. Perhaps of greater importance however, is

the explicit focus on the spatial processes giving rise to encounter data which enables researchers to study many aspects of spatial ecology from individual encounter history data, including resource selection or space usage (Royle et al. 2013), landscape connectivity (Royle et al. 2013b; Sutherland et al. 2014), spatial variation in density (Borchers and Efford 2008, Royle et al. 2013), and movement or dispersal (Schaub and Royle 2014, Ergon and Gardner 2014, Royle et al. *in review*).

As has been demonstrated throughout this book, reptiles represent an important component of many communities, are a group of animals in global decline, and can be extremely difficult to monitor. Many of the methods described in earlier chapters for monitoring, capturing and identifying individuals for reptilian populations lend themselves naturally to analysis using capture-recapture methods and should be preferred over indices of abundance like raw counts. Moreover, many of these sampling procedures are naturally spatial (trapping grids, line transect etc...) in which case we recommend analysis using spatial capture recapture methods in order to arrive at meaningful, spatial referenced abundance estimates as we demonstrated with the slow worms example.

XXX where should this next bit go??

We note that, while we only focussed on estimating the size of a population using marked individuals, another very important method for estimating abundance is distance sampling (Buckland et al. 2005). Unlike capture-recapture sampling, distance sampling requires only a single “snap-shot” sample of the population. For each detected individual distance from the observer is measured. Information about detection probability comes from an assumed model for the relationship between detection probability and distance to observer.

## Literature Cited

- Alho, J. M. (1990). Logistic regression in capture-recapture models. *Biometrics*, 623-635.
- Böhm, M., Collen, B., Baillie, J. E., Bowles, P., Chanson, J., Cox, N., & Cheylan, M. (2013). The conservation status of the worlds reptiles. *Biological Conservation*, 157, 372-385.
- Borchers, D. L., , Buckland, S. T. and W Zucchini. 2002. Estimating animal abundance: closed populations (Vol. 13). Springer Science & Business Media.
- Borchers, D.L. and M.G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64, 377-385.
- Boulanger, J., & McLellan, B. (2001). Closure violation in DNA-based mark-recapture estimation of grizzly bear populations. *Canadian Journal of Zoology*, 79(4), 642-651.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (2005).

Distance sampling. John Wiley & Sons, Ltd.

- Cagle, F. R. (1939). A system of marking turtles for future identification. *Copeia*, 1939(3), 170-173.
- Christy, M T., A A. Yackel, Adams, G H. Rodda, Julie A. Savidge, and Claudine L. Tyrrell. Modelling detection probabilities to evaluate management and control tools for an invasive species. *Journal of Applied Ecology* 47, no. 1 (2010): 106-113.
- Coull, B. A., & Agresti, A. (1999). The Use of Mixed Logit Models to Reflect Heterogeneity in Capture-Recapture Studies. *Biometrics*, 55(1), 294-301.
- Converse, S. J., & Royle, J. A. (2012). Dealing with incomplete and variable detectability in multi-year, multi-site monitoring of ecological populations. Design and Analysis of Long-term Ecological Monitoring Studies. Cambridge University Press, Cambridge, UK, 426-442.
- Dorazio, R. M., & Royle, J. A. (2003). Mixture models for estimating the size of a closed population when capture rates vary among individuals. *Biometrics*, 59(2), 351-364.
- Dorazio, R. M., Jelks, H. L., & Jordan, F. (2005). Improving Removal-Based Estimates of Abundance by Sampling a Population of Spatially Distinct Subpopulations. *Biometrics*, 61(4), 1093-1101.
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106, 598-610.
- Efford, M. G., Dawson, D. K., & Robbins, C. S. (2004). DENSITY: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation*, 27(1), 217-228.
- Ergon, T., & Gardner, B. (2014). Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture-recapture data. *Methods in Ecology and Evolution*, 5(12), 1327-1336.
- Efford, M. G. (2011). secr: Spatially explicit capture-recapture models. R package version, 2(0).
- Fiske, I., & Chandler, R. B. (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10), 1-23.
- Garden, J.G., McAlpine, C.A., Possingham, H.P., and Jones, D.N. (2007) Using multiple survey methods to detect terrestrial reptiles and mammals: what are the most successful and cost-efficient combinations?. *Wildlife Research* 34, 218-227.
- Gibbons, et al. (2000). The Global Decline of Reptiles, Dj Vu Amphibians Reptile species are declining on a global scale. Six significant threats to reptile

- populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *BioScience*, 50(8), 653-666.
- Grant, B. W., A. D. Tucker, J. E. Lovich, A. M. Mills, P. M. Dixon, and J. W. Gibbons. (1992). The use of coverboards in estimating patterns of reptile and amphibian biodiversity. *Wildlife 2001: Populations* 379-403.
- Grant, T. J. & Doherty, P. F. (2007). Monitoring of the Flat-Tailed Horned Lizard With Methods Incorporating Detection Probability. *The Journal of wildlife management*, 71(4), 1050-1056.
- Huggins, R. M. (1989). On the statistical analysis of capture experiments. *Biometrika*, 76(1), 133-140.
- Karanth, K. U., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79(8), 2852-2862.
- Kéry, M., & Schaub, M. (2012). Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.
- Kéry, M., & Royle, J. A. (2015). Applied Hierarchical Models. Academic Press.
- Laake, J., & Rexstad, E. (2008). RMark: an alternative approach to building linear models in MARK. Program MARK: a gentle introduction.
- Langtimm, C. A., Dorazio, R. M., Stith, B. M., & Doyle, T. J. (2011). New aerial survey and hierarchical model to estimate manatee abundance. *The Journal of Wildlife Management*, 75(2), 399-412.
- Mazerolle, M. J., Bailey, L. L., Kendall, W. L., Andrew Royle, J., Converse, S. J., & Nichols, J. D. (2007). Making great leaps forward: accounting for detectability in herpetological field studies. *Journal of Herpetology*, 41(4), 672-689.
- Meier, A. (2012). Reptilienaufwertungskonzept am Mueterschwandenberg. Bachelorarbeit. Zurich University of Applied Sciences, Wdenswil. 74 pp.
- Norris III, J. L., & Pollock, K. H. (1996). Nonparametric MLE under two closed capture-recapture models with heterogeneity. *Biometrics*, 639-649.
- Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife monographs*, 3-135.
- Paulissen, M. A., & Meyer, H. A. (2000). The effect of toe-clipping on the gecko *Hemidactylus turcicus*. *Journal of Herpetology*, 282-285.
- Pledger, S. (2000). Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics*, 56(2), 434-442.

- R Development Core Team. (2004). R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria.
- Reading, C. J., L. M. Luiselli, G. C. Akani, Xavier Bonnet, G. Amori, Jean-Marie Ballouard, E. Filippi, Guy Naulleau, D. Pearson, & L. Rugiero. (2010). Are snake populations in widespread decline?. *Biology Letters*, 6, 777-780.
- Royle, J. A. (2004). Generalized estimators of avian abundance from count survey data. *Animal Biodiversity and Conservation*, 27(1), 375-386.
- Royle, J.A., R.M. Dorazio and W.A. Link. (2007). Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics* 16, 67-85.
- Royle, J.A. and K.V. Young. (2008). A hierarchical model for spatial capture-recapture data. *Ecology* 89, 2281-2289.
- Royle, J. A. (2009). Analysis of capture-recapture models with individual covariates using data augmentation. *Biometrics*, 65(1), 267-274.
- Royle, J. A., Converse, S. J., & Link, W. A. (2012). Data Augmentation for Hierarchical Capture-recapture Models. arXiv preprint arXiv:1211.5706.
- Royle, J. A. and R. M. Dorazio. 2012. Parameter-expanded data augmentation for Bayesian analysis of capture-recapture models. *Journal of Ornithology* 152(2), 521-537.
- Royle, J. A., Chandler, R. B., Gazenski, K. D., & Graves, T. A. (2013). Spatial capture-recapture models for jointly estimating population density and landscape connectivity. *Ecology*, 94(2), 287-294.
- Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. (2013). Integrating resource selection information with spatial capture-recapture. *Methods in Ecology and Evolution* 4(6), 520-530.
- Royle, J. A., R. B. Chandler, R. Sollmann and B. Gardner. (2014). Spatial Capture-Recapture. Academic Press.
- Royle, J. A., Fuller, A. K., and Sutherland, C. (in review). Spatial capture-recapture models allowing for Markovian transience or dispersal. *Population Ecology*.
- Sacchi, R., Scali, S., Pellitteri-Rosa, D., Pupin, F., Gentili, A., Tettamanti, S. & Fasola, M. (2010). Photographic identification in reptiles: a matter of scales. *Amphibia-Reptilia*, 31(4), 489-502.
- Schaub, M., & Abadi, F. (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, 152(1), 227-237.
- Schaub, M., & Royle, J. A. (2014). Estimating true instead of apparent survival

- using spatial Cormack-Jolly-Seber models. *Methods in Ecology and Evolution*, 5(12), 1316-1326.
- Sutherland, C. S., Elston, D. A., & Lambin, X. (2014). A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. *Ecology*, 95(11), 3149-3160.
- Sutherland, C., A. K. Fuller and J. A. Royle. (2015). Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. *Methods in Ecology and Evolution* 6, 169-177.
- Tanner, M. A., & Wong, W. H. (1987). The calculation of posterior distributions by data augmentation. *Journal of the American statistical Association*, 82(398), 528-540.
- Tyrrell, C. L., Christy, M. T., Rodda, G. H., Yackel Adams, A. A., Ellingson, A. R., Savidge, J. A., Dean-Bradley, K., & Bischof, R. (2009). Evaluation of trap capture in a geographically closed population of brown treesnakes on Guam. *Journal of Applied Ecology*, 46(1), 128-135.
- Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). Analysis and management of animal populations. Academic Press.
- Yang, H. C., & Chao, A. (2005). Modeling animals' behavioral response by Markov chain models for capture-recapture experiments. *Biometrics*, 61(4), 1010-1017.
- Zylstra, Erin R., Robert J. Steidl, and Don E. Swann. Evaluating survey methods for monitoring a rare vertebrate, the Sonoran desert tortoise. *The Journal of Wildlife Management*, 74.6 (2010): 1311-1318.