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Estimating Abundance or Occupancy from Unmarked Populations

Brett T. McClintock[1] and Len Thomas[2]

[1] NOAA National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, WA, USA
[2] Centre for Research into Ecological and Environmental Modelling, School of Mathematics and Statistics, University of St. Andrews, St. Andrews, United Kingdom

Summary

When it comes to collecting field data, "you can't always get what you want" in population ecology. We are often interested in understanding the vital rates that drive population dynamics, such as fecundity or survival, but the realities of fieldwork under logistical and financial constraints often preclude us from collecting the data we would most like to have. Despite these challenges, there are plenty of ways to "get what you need" and make meaningful inferences about population status, trends, and habitat associations using relatively simple and inexpensive field sampling methods. Here, we focus on the estimation of abundance and species occurrence from unmarked population data. We provide an overview of common sampling and analysis methods for squeezing the most information out of unmarked population data while accounting for imperfect detection and other obstacles. These unmarked population methods include plot sampling, distance sampling, spatially replicated counts, removal sampling, and presence/absence sampling.

3.1 Introduction

From the perspective of an applied population ecologist, an ideal study population would consist of individually identifiable or "marked" organisms that could be observed at any time and for as long as we wish without disturbing them. Whether for a long-term investigation about the effects of global climate change or the shorter-term studies typical of graduate student projects, reliable inference about population patterns and dynamics from observations of a population of *marked individuals* would be considerably easier than observations of a study population consisting of indistinguishable and difficult-to-observe (or to manually mark) individuals. Some wildlife species possess easily distinguishable marks, including natural pelage coloration of some felids or acquired scars in some cetaceans, but otherwise this ideal study population rarely exists outside the artificial constructs of a well-designed field experiment. Instead, we must often contend with the reality that our study population may contain relatively few to no marked individuals, and that these individuals may be difficult to observe when conducting data collection surveys. This chapter focuses on using data from populations of *unmarked individuals* to estimate two quantities fundamental to understanding population dynamics and species distributions: *population abundance* and *species occurrence*.

3.1.1 Why Collect Data from Unmarked Populations?

Unmarked populations are not as informative for estimation of demographic parameters, such as survival, compared to marked populations. However, status, trends, and habitat associations can be inferred from unmarked populations, and there are entire books devoted to use of data from unmarked individuals for estimation of population abundance (Buckland et al. 2001, 2004, 2015) and species occurrence (MacKenzie et al. 2006). In deciding whether to collect and analyze data from an unmarked population, there are many issues to consider. When scientific hypotheses concern the role of demographic rates (i.e. recruitment, survival) and movements (i.e. immigration, emigration) as drivers of changes in abundance, then investment in capture-recapture methods for marked populations may be necessary (Chapters 7 and 9). However, a key advantage of unmarked population studies is that time and money need not be invested
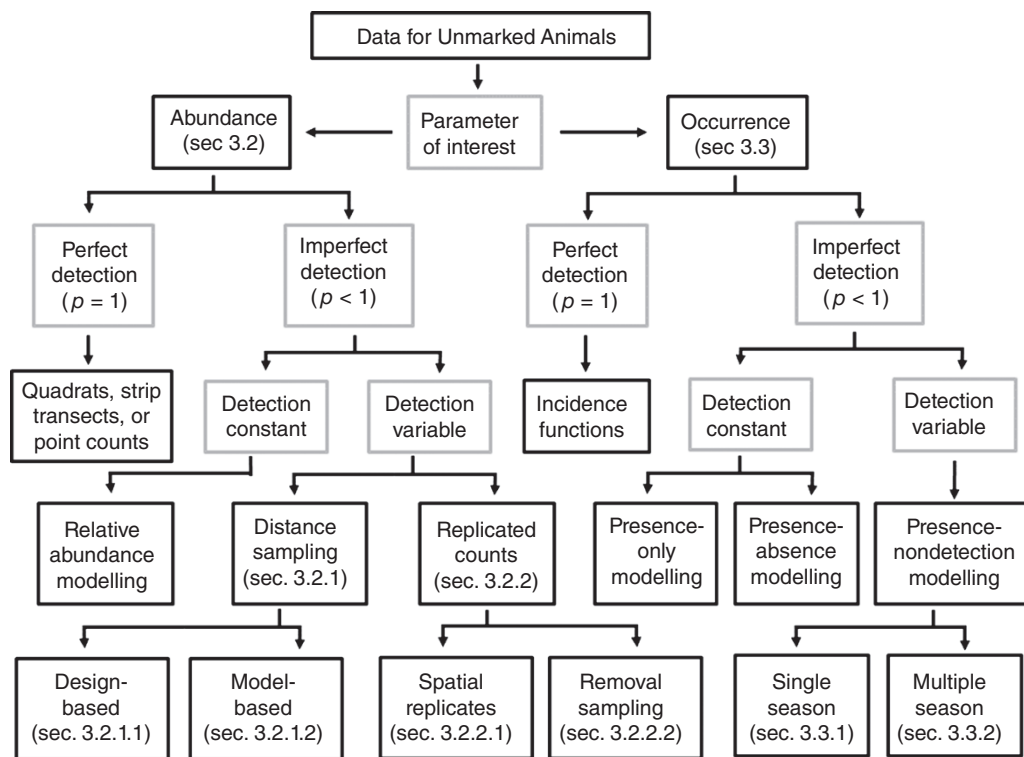
Figure 3.1 Decision tree for Chapter 3. Some of the most important considerations for the design and analysis of unmarked population studies include the item of ecological interest and detection probability (p).

in capturing and marking animals or, in the case of non-invasive genetic sampling, the collection and analysis of DNA samples (Lukacs and Burnham 2005, Bravington et al. 2016; Fewster et al. 2016; Chapter 5). Thus, limited resources can be invested in other aspects of the study design, thereby enabling a broader geographic or temporal scale of monitoring. Not only can capturing and marking animals be expensive in time and money, but it is also typically stressful and potentially harmful to wild animals. For species of conservation concern, unmarked population studies may be necessary because the capturing and marking of individuals is not politically or socially acceptable. Despite the limited information contained in unmarked data, in this chapter we will demonstrate how meaningful inferences about population abundance and species occurrence probability can be obtained using relatively simple and inexpensive field sampling methods for unmarked populations. A guide to this material is provided in Figure 3.1.

3.1.2 Relative Indices and Detection Probability

3.1.2.1 Population Abundance

Suppose one is interested in the size of an endangered population after protective management policies have been initiated. If a population of animals is endangered, physical capture of individuals for marking or genetic

sampling procedures may be prohibited. Inconveniently, many populations of individuals are not distinguishable from natural markings. As part of a monitoring plan, surveys of unmarked individuals are conducted throughout the study area each year. Whenever an individual is encountered during a survey, this datum is recorded.

If these surveys had perfect detection and all individuals in the population were encountered each year, raw counts of individuals would constitute annual estimates of population size or *abundance* (N). This example of a sampling scenario is often referred to as a *population census*. Population censuses are rare in wild animal populations because study areas are often too large (or inaccessible) to sample completely, and individuals present in the portion of the study area subject to sampling often go undetected. However, some populations are regularly censused with high success, such as nesting penguins. Typically, species that can be readily surveyed with complete detection are those where individuals are highly visible, occupy a discrete location, and can be distinguished by the observer. However, for the majority of populations where a population census is not possible, it may seem natural to assume that the number of individuals seen each year still reflects the underlying population size. In other words, if more individuals are seen each year, one may be inclined to conclude that the population increased during the study period. Under this assumption, the raw

counts (C) constitute an index of *relative abundance* for each year. However, this index is in fact a product of the *true abundance* (N) and the *probability of detection* (p):

$$E(C) = Np, \tag{3.1}$$

where $E(C)$ is the expected value for C. For example, suppose the rate of change in abundance (h) from year i to year $i + 1$ is $h = N_{i+1}/N_i$. From Eq. 3.1, we have:

$$E(h) = \frac{E(C_{i+1})}{E(C_i)} = \frac{N_{i+1}p_{i+1}}{N_i p_i} = h\frac{p_{i+1}}{p_i}. \tag{3.2}$$

Reliable inferences about changes in abundance from relative indices therefore depend on the critical assumption that detection probability is constant across surveys (i.e. $p_i = p_{i+1}$). It is now widely acknowledged that a constant probability of detection is generally an unrealistic assumption (Anderson 2001; Mazerolle et al. 2007; Johnson 2008; Archaux et al. 2012). The probability of detection during any given survey can depend on observer ability, environmental variables such as time of day, season, precipitation, habitat type, wind speed, and human disturbance, as well as species characteristics such as behavior, group size, or calling intensity. For example, Archaux et al. (2012) demonstrated by simulation that a detection probability difference between count surveys as small as 4–8% can lead to a 50–90% risk of a type I error with false rejection of the null hypothesis under sampling conditions that are commonplace in ecological studies. In a seven-year study of four species of forest birds in Utah, USA, Norvell et al. (2003) showed that the assumption of constant proportionality was violated and lead to differences in estimated trends for relative abundance compared to population size.

When individuals in a population are marked, it is possible to estimate p and make inferences about N and other demographic parameters using capture-recapture methods (Chapters 5 and 7). When the object of interest is unmarked and immobile, such as individual plants, nests, or sessile animals, spatial location can take the place of the mark in providing an identification, and detection probability can be estimated with capture-recapture protocols based on *repeated sampling* or *multiple observers* (Nichols et al. 2000). Things are not so easy for unmarked, mobile populations. However, with appropriate data collection and analysis, one can also estimate detection probability and reliably estimate N (or h) using a variety of different methods (Seber 1982; Borchers et al. 2002; Williams et al. 2002; Nichols et al. 2009).

3.1.2.2 Species Occurrence

Instead of abundance, suppose that one is interested in the spatial patterns and dynamics of *species occurrence*. In this case, so-called *presence/absence* surveys can be used to make inferences about the spatial distributions of species, and these methods do not require marked individuals. The sample units in presence/absence surveys are individual sites within a larger study region of interest. Surveys consist of visits to each site, where the species of interest is either encountered or not encountered, and the number of individuals encountered at each site may or may not be recorded. Assuming species occurrence is detected perfectly at each site, the *probability of species occurrence* for the study area may be estimated as x/n, where x is the number of sites where the species was detected and n is the total number of sites. Assuming perfect detection, one may infer patterns and dynamics in the species' distribution using *presence-only* or presence/absence modeling, such as incidence functions and related approaches (Hanski 1992, 1999; He and Gaston 2003; Phillips et al. 2006; Yackulic et al. 2012a). However, it is now widely recognized that presence/absence data are also subject to imperfect detection, and presence/absence data are perhaps more appropriately described as *detection/nondetection* data (MacKenzie et al. 2002; He and Gaston 2003; Tyre et al. 2003; MacKenzie 2005).

Similar to using raw counts to infer abundance, problems arise when attempting to make inferences about species occurrence under imperfect detection. The issue is that the number of sites with detections x is a function of both the *probability of site occupancy* (ψ) and the *probability of detection* for the species at a site (p):

$$E(x) = pn\psi. \tag{3.3}$$

Failing to account for $p < 1$ will therefore result in underestimation of species occurrence. Now suppose the finite rate of change in occupancy from year i to year $i + 1$ is $h = \psi_{i+1}/\psi_i$. From Eq. 3.3, we have:

$$E(h) = \frac{E(x_{i+1})}{E(x_i)} = \frac{\psi_{i+1}p_{i+1}}{\psi_i p_i} = h\frac{p_{i+1}}{p_i}. \tag{3.4}$$

Attempting to infer changes in occupancy from an index of *relative occupancy* therefore depends on the assumption that p is constant across surveys. If one is willing to assume a constant detection probability, then the relative patterns and dynamics of species distribution can be investigated using presence-only and presence/absence modeling without explicitly accounting for detection probability (Phillips et al. 2006; Royle et al. 2012; Yackulic et al. 2012a). However, for many animals, and even plants (Kéry and Gregg 2004; Chen et al. 2012), it will more often be the case that detection is imperfect (i.e. $p < 1$) and is not constant among observers, sampling occasions, or sites. By using repeated sampling, one can use detection/nondetection data to estimate both site-level probabilities of detection and occurrence, as well as local extinction and colonization rates.

3.1.3 Hierarchy of Sampling Methods for Unmarked Individuals

A complete population census represents the most informative sampling method for an unmarked population. More commonly, study areas are too large to sample completely but individuals that are exposed to sampling are perfectly detected, allowing the use of uncorrected counts from sampled portions of the study area to estimate regional abundance (or density). Such *plot sampling* methods include quadrats (square plots), strip transects (rectangular plots), and point counts (circular plots, Seber 1982; Buckland et al. 2001; Borchers et al. 2002; Williams et al. 2002).

Given R plots each of size a, randomly selected from within a study area of size A, and containing c individuals, then abundance $(\hat{N})$ may be estimated as

$$\hat{N} = \frac{c}{Ra}A \tag{3.5}$$

and density $(\hat{D})$ as

$$\hat{D} = \frac{\hat{N}}{A} = \frac{c}{Ra}. \tag{3.6}$$

A simulated strip transect example is shown in Figure 3.2. Strip transects are often used for aerial surveys of conspicuous, common animals. For strip transects, we can modify the above formulae to accommodate the area sampled by each strip. In the example, $R = 10$ strips of half-width $w = 150$ m and length $l_i = 20$ km ($i = 1, …, R$) were placed according to a systematic random design in a study area of size $A = 560$ km^2. Hence, we now have
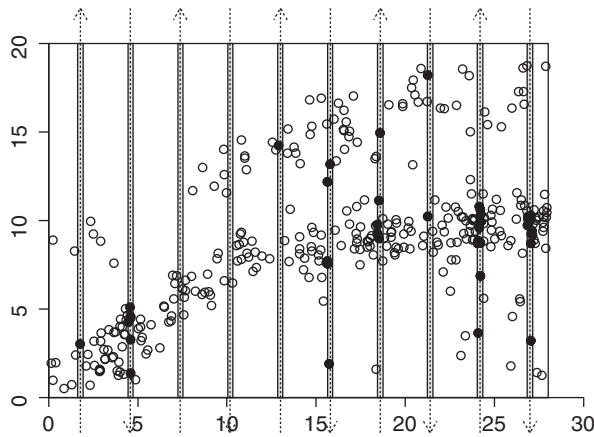
Figure 3.2 A simulated example strip transect survey that was created using the `wisp` package in R; the population comes from the `seal.pop` dataset. The surveyed strips are shown in gray with dashed lines indicating the tracklines taken during the survey. Animal locations occur within the simulated landscape (white circles), and all animals within the surveyed strips are assumed to be detected (black circles).

$$\hat{N} = \frac{c}{2wL}A, \tag{3.7}$$

and

$$\hat{D} = \frac{\hat{N}}{A} = \frac{c}{2wL}, \tag{3.8}$$

where $L = \sum_{i=1}^{R} l_i$. Assuming all $c = 40$ individuals in the strips were counted, we obtain $\hat{N} = 373$ and $\hat{D} = 0.67$ individuals km^{-2}, and because the analysis is based on a simulation, we know the true values were 345 and 0.62, respectively. Variance is calculated treating transect as the sampling unit; methods for *systematic random designs* such as this are discussed in Fewster et al. (2009). Applying the "O2" estimator of Fewster et al., the coefficient of variation (CV – standard error divided by estimate) on the above estimates is 0.23. Systematic random survey designs are generally more efficient than *completely random designs*, in the sense that they produce lower variance for the same survey effort.

When detection in the areas exposed to sampling is not perfect, one must account for $p < 1$ to reliably estimate abundance or species occurrence. Detection probability is often considered a "nuisance" parameter that is of little interest from an ecological perspective. However, because the detection process must be properly accounted for to make reliable inferences about underlying ecological processes, detection probability shall be the central theme of our chapter. Fortunately, numerous study designs facilitate simultaneous estimation of detection probability and ecological parameters of interest from unmarked populations. If distances to detected individuals can be measured, then *distance sampling methods* can be used to simultaneously estimate detection probability and abundance. However, if it is not possible to estimate distances to detected individuals, but surveys are spatially or temporally replicated, then *repeated counts* can be used to estimate detection probability and abundance.

Some animal populations are not immediately amenable to the above approaches, but nevertheless may reliably be surveyed using modifications of the methods. For example, cottontop tamarin monkeys (*Saguinus oedipus*) are endemic to Colombian forests, but are not suitable for standard count-based methods, being highly cryptic and showing strong avoidance of observers. However, monkeys can be induced to approach observers with playbacks of conspecific vocalizations; exploiting this behaviour led to the development of a *lure strip transect* by Savage et al. (2010) to derive the first range-wide population estimate. Similarly, Buckland et al. (2006) used acoustic lures in a point-based sampling scheme to derive an estimate of detection probability of Scottish Crossbills (*Loxia scotica*).

One option that is often useful when the animals themselves are hard to survey is to survey animal signs such as

whale surface blows, carnivore tracks, songbird calls, primate nests, or hare pellets. The density of these alternative, easier to measure, objects (often called "cues") can then be linked to animal density by using one or more *multipliers* or conversion factors, which usually require separate estimation using secondary surveys. For example, Laing et al. (2003) discuss methods for estimating deer dung deposition and decomposition rates, for estimation of deer density using deer dung collected along transect surveys. Some species that are hard to detect visually make frequent, loud vocalizations that can be transmitted for long distances through the environment (e.g. many cetacean species, forest elephants). Passive acoustic density estimation is a rapidly expanding field for monitoring of secretive species (Marques et al. 2013).

Multipliers are also useful when some proportion of the population can be surveyed using a standard method, and this proportion can be estimated. For example, *aerial strip transect surveys* have become more widely used now that it is possible to replace a human observer on the vehicle with a high-definition camera or video system (Buckland et al. 2012; Conn et al. 2014). For marine mammals, some proportion of animals will be underwater when the survey vehicle passes over, but if this proportion can be estimated from auxiliary information, such as a sample of tagged animals, then correction factors can be included as multipliers in the denominator of the standard strip transect formula (Eq. 3.7).

In the absence of counts of detected individuals, presence/absence surveys represent the least-informative sampling method for unmarked populations. These data represent a coarse summary of population structure and dynamics that is also subject to potential biases induced by imperfect detection at the site level. However, using repeated sampling, detection/nondetection data can be used to investigate complex hypotheses about the patterns and dynamics of species occurrence, while still accounting for imperfect detection. As we shall see, there is a fundamental relationship between abundance and species occurrence, and under certain conditions, one may even be able to estimate abundance from detection/nondetection data.

In the rest of this chapter, we focus on developing a conceptual understanding of the various methods used in abundance and occupancy estimation for unmarked animals (Figure 3.1); we limit our treatment of issues associated with survey design and field methods. However, good design and execution are key to the success of all of these methods. Anyone planning on putting these methods into practice would be well advised to consider these issues carefully, and undertake pilot surveys and pilot analyses before starting in earnest. Poor analyses

can typically be redone at low cost; the same is not true if a repeat collection of field data is required!

3.2 Estimating Abundance (or Density) from Unmarked Individuals

3.2.1 Distance Sampling

Distance sampling methods were originally developed to estimate abundance (or density) for unmarked populations where $p < 1$. A comprehensive review of the history and methods of distance sampling, as well as practical considerations for the design and implementation of these studies, is provided by Buckland et al. (2001, 2004, 2015). A large and growing literature describes the extension or modification of these methods for nearly all imaginable sampling situations, but only a fraction of these can be covered here. We focus on the fundamentals of estimating abundance with *distance sampling data* collected from line and point transects. We do not cover the practicalities of survey design and field methods, although getting these right is absolutely key to obtaining reliable results – the reader is referred to chapters 2 and 4 in Buckland et al. (2015), chapter 7 in Buckland et al. (2001), or chapter 7 in Buckland et al. (2004).

We first describe *design-based* (or *classical*) distance sampling analysis methods (Buckland et al. 2001; Buckland et al. 2015, Chapter 5). We then consider recent *model-based* distance sampling analysis methods (Hedley and Buckland 2004; Royle et al. 2004; Buckland et al. 2015, chapters 7 and 8 of Kéry and Royle 2015; see review by Miller et al. 2013a). The two terms are convenient for distinguishing different approaches to distance sampling, but design-based distance sampling is a bit of a misnomer. Both approaches use model-based methods for describing variation in detection probability within the sampled areas. The key difference is that design-based distance sampling methods use assumptions about random transect placement to extrapolate from estimated abundance in the sampled area to abundance over the entire survey region, whereas model-based distance sampling methods use a spatial model of animal distribution for extrapolation. The key advantage of design-based methods is that we can ensure the assumptions are met through good survey design, whereas for model-based methods we cannot be sure that the required assumptions about animal distribution are correct. On the other hand, model-based methods have relaxed requirements for the sampling design, and may therefore be better able to accommodate nonrandom sampling designs such as opportunistic sampling. However, flexibility does not mean that model-based approaches can salvage a poorly designed study. Relative to the desired level of inference,

reliable use of model-based approaches will necessarily depend on both the appropriateness of the model and on the quality of available data, which in turn depends on the sampling design. For a detailed discussion of model-based versus design-based inference in the context of distance sampling and animal abundance estimation in general, see Borchers et al. (2002).

3.2.1.1 Classical Distance Sampling

3.2.1.1.1 Line and Point Transects

Consider the *strip transect scenario* described in Section 3.1.3 and shown in Figure 3.2. To meet the assumption that all individuals in the strip are detected (i.e. $p = 1$), the strips have to be very narrow, so that they can be searched thoroughly as the observer moves down the trackline. Detecting all animals out to the boundary of the strip implies that there will be many animals just outside the strip that are also detected, but cannot be counted. Hence strip transect (and other plot sampling) methods are inefficient in the sense that they do not use all of the data potentially available. The survey design is fine for animals that occur at high density, where a reasonable sample can be obtained even using small plots, but it is not optimal for animals that occur at lower density, or are harder to detect, so that the plots must be prohibitively small to ensure $p = 1$. Distance sampling methods relax the assumption that all individuals must be detected, thereby allowing a larger area to be included in the sample, and hence more data to be collected (compare Figures 3.2 and 3.3a). The penalty for this is that we must now account for the animals missed. From Eqs. 3.1, 3.5, and 3.6, we can estimate abundance (N) and density (D) corrected for imperfect detection ($p < 1$):

$$\hat{N} = \frac{c}{2wL\hat{p}}A, \tag{3.9}$$

and

$$\hat{D} = \frac{\hat{N}}{A} = \frac{c}{2wL\hat{p}}. \tag{3.10}$$

Hence, to reliably estimate abundance (or density) when $p < 1$, one must be able to reliably estimate p.

Line transect surveys are the distance sampling equivalent of a strip transect (Figure 3.3a). Observers travel along randomly placed lines within the study area, and whenever an individual is detected, the perpendicular distance from the line to the individual is measured and recorded. Alternatively, the radial distance and sighting angle can be recorded in the field and then used to calculate the perpendicular distance. The other common type of distance sampling survey is a *point transect* (also called a *variable circle plot*), which is an extension of the point count plot sampling method. In point transect surveys, observers visit randomly placed points within the study area and record the radial distance from the point to any detected individuals (Figure 3.3b).

Distance sampling theory allows for individuals in the sampled areas to go undetected by exploiting the tendency for detectability to decrease with increasing distance from the line or point. Buckland et al. (2001, chapters 4 and 6) discuss some of the relative advantages of line and point transects, but where feasible, line transect distance sampling methods are generally considered more efficient, accurate, and robust (Bollinger et al. 1988). However, sampling techniques are often linked to habitat structure. For example, line transects are typically easier to implement in open habitats like grasslands or ocean,
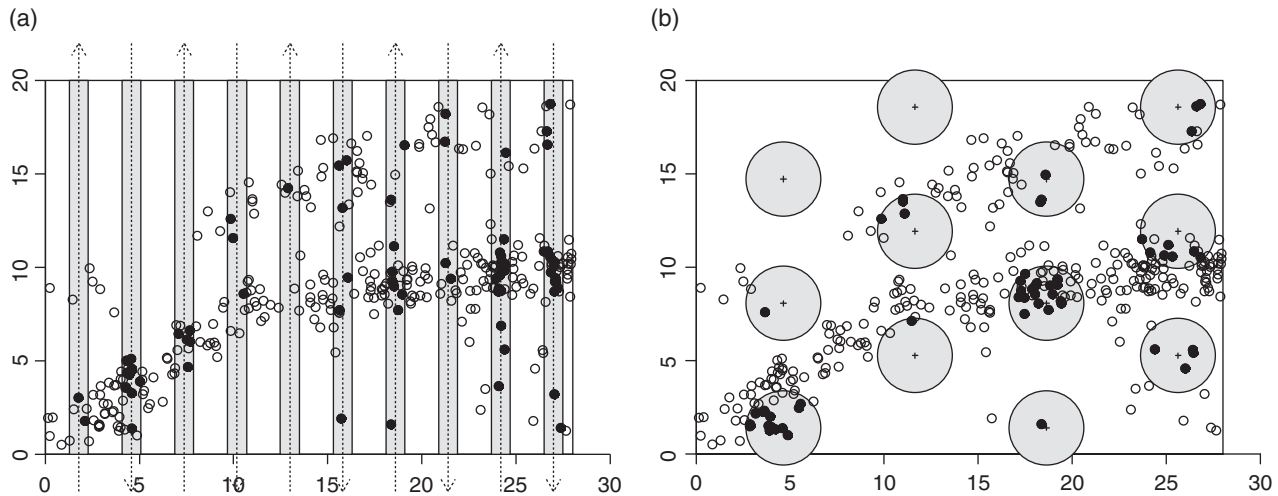
Figure 3.3 Examples of (a) line transect and (b) point transect sampling. Detected and undetected animals are shown as black and white circles, respectively. Note that compared with the strip transect survey of Figure 3.2, the line transect covers a larger area, but some individuals within the covered area are missed. Individuals closer to the line or point are more likely to be detected.

whereas point transects are more often used in closed or rugged habitats such as forests or mountains.

In cases where animals occur in distinct *clusters* (groups, flocks, herds, etc.), it is often easier to treat the cluster as the object that is sampled, recording the distance to the center of the cluster and, separately, the cluster size. Eqs. 3.9 and 3.10 then give the abundance and density of clusters; to convert to abundance and density of individuals one needs to include an additional term for population mean cluster size. In some cases, this can be reliably estimated by the mean of the observed cluster sizes. More often, however, cluster size is only recorded accurately at short distances; various methods are available to correct for any *size bias* for observations of clusters at longer distances (see Buckland et al. 2001, Section 3.5).

The density estimators using line or point transects are necessarily different because the geometry of the sampling frame differs, but both approaches have three key assumptions in common: (i) all individuals located on the line or point are detected; (ii) animal movements are negligible; and (iii) all distances (and angles, if necessary) are measured accurately. A fourth assumption is that detections are independent, but the classical methods are robust to violations of this assumption.

Based on the observed distances $x = (x_1, x_2, \ldots, x_c)$ to c detected individuals from line or point transect surveys, the basic strategy underlying classic distance sampling methods is a combination of design- and model-based approaches. Model-based methods are used to describe the detection process as a decreasing function of distance, and, given a model for the detection process, design-based methods are used to make inferences about density (or abundance). The *detection function*, $g(x \mid \theta)$, is a model for the detection process that generated the observed distance data (x) as a function of (unknown) detection process parameter(s), θ. Specifically, $g(x \mid \theta)$ is the probability of detecting an object at distance x from the line or point, conditional on the model parameters θ. Hence, $g(0 \mid \theta) = 1$ based on assumption 1. Careful specification of $g(x \mid \theta)$ is paramount to reliable estimation of θ and D (or N) from the observed distances x. Regardless of the exact form of the model, we can estimate the average detection probability, p, from the fitted detection function for line transects:

$$\hat{p} = \frac{\int_0^w \hat{g}(x \mid \theta)dx}{w}, \tag{3.11}$$

or the detection function for point transects:

$$\hat{p} = \frac{2 \int_0^w x\hat{g}(x \mid \theta)dx}{w^2} \tag{3.12}$$

(for full derivations of these estimators, see chapter 2 of Buckland et al. 2001). Here, w is the *truncation distance*, or the distance beyond which detections are ignored in the estimation of density; proper truncation of outliers can greatly aid in the modeling of the detection function (see Buckland et al. 2001, pp. 15–17). The estimates of p can then be used to obtain estimates of density (or abundance) from Eqs. 3.9 and 3.10 (or the equivalent for point transects). Fortunately, given a specified form for the detection function $g(x \mid \theta)$, free software tools are available for estimating θ and therefore N or D (Section 3.4), thereby precluding the need for us to dust off our undergraduate calculus texts.

3.2.1.1.2 Specification of the Detection Function g(x | θ)

Histograms of distance sampling data can help provide some initial insights about the purpose of the detection function. Figure 3.4a shows the distance to detected individuals from the example in Figure 3.3a, in 50 m intervals. Note the tendency for fewer individuals to be detected at greater distances from the line. We have described the detection function as a mathematical model for detection probability as a function of the measured distances to individuals detected from line or point transect surveys. There are many different models that could be used for this purpose, but decades of research have converged on a relatively small, but flexible, set of models to choose from.

Buckland (1992) synthesized much previous work and developed a unified formulation for specifying a suite of detection functions that are commonly used by practitioners. The strategy is to select a few models for $g(x \mid \theta)$ that tend to exhibit desirable qualities, such as generality, flexibility, and efficiency. In terms of shape, it is desirable for detection functions to be monotonically decreasing with a "shoulder" near the line or point. The width of the shoulder indicates the distance from the line or point to which detection remains nearly certain – this is something that is typically, at least partly, under the control of the observers; a wider shoulder leads to more robust inference. Truncation is often used to remove outlier observations recorded at unusually large distances, further improving inference (Buckland et al. 2001, pp. 15–17).

Many models for the detection function $g(x \mid \theta)$ could exhibit these qualities, but Buckland (1992) proposed detection functions using the following conceptual form:

$$g(x \mid \theta) \propto \text{key}(x \mid \theta_k)[1 + \text{series}(x \mid \theta_s)],$$

where $\text{key}(x \mid \theta_k)$ is a *key function* that serves as baseline for the model, and $\text{series}(x \mid \theta_s)$ is a *series expansion* used to adjust the key function. The key function alone can often suffice, but a series expansion can help improve the fit of

(a) Observed distances

(b) Half-normal
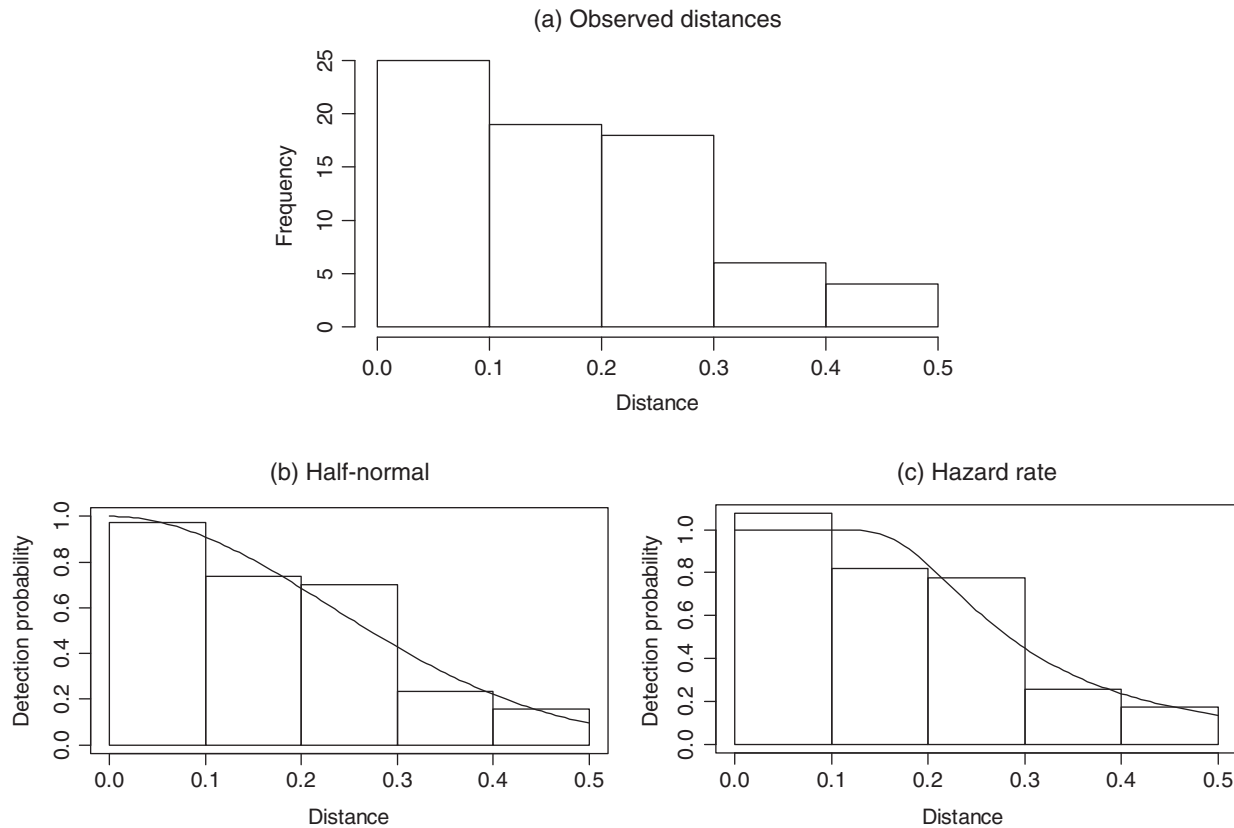
(c) Hazard rate

Figure 3.4 (a) Histogram of observed distances to detected individuals in the line transect example from Figure 3.3a. (b) and (c) Detection functions fitted to these data using half-normal (b) and hazard-rate (c) models without series expansions. Histograms of the distances are also shown in (b) and (c), scaled so that the area of the histogram is the same as the area under the fitted functions. The half-normal model has a lower AIC value and so is the preferred model, although both AIC values and estimated average detection probability, $\hat{p}$, are similar (see text).

Table 3.1 Recommended models for detection functions of the form $g(x \mid \theta) = \text{key}(x \mid \theta_k)[1 + \text{series}(x \mid \theta_s)]$, where x is distance from the line, θ_k are the key function parameters, θ_s are the series expansion parameters, and w is the truncation point (i.e. distances exceeding w are either not recorded or removed before analysis). The series expansion terms depend on a scaled value of x, $x_s = x/w$ or $x_s = x/\sigma$.

		Series expansion			
Key function	θ_k	Cosine	Simple polynomial	Hermite polynomial	θ_s
Uniform, $1/w$		$\sum_{j=1}^{m} a_j \cos(j\pi x_s)$	$\sum_{j=1}^{m} a_j(x_s)^{2j}$		a_j
Half-normal, $\exp(-x^2/2\sigma^2)$	σ	$\sum_{j=2}^{m} a_j \cos(j\pi x_s)$		$\sum_{j=2}^{m} a_j H_{2j}(x_s)$	a_j
Hazard-rate, $1 - \exp(-(x/\sigma)^{-b})$	σ, b	$\sum_{j=2}^{m} a_j \cos(j\pi x_s)$	$\sum_{j=2}^{m} a_j(x_s)^{2j}$		a_j

Source: Adapted from Buckland et al. (2001, p. 47).

the key function to the distance data. Buckland et al. (2001) recommend three key functions and three *m*th-order series expansions (Table 3.1). Figure 3.4b and c show detection functions for the *half-normal* and *hazard-rate models* without series expansions, fit to example data from Figure 3.4a. Standard likelihood-based analysis methods can be used to fit models and estimate

parameters of the detection function, and selection among candidate models can be accomplished using likelihood-based model selection procedures (Chapter 2). Additional model structures explaining variation in detection probability, such as observer, environmental, or species covariates, can also be incorporated into this framework (Marques and Buckland 2004; Marques et al. 2007).

Estimating variance of $\hat{N}$ and $\hat{D}$ involves combining estimated variances from the random components that make up the abundance and density estimates: number of observations (c), detection probability (p), and where applicable, population mean cluster size. Details of these procedures and calculation of related quantities such as coefficient of variation and confidence intervals, are given in Buckland et al. (2001, Section 3.6), although the standard method of calculating variance in c has changed based on recommendations of Fewster et al. (2009).

For the example line transect data, $\hat{p}$ is 0.56 (SE 0.05) for the half-normal and 0.62 (SE 0.07) for the hazard rate models; AIC (Akaike's Information Criterion) is −121.53 and −119.13 respectively, and so the half-normal model would be selected based on lowest AIC. Given this model, and using Eqs. 3.9 and 3.10 with $c = 72$ individuals and $w = 0.5$ km, we estimate that $\hat{N} = 360$ and $\hat{D} = 0.64$ individuals km^{-2}, which are close to the true values of 345 and 0.62 respectively. It is instructive to compare the estimates of uncertainty from the strip and line transect surveys: the former had a CV of 0.23 while the latter was somewhat more precise, with a CV of 0.20. Hence, even though line transect analysis requires estimating the detection function as an additional quantity, the additional uncertainty that this generates in the final estimate was more than compensated for by the reduction in uncertainty from being able to survey a larger area by having a longer truncation distance (w).

We were also rather generous in assuming all individuals in the strips were detected for the strip transect survey, given that the estimated detection probability at the strip transect boundary of 150 m was estimated, from the line transect data, to be 0.8. Hence, even when undertaking a strip transect survey, it is worthwhile to record the perpendicular distance to detected individuals, as a way to check the assumption that all animals are detected (see Buckland et al. 2001, pp. 335 for another example).

The above example is somewhat artificial, being based on simulated data. Numerous real-world worked examples exist, including seven case studies in chapter 8 of Buckland et al. (2001), many of which have accompanying data available as sample datasets in Program `Distance`. Three other examples in order of increasing complexity include: Williams and Thomas (2007), Marques et al. (2007) and Durant et al. (2011). A simplified version of an analysis from the latter paper is given in Box 3.1. Last, Buckland et al. (2015) provide numerous examples, with data and `R` code on an associated website.

Much of the modern research in classic distance sampling seeks to eliminate, relax, or better cope with various assumptions about the detection process. Extended models include *multiple-observer* or *mark-recapture distance*

sampling to allow for $g(0\,|\,\theta) < 1$ (Laake and Borchers 2004; Borchers et al. 2006; Buckland et al. 2010), animals moving in response to observers (Fewster et al. 2008), transect placement that is not fully random (Marques et al. 2010), and measurement error in detection distance (Marques 2004; Borchers et al. 2010). Avoidance of the observer is more common in point transects than line transects, and the issue often requires left-truncation of the distance data, thereby creating a point "donut." General recommendations for point transect surveys were reviewed by Sólymos et al. (2013) and Matsuoka et al. (2014).

3.2.1.2 Model-Based Distance Sampling

Classic distance sampling methods have strict requirements about the design of sampling surveys, thereby avoiding assumptions about spatial distribution of individuals within the study area. It is not required that individuals be *randomly distributed* within the study area (e.g. Poisson), instead that transects are randomly placed within the study area. This requirement ensures the individual-to-transect distances are random, from a known distribution (e.g. uniform in the case of a line transect), and hence allows the distance to *observed individuals* to be used to draw inferences about detectability. Randomly placed lines or points also ensure that the estimated density from the sampled area also applies to the entire study area.

In contrast, model-based distance sampling methods do not require these key assumptions about the sampling design. Model-based methods instead rely on assumptions about the spatial distribution of individuals within the sampled region. By including a model for local abundance, covariates for habitat type, region, or other factors may be used to explain variability in both abundance and detection in sampled areas, as well as make predictions about abundance in unsampled areas. Model-based methods are therefore better suited for *opportunistic sampling*. Another potential advantage is that the model may explain spatial variation in density through use of appropriate covariates, in contrast to design-based methods where spatial variability within strata contributes to estimator variance. Hence model-based methods may produce more precise estimates. One strong disadvantage, however, is that model-based methods rely on a model for animal distribution within the study area – if this model is incorrect (and remember that all models are wrong) then estimates may be biased, and variances may be wrong. We do not usually control the animal distribution, so we cannot know completely whether our models are right, or nearly so. By contrast, in classic, design-based methods, the assumptions are about the design, and we are in control of that.

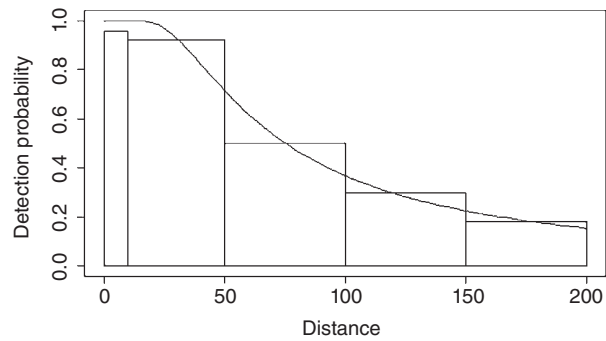**Box 3.1 Estimating Density from a Line Transect Survey Using Classical Methods**

Durant et al. (2011) estimated the seasonal and habitat-specific density, as well as temporal trends, of seven carnivore species using line transects surveys performed within a 3000 km² section of Serengeti National Park, Tanzania. Here, we focus on one species, the spotted hyaena (*Crocuta crocuta*). Our analysis is a simplified version of the one by Durant et al. using the four surveys performed in the wet and dry season in 2002–3 (hereafter 2002) and the wet and dry season of 2005 (see paper for complications that are inherent in use of earlier survey data). Approximately 30 transects, placed according to a systematic random design with 2 km transect spacing and totaling approximately 1200 km, were surveyed on each occasion, where the exact number varied by occasion depending on random start point and orientation. Sightings were of clusters (or groups) of individuals, and for each sighting the species and cluster size was recorded, as well as the estimated distance from the center of the cluster to transect, in one of nine intervals: 0–10, 10–50, 50–100, 100–150, 150–200, 200–300, 300–400, 400–500, and >500 m.

For spotted hyaenas, 494 groups were sighted. We follow Durant et al., in truncating the data at 200 m, leaving 389 groups sighted within this distance. We fit the detection function models given in Table B3.1.1, allowing up to two series expansion terms. The model would be sufficient if our interest were only in an overall density estimate, however, a goal of the analysis was to estimate density for two habitat strata within the surveys (long grass plains, LGP, and short grass plains, SGP), and it is possible that hyaena detectability varied by habitat or survey. Hence, we also fit multiple covariate models with habitat, year, and season as factor covariates (see Marques et al. 2007 for an accessible introduction to multiple covariate distance sampling). Last, we tried models that included cluster size as a continuous covariate, in case larger clusters were easier to spot. The AIC-best models (ΔAIC < 2) were as follows (HR means hazard rate and HN half-normal; cos(2) means cosine series expansion of order 2):

We observe that the AIC-best model is the HR with no series expansion terms, but that all of the other models that are close in terms of AIC, and have similar estimated

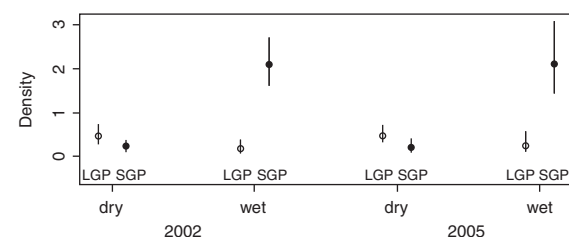
Figure B3.1.1 Fit of the hazard-rate model to detections at 50 m intervals to groups of spotted hyenas.

average detection probabilities ($\hat{p}$). These results are typical for "good" distance sampling data with a wide shoulder of high detectability at short distances. Goodness-of-fit for the selected model can be assessed by comparing the fitted detection function to a scaled histogram of the distances (see plot) as well as via a χ^2-test (other tests are available for data not collected in intervals). The fit of the hazard-rate model is good ($\chi^2 = 0.34$ with 2 d.f.; $p = 0.84$, Figure B3.1.1). Durant et al. looked for evidence of variation in cluster size between habitats or surveys and found no differences, so we follow the authors in estimating population mean cluster size as the mean of the observed cluster sizes (1.91; CV 0.05).

Density estimates were calculated by habitat and survey using Eq. 3.10, with an additional multiplier for mean cluster size. Variances and confidence intervals were derived using the standard methods described by Buckland et al. (2001, Section 3.6), except that when calculating variance in counts, *c*, a variance estimator was used that accounts for the systematic random design (estimator O2 of Fewster et al. 2009). The results are shown below (Figure B3.1.2). The results clearly demonstrate that density in the wet season is higher than the dry in the SGP habitat but not in the LGP. The findings are consistent with a "commuter" system, where Serengeti hyaenas have been observed to commute long distances from their clan territory to areas, like SGP in the wet season, where the density of migratory prey is high.

Analyses reported here were performed in the `Distance` software but almost identical results were obtained using the `Distance` package in R, which was also used to produce the plots.

Table B3.1.1 Model selection for detection functions for counts of spotted hyaenas.

	No. of parameters	AIC	ΔAIC	$\hat{p}$	$CV(\hat{p})$
HR (no series expansion)	2	1142.83	0.0	0.48	0.10
HN cos(2)	2	1142.93	0.10	0.46	0.07
HN cos(2) + cluster size	3	1143.98	1.15	0.46	0.04
HN cos(2) + season	3	1144.40	1.57	0.46	0.04
HN cos(2) + habitat	3	1144.47	1.64	0.46	0.04
HN cos(2) + year	3	1144.53	1.70	0.46	0.04
HR + cluster size	3	1144.72	1.89	0.50	0.04

Figure B3.1.2 Estimates of density for spotted hyenas during the dry and wet seasons in the long grass plains (LGP) and short grass plains (SGP). Dots are the estimates and vertical lines are 95% confidence intervals.

Relative to classic methods, development of model-based distance sampling methods is still at an early stage. As such, there remains room for much theoretical and practical development. Here, we will briefly describe some of the notable developments in model-based distance sampling.

Hedley and Buckland (2004) and Royle et al. (2004) were among the earlier developments in model-based distance sampling methods, and both seek to account for imperfect detection while incorporating environmental covariates that explain local variation in abundance within the study region of interest. Hedley and Buckland (2004) approached the problem from a classic distance sampling perspective and proposed a model conditioned on detection: the conditional distribution of x given that the observation appeared in the sample c. However, they found it simpler in practice to attack the problem in a *two-stage approach*: first to fit a detection function model to the distance data, and then conditional on this model, to fit a spatial density surface model to the corrected count data. Two-stage approaches are analytically more tractable than direct modeling of both density and observation processes. Because the transects are usually narrow compared to the size of the study area, there is also little to be learned about the large-scale spatial distribution of animals from the distances of observed animals from the transects – this provides further justification for a two-stage approach. One disadvantage of such an approach, however, is that it is not straightforward to propagate uncertainty from the first stage based on detection function modeling through to the second stage of density surface modeling. A review of model-based methods, with an emphasis on practical two-stage approaches, is given by Miller et al. (2013a), who also provide an example application with accompanying computer code. For the remainder of this section, we focus mainly on *one-stage approaches*.

Royle et al. (2004) approached the problem from a hierarchical modeling perspective and used an *unconditional* model that is the joint distribution of x and c. The approach groups the distance data for each of R transects into J distance classes, such that the distance data for sample unit (or site) i are $\boldsymbol{x}_i = (x_{i1}, x_{i2}, \dots, x_{iJ})$ for $i = 1, \dots, R$, with distance group end points (e_0, e_1), (e_1, e_2), …, (e_{J-1}, e_J). Typically, $e_0 = 0$ and $e_J = w$. For these grouped distance data, the probability that an individual is present at site i and detected in distance class j is calculated by the following function for line transects:

$$\pi_{ij} = \frac{\int_{e_{j-1}}^{e_j} g(x \mid \theta)dx}{e_j - e_{j-1}}, \qquad (3.13)$$

and by a similar function for point transects:

$$\pi_{ij} = \frac{2\pi \int_{e_{j-1}}^{e_j} x g(x \mid \theta)dx}{\pi e_J^2.} \qquad (3.14)$$

Similar to classic distance sampling, the detection function $g(x \mid \theta)$ can incorporate site-level covariates to explain variability in π_{ij}.

It is then assumed that the $\boldsymbol{x}_i$ follow a multinomial distribution with an unknown index N_i, the local population size at site i. A simple model for N_i is:

$$N_i \sim \text{Poisson}(\lambda a_i), \qquad (3.15)$$

where we assume the $\boldsymbol{x}_i$ are derived from an underlying (homogeneous) Poisson point process for the distribution of individuals in the study area, and the intensity parameter λ is the expected local density of individuals in each site (of area a_i). For line transects of length l_i, $a_i = 2e_J l_i$, and for point transects, $a_i = \pi e_J^2$. After integrating the multinomial likelihood for $\boldsymbol{x}_i$ over the random effects distribution for N_i, the resulting likelihood for $\boldsymbol{x}_i$ is

$$L(\lambda, \theta \mid \boldsymbol{x}_i) = \prod_{j=1}^{J} \text{Poisson}\left(x_{ij}; \lambda a_{ij} \pi_{ij}\right), \qquad (3.16)$$

where $a_{ij} = 2l_i(e_j - e_{j-1})$ for line transects, and $a_{ij} = \pi e_J^2$ for point transects. Density (and its variance) can then be estimated for each of the R sites using standard likelihood-based analysis methods.

From an ecological perspective, this formulation is quite interesting because it allows local abundances to be related to site-specific covariates such as habitat. The underlying distribution of animals in the study area need not be the same across sites, and Eqs. 3.15 and 3.16 can be relatively easily extended to an *inhomogeneous point process* that is a function of the covariates believed to influence local abundance (Box 3.2). Here, "inhomogeneous" refers to distributions that are not spatially uniform. For example, the degree of habitat fragmentation within a site may be related to lower local densities. The relationship can be investigated using the log link function:

$$\log(\lambda_i) = \alpha + f_i \beta, \qquad (3.17)$$

where f_i is some measure of fragmentation for site i, β is a slope parameter describing the relationship between f_i and local abundance, and α is an intercept parameter. In this manner, if measurable covariates can adequately explain variability in local densities, and these covariates can be measured in areas not exposed to distance sampling (e.g. from GIS records), it is possible to make predictions about local densities in unsampled areas. Conn et al. (2014) provide an example where aerial transect

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Box 3.2 Covariates and Link Functions

Ecological hypotheses about factors that influence detection probability, abundance, or species distribution can be investigated through the use of link functions (Table B3.2.1) that relate the parameter of interest (θ) to measurable covariates (X). When θ is a probability (i. e. $0 \leq \theta \leq 1$), a common link function is the logit link:

$$\theta = \frac{\exp(X\beta)}{1+\exp(X\beta)} \tag{3.18}$$

or, equivalently,

$$\text{logit}(\theta) = \log\left(\frac{\theta}{1-\theta}\right) = X\beta, \tag{3.19}$$

where

$$X\beta = \sum_{j=1}^{r} x_j\beta_j. \tag{3.20}$$

The parameter vector β therefore describes the relationship(s) between θ and r measurable covariates x_j ($j = 1, \ldots, r$). Note that it is common for β_1 to be designated

Table B3.2.1 Common link functions and covariates relevant to models of abundance or species occurrence under imperfect detection.

Parameter	Link function	Example covariates (x)
Detection probability (p)	logit	observer, weather conditions, habitat, effort
Mean density (λ)	log	habitat, elevation, region
Occupancy probability (ψ)	logit	habitat, elevation, region

as an intercept term by setting $x_1 = 1$. When θ is non-negative (i. e. $\theta \geq 0$), the log link function is often used:

$$\theta = \exp(X\beta)$$

or, equivalently,

$$\log(\theta) = X\beta.$$

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surveys were used in conjunction with spatial covariates for sea surface ice, temperature, and other factors to estimate local densities for three species of seals that are associated with sea ice in the Bering Sea – a study area the size of Texas!

The N_i were integrated out of the likelihood (Eq. 3.16), and estimates for N_i cannot be obtained directly from the likelihood. However, N_i can be estimated as a derived parameter conditional on $\hat{\pi}_i$ and $\hat{\lambda}_i$ using an empirical Bayes procedure[1]:

$$\Pr\left(N_i = k \mid x_i, \hat{\lambda}_i, \hat{\pi}_i\right) = \frac{\Pr(x_i \mid N_i = k, \hat{\pi}_i)\Pr\left(N_i = k \mid \hat{\lambda}_i\right)}{\sum_{j=0}^{\infty}\Pr(x_i \mid N_i = j, \hat{\pi}_i)\Pr\left(N_i = j \mid \hat{\lambda}_i\right)}, \tag{3.21}$$

which, for the Poisson local population model, provides the basis for the so-called *best unbiased predictor* of N_i (Royle et al. 2004):

$$E(N_i \mid x_i) = \sum_{j=1}^{J} x_{ij} + \hat{\lambda}_i a_i\left(1 - \sum_{j=1}^{J}\hat{\pi}_{ij}\right). \tag{3.22}$$

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1 This is based on the famous conditional probability theorem attributed to the Rev. Thomas Bayes (1701–1761), $\Pr(A \mid B) = \dfrac{\Pr(B \mid A)\Pr(A)}{\Pr(B)}$.

For simplicity, we have focused on an inhomogeneous Poisson point process model for explaining variability in local abundance, but there are many alternative models available for N_i that allow even greater flexibility in specifying various forms of spatial variation (Royle and Dorazio 2006; Royle et al. 2007; chapter 24 of Kéry and Royle 2015). However, it should be noted that although model-based approaches do not require strict random placement of line or point transects with respect to the distribution of individuals within the study area, reliable inferences to unsampled areas *still* require that the distribution of individuals in the sampled areas is representative of that in the unsampled areas. Careful study design is therefore still a requisite for reliable predictions about local abundance in unsampled areas when using model-based distance sampling methods.

Example datasets and R code utilizing these methods can be found in Royle et al. (2004) and extensions (Chandler et al. 2011; Chelgren et al. 2011; Sillett et al. 2012). Sillett et al. (2012) estimated local and total population densities for Island Scrub-Jays (*Aphelocoma insularis*) as a function of habitat-level covariates, finding higher jay densities in low-elevation chaparral habitat. Johnson et al. (2010) generalized the approach of Hedley and Buckland (2004) by implementing a full likelihood-based approach for the simultaneous estimation of detection probability and an (in)homogeneous spatial point

process, and Conn et al. (2012, 2013) developed other promising model-based extensions for multiple-observer distance sampling surveys that can accommodate species misidentification.

3.2.2 Replicated Counts of Unmarked Individuals

In distance sampling, the detection distances supply the information needed to estimate detection probability from (typically unreplicated) counts of unmarked individuals. The collection of distance sampling data is not always feasible or appropriate, and logistics often depend on the specific species of interest and sampling conditions in the field. For example, even with modern laser rangefinders, estimating distances to all individuals seen or heard during surveys can be difficult, and both accuracy and precision may depend on whether the cue for initial detection is visual or auditory. Auditory cues can be especially challenging for distance sampling because both distance *and* location must usually be estimated. However, when count surveys are temporally replicated, repeated surveys allow detection probability and therefore abundance to be estimated from unmarked counts without any need for distance data. Examples of study designs include *spatially replicated counts* (Royle 2004a) and *removal models* (Farnsworth et al. 2002; Royle 2004b). Many of these methods share similarities with model-based distance sampling approaches.

3.2.2.1 Spatially Replicated Counts

In the case of spatially replicated counts, we consider counts of unmarked individuals detected during T visits to R sample units (or sites). Let y_{it} denote the number of distinct individuals counted at site i ($i = 1, \dots, R$) on sampling occasion t ($t = 1, \dots, T_i$). Note that the number of sampling occasions, T_i, is allowed to vary among sites. The model has three assumptions: (i) the local population in each site is closed to birth, death, immigration, and emigration during the sampling period; (ii) counts at each site are independent; and (iii) individuals are not double-counted within a single sampling occasion.

Utilizing information about detection probability and local abundance afforded by repeated sampling, it is natural to assume that the counts for each site, $\boldsymbol{y_i} = (y_{i1}, y_{i2}, \dots, y_{iT_i})$ for $y_{it} \in \{0, 1, 2, \dots, N_i\}$, are binomial random variables with an unknown index N_i, the local population size at each site, and detection probability p:

$$L(N_i, p \mid \boldsymbol{y}_i) = \prod_{t=1}^{T_i} \binom{N_i}{y_{it}} p^{y_{it}} (1-p)^{N_i - y_{it}}. \tag{3.23}$$

Even with a constant detection probability, this likelihood is notoriously unstable and sensitive to small perturbations in the data. Instability is exacerbated by a tendency

for repeated count data to be sparse, with some sites having few or no detections (Box 3.3). In fact, until recently, this repeated count sampling protocol was not widely used. Royle (2004a) proposed a hierarchical modeling solution to the problem by specifying a model for the local abundance at each site (N_i). There are many options for these so-called *N-mixture* models, but a natural choice in this case is the Poisson distribution:

$$N_i \sim \text{Poisson}(\lambda), \tag{3.24}$$

with local abundance rate parameter λ, defined as the density per site or mean local abundance. Maximum likelihood analysis may then proceed using the integrated likelihood:

$$L(p, \lambda \mid \boldsymbol{y}_1, \boldsymbol{y}_2, \dots, \boldsymbol{y}_R)$$
$$= \prod_{i=1}^{R} \left[\sum_{N_i = \max(\boldsymbol{y}_i)}^{\infty} \left(\prod_{t=1}^{T_i} \text{Binomial}(y_{it}; N_i, p) \right) \text{Poisson}(N_i; \lambda) \right]. \tag{3.25}$$

Note that a similar integrated likelihood approach was used to derive Eq. 3.16, but in this case the integrated likelihood is not of a standard form (e.g. Poisson). Given a maximum likelihood estimate (MLE) for λ, an estimate of total abundance across the R sites in the sampled area is

$$\hat{N} = R\hat{\lambda}, \tag{3.26}$$

with variance approximated by the delta method:

$$\text{var}(\hat{N}) = R^2 \text{var}(\hat{\lambda}). \tag{3.27}$$

Similar to distance sampling (Eq. 3.21), the N_i are integrated out of the likelihood (Eq. 3.25), and estimates for N_i are not obtained from the likelihood. However, these again can be estimated (conditional on $\hat{p}$ and $\hat{\lambda}$) using an empirical Bayes procedure:

$$\Pr(N_i = k \mid \boldsymbol{y}_i, \hat{\lambda}, \hat{p}) = \frac{\Pr(\boldsymbol{y}_i \mid N_i = k, \hat{p}) \Pr(N_i = k \mid \hat{\lambda})}{\sum_{j=0}^{\infty} \Pr(\boldsymbol{y}_i \mid N_i = j, \hat{p}) \Pr(N_i = j \mid \hat{\lambda})}. \tag{3.28}$$

Conveniently, this expression also allows estimation of the probability of species occurrence for sites with no detections:

$$\hat{\psi}_i = 1 - \Pr(N_i = 0 \mid \boldsymbol{y}_i, \hat{\lambda}, \hat{p}) \tag{3.29}$$

(Royle et al. 2005). We will return to this relationship between local abundance and site occupancy in Section 3.3.

One of the advantages of the modeling approach above is an ability to incorporate *covariate information* about

Box 3.3 Estimating Abundance from Spatially Replicated Counts

Kéry et al. (2005) estimated abundances for eight species of bird in Switzerland using the spatially replicated count model of Royle (2004a). Here, we demonstrate this modeling approach using data from one of these species, Mallards (*Anas platyrhynchos*). Survey data were collected in 2002 during $T = 2$ or 3 visits to 235 sites throughout Switzerland. Mallards were detected at 40 sites, but counts tended to be quite low, with 87% of visits detecting no Mallards and 8% of visits detecting a single individual. In addition to counts, several temporal and site-level covariates that were believed to influence detection probability or local abundance were recorded. The covariates included date, elevation, and percent forest cover. Kéry et al. (2005) suspected detection probability might vary with date and elevation because activity associated with breeding was expected to decline during the study, but less so at higher elevations due to later breeding at higher altitudes. Based on the natural history of Mallards, they also suspected Mallards would have higher densities at lower elevations and in areas with less percent forest cover. Based on AIC, they found the best-supported models included

$$\text{logit}(p_{it}) = \alpha_0 + (\text{date})_{it}\alpha_1 + (\text{date})_{it}^2\alpha_2 + (\text{date})_{it}(\text{elev})_i\alpha_3$$
$$+ (\text{date})_{it}^2(\text{elev})_i\alpha_4$$
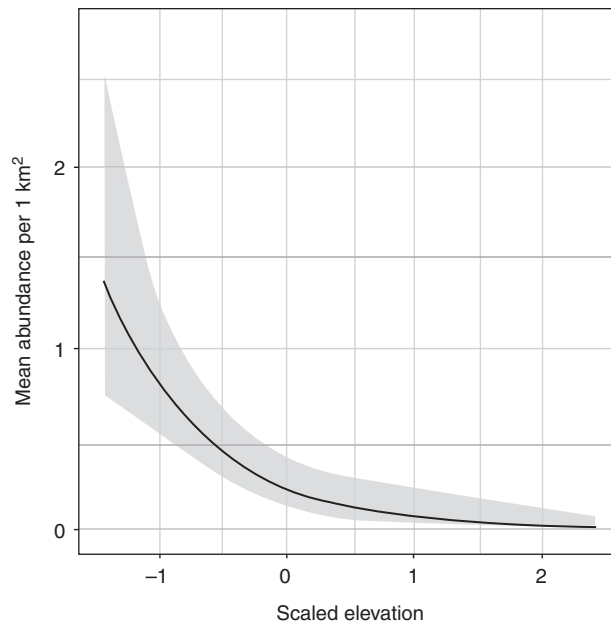
for detection probability at site *i* during visit *t*, and

$$\log(\lambda_i) = \beta_0 + (\text{elev})_i\beta_1 + (\text{forest})_i\beta_2$$

for mean local abundance at site *i*.

Estimates of the coefficients were based on standardized values for the set of covariates (Table B3.3.1). The estimates indicate that surveys occurring later in the season and at higher elevations tended to have lower detection probabilities. Perhaps more interesting from an ecological perspective, the estimates for β_1 and β_2 supported the hypothesis that sites at higher elevations

Table B3.3.1 Estimates of slope coefficients for the effects of standardized covariates on abundance of Mallards.

Parameter	Estimate	SE
α_0	0.01	0.27
α_1	−0.37	0.25
α_2	−0.33	0.17
α_3	−0.14	0.25
α_4	−0.38	0.17
β_0	−1.47	0.30
β_1	−0.92	0.30
β_2	−0.81	0.22

Figure B3.3.1 Estimates of density for Mallards (per km^2) as a function of scaled elevation. 95% confidence intervals are shaded.

(Figure B3.3.1) or with more forest cover (Figure B3.3.2) tended to have lower densities of Mallards. Across all sites, Kéry et al. (2005) estimated the total population size as $\hat{N} = 104$ (95% CI: 67–152), with a mean estimated density of 0.43 (95% CI: 0.28–0.64) Mallards per 1 km^2.
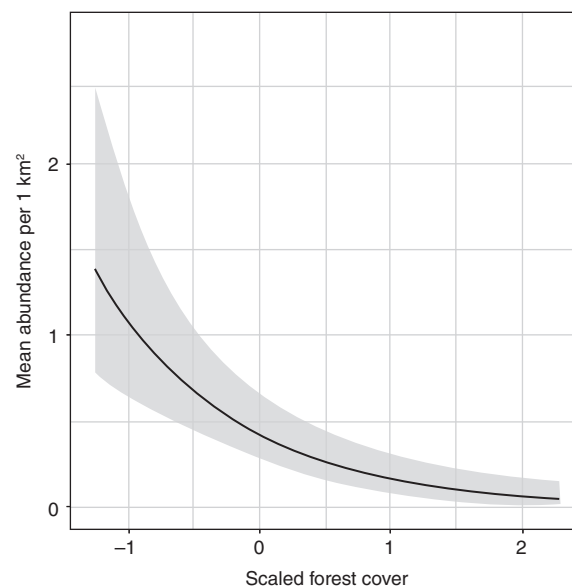
Figure B3.3.2 Estimates of density for Mallards (per km^2) as a function of scaled forest cover. 95% confidence intervals are shaded.

detection and local abundance. Either objective can be easily achieved using standard link functions:

$$\log(\lambda_i) = \alpha + \sum_{j=1}^{r} x_{ij}\beta_j, \qquad (3.30)$$

or

$$\text{logit}(p_{it}) = \alpha + \sum_{j=1}^{r} x_{ij}\beta_j + \sum_{k=1}^{q} z_{tk}\delta_k, \qquad (3.31)$$

where x_{ij} ($j = 1, \dots, r$) are r measurable covariates for site i, and z_{tk} ($k = 1, \dots, q$) are q measurable covariates for sampling occasion t (Box 3.3). Note that spatial variation in local abundance that is not explained by the measurable covariates can be incorporated using additional distributional assumptions. For example, Royle and Dorazio (2006) accounted for substantial spatial heterogeneity when estimating local abundance for a species of stream fish, the Okaloosa darter (*Etheostoma okaloosae*), by assuming $\log(\lambda_i)$ is a normally distributed random variable with unknown mean (μ_i) and variance (σ^2). When there is spatial variation in local abundance, an estimate of total abundance for the sampled area is $\hat{N} = \sum_{i=1}^{R} \hat{\lambda}_i$. Assuming the r covariates can be measured over a larger region, including unsampled sites with no count data, a total population estimate can be obtained by summing all $\hat{\lambda}_i = \hat{\alpha} + \sum_{j=1}^{r} x_{ij}\hat{\beta}_j$ over the entire region of interest.

Spatially replicated count methods have been applied to many vertebrate species, including amphibians (Dodd and Dorazio 2004; Mazerolle et al. 2007), birds (Royle 2004a; Kéry and Royle 2010; Riddle et al. 2010), and mammals (Zellweger-Fischer et al. 2011). These count methods have also been extended to open populations, thereby relaxing the closure assumption (Kéry et al. 2009; Chandler et al. 2011; Dail and Madsen 2011; Zipkin et al. 2014). When double counting occurs within sampling occasions, for example because of animal movements, Chandler and Royle (2013) use a design-induced spatial dependence among counts to estimate density, although, in practice, this approach is best suited to studies with at least some marked individuals in the population.

Although spatially replicated count methods have received a great deal of attention in recent years, a major problem with these methods is that unless detection probability is constant across sites, then a correct model for detectability must be specified. When the factors driving detectability can be identified and reliably measured, then some limited modeling of detectability is possible (Eq. 3.31). However, if there is any correlation between detection-related covariates and density-related covariates, then reliable inference is not possible because the two sets of parameters are confounded. In our opinion,

these methods should therefore be relied upon more as a last resort because other survey methods based on distance sampling or capture-recapture allow detectability to be estimated independently of density. There is no free lunch in population ecology, and repeated count methods require strong and largely untestable assumptions about detectability (Barker et al. 2018, Link et al. 2018).

3.2.2.2 Removal Sampling

A popular technique for estimating the size of exploited populations such as fisheries, *removal sampling methods* also involve counts of unmarked individuals that are detected during T visits to R sample units (or sites). As the name implies, removal methods were originally developed to estimate abundance when individuals are trapped and removed from the population (Hilborn and Walters 1992). However, if captured individuals can be temporally removed and then released after sampling is completed (Jung et al. 2005), applications of removal sampling methods need not be limited to harvested populations. In fact, if one can keep track of individuals after they are initially detected, then no physical removal is required (Farnsworth et al. 2002).

There are numerous models for estimating abundance using counts arising from removal sampling protocols (Zippin 1958; Otis et al. 1978; Farnsworth et al. 2002; Williams et al. 2002, pp. 320–325; Royle 2004b), but each uses the decline in numbers of individuals detected for the first time across the T sampling occasion to inform the estimation of detection probability. All of these removal approaches make two assumptions: (i) the population in each site is closed to birth, mortality, and movement during the sampling period of interest; and (ii) there is no double-counting of individuals across the T sampling occasions.

The general removal design under consideration involves counts for the number of individuals first detected during each sampling occasion, $y_i = (y_{i1}, y_{i2}, \dots, y_{iT})$, for site $i = 1, \dots, R$. For illustration, if we assume $T = 2$, $y_{i1} > y_{i2}$ and a constant detection probability, a simple removal estimator is:

$$\hat{N}_i = \frac{y_{i1}^2}{y_{i1} - y_{i2}} \qquad (3.32)$$

(Zippin 1958). This model has been generalized for $T > 2$ with time variation in detection probability (Otis et al. 1978; White et al. 1982), as well as for $T > 3$ with individual heterogeneity in detection probability (Pledger 2000). The familiar closed population capture-recapture models (e.g. models "M_b," "M_{tb}," "M_{bh}," and "M_{tbh}") are discussed elsewhere in Chapter 5. As with capture-recapture models for marked animals, removal models for unmarked animals that do not account for

individual heterogeneity or other sources of variability in detection probability can yield biased estimates of abundance.

Motivated by avian point counts, Farnsworth et al. (2002) developed a practical removal sampling protocol for unmarked populations that allows modeling of individual heterogeneity in detection probability when $T = 3$. The authors proposed partitioning a single visit (of duration K minutes) to R points within the study area into $T = 3$ intervals of length k_t, such that $\sum_{t=1}^{3} k_t = K$. For each point, the $y_i = (y_{i1}, y_{i2}, y_{i3})$ then consists of the number of individuals first detected in each of the intervals. *Individual heterogeneity* in detection probability is characterized by partitioning N into two groups; group 1 consists of individuals that are easily detected (with probability of detection during the first interval equal to 1), and group 2 includes those that are more difficult to detect (with probability of detection within one minute p). All individuals in group 1 (and some individuals from group 2) are therefore detected in the first interval (of length k_1). Defining c as the expected proportion of the population in group 2, $q = 1 - p$, $y_{.t} = \sum_{i=1}^{R} y_{it}$, and $y_{..} = \sum_{t=1}^{3} y_{.t}$, the model likelihood is multinomial:

$$L(c,p \mid y_1, y_2, \dots y_R)$$
$$= \frac{y_{..}!}{y_{.1}! y_{.2}! y_{.3}!} \left[\frac{1 - cq^{k_1}}{1 - cq^{K}} \right]^{y_{.1}} \left[\frac{cq^{k_1}(1 - q^{k_2})}{1 - cq^{K}} \right]^{y_{.2}} \left[\frac{cq^{k_1 + k_2}(1 - q^{k_3})}{1 - cq^{K}} \right]^{y_{.3}}.$$

$$(3.33)$$

Abundance for the sampled area can then be estimated as:

$$\hat{N} = \frac{y_{..}}{\hat{p}}. \tag{3.34}$$

When the size of the sampled area is known (e.g. from fixed-radius point counts), then density can be estimated as:

$$\hat{D} = \frac{\hat{N}}{A} \tag{3.35}$$

with variance calculated as:

$$\text{var}(\hat{D}) = \frac{y_{..}^{2} \text{var}(\hat{p})}{A^{2} \hat{p}^{4}} + \frac{y_{..}(1 - \hat{p})}{A^{2} \hat{p}^{2}}, \tag{3.36}$$

where A is the total area sampled (e.g. the sum of the areas within each fixed-radius point).

Farnsworth et al. (2002) used this approach to demonstrate strong differences in detectability for 15 bird species in Great Smoky Mountains National Park, USA, that could be attributed to variation in call intensity, time of day, and observer ability. From a practical perspective, the design can be useful because physical removal is not required. However, one must be able to distinguish newly detected individuals from those previously detected, which can be difficult for mobile or nonterritorial species.

We also note that for $T > 3$, the removal models allowing individual heterogeneity proposed by Norris and Pollock (1996) and Pledger (2000) may be preferable because these models do not assume that any group has detection probability equal to 1.

Using a similar integrated likelihood approach to that already described for model-based distance sampling (Eq. 3.16) and spatially replicated counts (Eq. 3.25), Royle (2004b) proposed a model of local abundance for removal data that assumes the y_i ($i = 1, \dots, R$) from each site are multinomial random variables with local population index N_i and cell probabilities $\pi_i = (\pi_{i1}, \pi_{i2}, \dots, \pi_{iT_i})$, where

$$\pi_{it} = p_{it}(1 - p_{it})^{t-1}, \tag{3.37}$$

and p_{it} is the probability of detection for site i on sampling occasion t. Therefore, π_{it} is the probability that an individual in site i is detected for the first time and removed during the tth sampling occasion ($t = 1, \dots, T_i$). The number of sampling occasions, T_i, is allowed to vary among sites. As before, a natural model for local abundance is

$$N_i \sim \text{Poisson}(\lambda_i), \tag{3.38}$$

which yields a now familiar integrated likelihood:

$$L(\lambda_i, p_i \mid y_i) = \prod_{t=1}^{T_i} \text{Poisson}(y_{it}; \lambda_i \pi_{it}). \tag{3.39}$$

Both λ_i and p_{it} may be modeled using site-level (i) and temporal (t) covariates as in Eqs. 3.30 and 3.31. As before, the local abundances (conditional on $\hat{\pi}_i$ and $\hat{\lambda}_i$) can be estimated using an empirical Bayes procedure (Eq. 3.21) which, for the Poisson local population model, yields the best unbiased predictor of N_i:

$$E(N_i \mid y_i) = \sum_{t=1}^{T_i} y_{it} + \hat{\lambda}_i \left(1 - \sum_{t=1}^{T_i} \hat{\pi}_{it} \right). \tag{3.40}$$

The removal sampling methodology of Royle (2004b) has been applied to a diverse range of wildlife species, including fish (Royle and Dorazio 2006), amphibians (Royle and Dorazio 2008, pp. 291–294), and birds (Royle 2004b).

3.3 Estimating Species Occurrence under Imperfect Detection

Despite its relative infancy, the past two decades have seen an explosion in the development and application of methods for estimating *species occurrence* under imperfect detection. Prior to these developments, presence/absence data were typically used to infer patterns and dynamics in occupancy through incidence functions (Hanski 1992) or other methods that do not account for detection

probability (He and Gaston 2003). In some situations, it may be perfectly reasonable to assume species are detected without error, which is analogous to a complete population census as described previously. For example, if relatively small sample units or sites within a study area are visited to determine the presence or absence of a particular species of vascular plant, then it may be unlikely that the species would go undetected in any site that is occupied (but then again, see Kéry and Gregg 2004; Chen et al. 2012). Unfortunately, this scenario does not apply to most animals, and species that are relatively small, or have cryptic or elusive behaviour, are especially problematic. Even potential proxies for species presence, such as tracks, scats, or nests, can be difficult to detect. Much recent research has therefore focused on the estimation of patterns and dynamics in site occupancy when species detection is not perfect (i.e. $p < 1$).

Recent reviews of the history and methods of occupancy models, as well as practical considerations for the design of these studies, are provided by MacKenzie et al. (2006), Royle and Dorazio (2008), Bailey et al. (2014), and Guillera-Arroita (2016). Here, we focus on the basics of occupancy estimation for a single species when $p < 1$, as well as some exciting recent developments. All of these methods use repeated sampling protocols to inform the detection process, thereby allowing inferences about species occurrence from detection/nondetection data.

3.3.1 Single-Season Occupancy Models

We begin with the *single-season occupancy model* originally presented by MacKenzie et al. (2002), which provides a foundation for extensions that follow. The sampling scenario under consideration involves surveys for a species at R distinct sample units (or sites), and each site is surveyed on T sampling occasions. We assume the occupancy status of each site is closed, such that there is no site colonization or extinction during the sampling period. The species is either detected or not detected during each of the T surveys at each of the R sites. We assume the species is never falsely detected when the species is absent from a site, i.e., there are no *false positive species detections*. When the species is present at a site, the species may be detected (with probability p) or may not be detected (with probability $1 - p$). We also assume that the detection of the species at one site is independent of detecting the species at any other site.

Similar to capture-recapture methods for marked animals (Chapters 5 and 7), we can summarize the detection data for each site using an *encounter history*. For illustration, consider an occupancy study of a calling anuran species with $T = 3$ sampling occasions at each of $R = 30$ ponds. If the species is heard during the tth visit at the ith site, we shall denote this with a "1". If the species is

Table 3.2 The $2^T = 8$ possible encounter histories (h_i) and their respective probabilities, $\Pr(h_i \mid \psi, p_i)$, for a single-season occupancy study with $T = 3$ sampling occasions. Here we allow the conditional (on presence) probability of detection (p_{it}) to vary by both site (i) and occasion (t).

h_i	$\Pr(h_i \mid \psi, p_i)$
000	$\psi \prod_{t=1}^{T}(1 - p_{it}) + 1 - \psi$
100	$\psi p_{i1}(1 - p_{i2})(1 - p_{i3})$
010	$\psi(1 - p_{i1})p_{i2}(1 - p_{i3})$
110	$\psi p_{i1} p_{i2}(1 - p_{i3})$
001	$\psi(1 - p_{i1})(1 - p_{i2})p_{i3}$
101	$\psi p_{i1}(1 - p_{i2})p_{i3}$
011	$\psi(1 - p_{i1})p_{i2}p_{i3}$
111	$\psi p_{i1} p_{i2} p_{i3}$

not detected, we denote this with a "0". The encounter history for each of the ponds is then a vector of 1s and 0s (Table 3.2). For example, the encounter history "101" indicates the species was detected at a site on the first and third sampling occasions, but was not detected on the second. In a closed population, a site with an encounter history containing at least one detection is occupied by the species. If ψ denotes the probability of species occurrence across the R sites, and p_t is the probability of detecting the species at an occupied site on occasion t, we observe the encounter history $h_i = (h_{i1}, h_{i2}, h_{i3}) = 101$ at site i with probability

$$\Pr(h_i = 101) = \psi p_1 (1 - p_2) p_3. \qquad (3.41)$$

Things are a bit more tricky when a site has the detection history $h_i = 000$. In this case, we do not know if the species was *truly absent* from the site (with probability $1 - \psi$), or if the species was indeed present (with probability ψ) but observers *failed to detect* the species on all three sampling occasions [with probability $(1 - p_t)^3$]:

$$\Pr(h_i = 000) = \left[\psi \prod_{t=1}^{T}(1 - p_t) \right] + (1 - \psi). \qquad (3.42)$$

The formulation allows the specification of a general model likelihood for ψ and $p = (p_1, p_2, \dots, p_T)$ given the encounter histories summarizing the T_i ($i = 1, \dots, R$) sampling occasions for all R sites:

$$
\begin{aligned}
&L(\psi, p \mid h_1, h_2, \dots, h_R) \\
&= \prod_{i=1}^{R} \left\{ \left[\psi \prod_{t=1}^{T_i} p_t^{h_{it}} (1 - p_t)^{1 - h_{it}} \right] + (1 - \psi) I\left(\sum_{t=1}^{T_i} h_{it} = 0 \right) \right\},
\end{aligned}
$$
$$(3.43)$$

where $I\left(\sum_{t=1}^{T_i} h_{it} = 0 \right)$ is an indicator function taking the value 1 when $\sum_{t=1}^{T_i} h_{it} = 0$ (i.e. the species was never

detected at site *i*), and 0 otherwise. Likelihood-based methods may therefore be used to simultaneously estimate occupancy and detection probability.

One of the advantages of this occupancy modeling approach is its ability to incorporate covariates that may help explain site occupancy or detection probability (Box 3.4). Using the logit link function, covariate modeling of ψ enables a broad range of ecological hypotheses to be investigated:

$$\text{logit}(\psi_i) = \alpha + \sum_{j=1}^{r} x_{ij}\beta_j, \tag{3.44}$$

where $\boldsymbol{x}_i = (x_{i1}, x_{i2}, \dots, x_{ir})$ is a collection of *r* measurable covariates that are believed to influence the probability of occupancy at site *i* (ψ_i), α is an intercept parameter, and the β_j are slope parameters describing the relationship between x_{ij} and site occupancy. As in Eq. 3.31, covariates may also be used for modeling detection probability:

$$\text{logit}(p_{it}) = \alpha + \sum_{j=1}^{r} x_{ij}\beta_j + \sum_{k=1}^{q} z_{ik}\delta_k. \tag{3.45}$$

Similar to repeated count methods (Section 3.2.2.1), if there is correlation between species occupancy and detectability, then the two become confounded. There are therefore limitations as to what relationships can be properly accounted for, and careful consideration of these limitations is important in the design and analysis of occupancy studies (see MacKenzie et al., 2006).

3.3.2 Multiple-Season Occupancy Models

Single-season occupancy models are useful for examining occupancy during the snapshot of time spanning the *T* sampling occasions. However, we are often interested in patterns and dynamics of species occurrence over time. Suppose that instead of a single sampling period of *T* occasions where we assume that sites are closed to changes in occupancy status, we conduct *M* sampling periods of $T_m (m = 1, \dots, M)$ occasions. We will still assume that the sites are closed to changes in occupancy *within* each of the *M* sampling periods, but not *between* these periods. A *multiseason occupancy model* allows us to investigate changes in site occupancy through time, as previously unoccupied sites become occupied and previously occupied sites become unoccupied.

To investigate species occurrence dynamics under imperfect detection, some additional parameters are required. In addition to ψ_m and p_{mt} for $m = 1, \dots, M$ and $t = 1, \dots, T_m$, multiseason occupancy models also estimate the probabilities of local colonization and local extinction. The *probability of local colonization* (γ_m) is the probability that a site unoccupied during sampling period *m* is occupied during period *m* + 1. The *probability of local extinction* (ϵ_m) is the probability that a site occupied during sampling period *m* is unoccupied during period *m* + 1. With these additional occupancy dynamics parameters, probabilistic arguments may still be used to model encounter histories and estimate ψ, *p*, γ, and ϵ for multiple seasons (MacKenzie et al. 2003).

Consider the case for $M = 2$, $T_1 = T_2 = 3$, and the complete encounter history $\boldsymbol{h}_i = (\boldsymbol{h}_{i1}, \boldsymbol{h}_{i2}) = 010\ 000$. The probability of observing the detection history $\boldsymbol{h}_{i1} = (h_{i11}, h_{i12}, h_{i13}) = 010$ during the first sampling period is:

$$\Pr(\boldsymbol{h}_{i1} = 010) = \psi_1(1 - p_{11})p_{12}(1 - p_{13}). \tag{3.46}$$

In this case, site *i* was clearly occupied during the first period of sampling. For the second period of sampling, the site could have remained occupied (with probability $1 - \epsilon_1$) or become unoccupied (with probability ϵ_1). The probability of observing $\boldsymbol{h}_{i2} = (h_{i21}, h_{i22}, h_{i23}) = 000$ for the second sampling period is therefore:

$$\Pr(\boldsymbol{h}_{i2} = 000) = (1 - \epsilon_1)\prod_{t=1}^{3}(1 - p_{2t}) + \epsilon_1. \tag{3.47}$$

Hence, the probability of observing the complete detection history, $\Pr(\boldsymbol{h}_i = 010\ 000)$, is simply the product of Eqs. 3.46 and 3.47.

A more complicated case arises when $\boldsymbol{h}_i = 000\ 000$. Here, the occupancy status of site *i* is never known with certainty, and all combinations of occupancy, local extinction, and local colonization are possible: (i) the site was occupied during both sampling periods, but not detected, with probability $\psi_1\prod_{t=1}^{3}(1 - p_{1t})(1 - \epsilon_1)\prod_{t=1}^{3}(1 - p_{2t})$; (ii) the site was occupied, but not detected, during the first sampling period and unoccupied during the second period, with probability $\psi_1\prod_{t=1}^{3}(1 - p_{1t})\epsilon_1$; (iii) the site was unoccupied during the first sampling period and occupied, but not detected, during the second sampling period, with probability $(1 - \psi_1)\gamma_1\prod_{t=1}^{3}(1 - p_{2t})$; or (iv) the site was unoccupied during both sampling periods, with probability $(1 - \psi_1)(1 - \gamma_1)$. Hence, the expression must combine all four possible scenarios:

$$
\begin{aligned}
&\Pr(\boldsymbol{h}_i = 000\ 000 \mid \psi_1, \epsilon_1, \gamma_1, \boldsymbol{p}) \\
&= \psi_1\prod_{t=1}^{3}(1 - p_{1t})\left[(1 - \epsilon_1)\prod_{t=1}^{3}(1 - p_{2t}) + \epsilon_1\right] \\
&\quad + (1 - \psi_1)\left[\gamma_1\prod_{t=1}^{3}(1 - p_{2t}) + (1 - \gamma_1)\right].
\end{aligned} \tag{3.48}
$$

Occupancy for the second sampling period may then be derived as $\psi_2 = \psi_1(1 - \epsilon_1) + (1 - \psi_1)\gamma_1$. Clearly, the probability statements for large *M* can become complicated
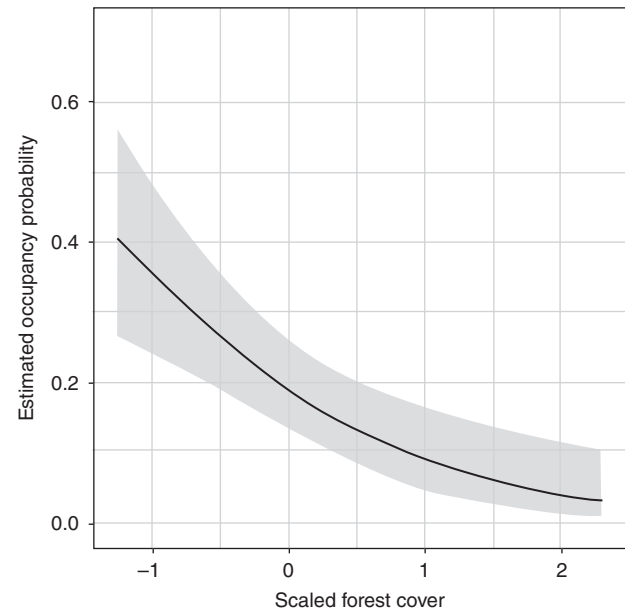
Box 3.4 A Single-Season Occupancy Analysis

Returning to the Mallard data of Kéry et al. (2005) that was described in Box 3.3, we will now use these data to estimate the probability of species occurrence using the standard single-season occupancy model of MacKenzie et al. (2002). During $T = 2$ or 3 visits to $R = 235$ sites throughout Switzerland, Mallards were detected at 40 sites. If only a single visit had been made to each site, then the $x = 31$ sites where Mallards were detected on the first visit would yield the naive estimate of occurrence probability $\hat{\psi} = \dfrac{x}{R} = \dfrac{31}{235} = 0.13$. Using the single-season occupancy model that accounts for imperfect detection, we can model both the probability of occurrence and detection probability as a function of covariates using the logit link function. Here are AIC rankings for a candidate model set including elevation (elev), percent forest cover (forest), or intercept-only (.) effects on ψ, as well as date, elevation, and intercept-only effects on detection probability (p) (Table B3.4.1).

We see there is some evidence of a seasonal effect on detection probability, but based on the AIC weights, this evidence is not overwhelming. Consistent with the original analysis of Kéry et al. (2005), both elevation and forest cover were found to affect the probability of species occurrence. Unconditional on elevation or forest cover, the mean estimate for ψ from model $\psi(.)p(date)$ was 0.20 (95% CI: 0.14–0.26), which is significantly higher than the naive estimate of 0.13. The mean estimate for p from model $\psi(elev + forest)p(.)$ was 0.67 (95% CI: 0.57–0.76), indicating that on average there was a 67% chance that a Mallard would be detected during a survey of an occupied site. When plotting site occupancy as a function of elevation or forest cover, the estimated probability of a

site being occupied declines with increasing elevation (Figure B3.4.1) or increasing percent forest cover (Figure B3.4.2).
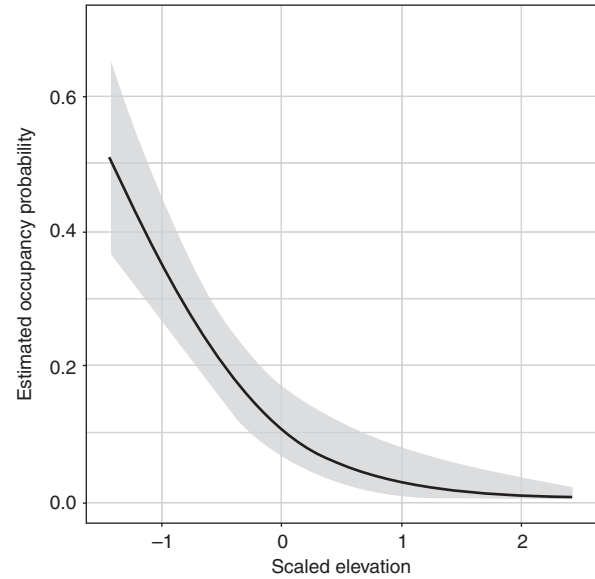
Figure B3.4.1 Estimates of the probability of occupancy for Mallards as a function of scaled elevation. 95% confidence intervals are shaded.

Table B3.4.1 Model selection for the effects of standardized covariations on the probability of occupancy for Mallards.

Model	No. of parameters	AIC	ΔAIC	AIC weight
$\psi(elev + forest)p$ $(date)$	5	314.4	0.0	0.59
$\psi(elev + forest)p(.)$	4	315.1	0.8	0.40
$\psi(elev)p(date)$	4	323.8	9.5	0.01
$\psi(elev)p(.)$	3	324.4	10.1	0.00
$\psi(forest)p(date)$	4	341.6	27.3	0.00
$\psi(forest)p(.)$	3	350.7	36.4	0.00
$\psi(.)p(date)$	3	355.5	41.2	0.00
$\psi(.)p(.)$	2	360.3	45.9	0.00

Figure B3.4.2 Estimates of the probability of occupancy for Mallards as a function of scaled forest cover. 95% confidence intervals are shaded.

and tedious, but matrix notation makes the problem tractable (MacKenzie et al. 2003, 2006).

For general M, the multiple-season occupancy model likelihood is:

$$L(\psi_1, \boldsymbol{\gamma}, \boldsymbol{\epsilon}, \boldsymbol{p} \mid \boldsymbol{h}_1, \boldsymbol{h}_2, \ldots, \boldsymbol{h}_R) = \prod_{i=1}^{R} \Pr(\boldsymbol{h}_i). \qquad (3.49)$$

Likelihood-based analysis methods may be used to estimate parameters and derive the probability of occupancy during sampling period m using the recursive relationship

$$\psi_m = \psi_{m-1}(1 - \epsilon_{m-1}) + (1 - \psi_{m-1})\gamma_{m-1}. \qquad (3.50)$$

Similar to the single-season occupancy model, site-level or temporal covariates for probabilities of site occupancy (ψ_{im}), local colonization (γ_{im}), local extinction (ϵ_{im}), and detection (p_{imt}) can be incorporated into the model parameters using logit link functions (Box 3.2).

3.3.3 Other Developments in Occupancy Estimation

The basic single- and multiseason occupancy models described above have been extended to accommodate more complicated hypotheses about species occurrence and the species detection process. The methodological explosion cannot be covered in its entirety here, but many of these developments are covered in MacKenzie et al. (2006), Royle and Dorazio (2008), and Bailey et al. (2014). Here, we briefly review a few of these extensions.

3.3.3.1 Site Heterogeneity in Detection Probability

Similar to other methods described in this chapter, heterogeneity in detection probability among sites can bias estimators of species occurrence (McClintock et al. 2010a; Miller et al. 2015). One of the earliest extensions of occupancy estimation methods sought to accommodate site heterogeneity in detection probability beyond that explained by measurable covariates believed to influence detection. These "generic" individual heterogeneity models are often needed for reliable inference about species occurrence when it may not be possible to identify, measure, or control for all important sources of variation in detection probability through study design. Occupancy models allowing *heterogeneity in detection* assume that the probability of detection probability at each site (p_i) is a random variable from some distribution, usually referred to as a *mixture distribution* (Royle 2005).

3.3.3.2 Occupancy and Abundance Relationships

In Section 3.2.2.1, we touched on a fundamental relationship between local abundance and the probability of site occupancy:

$$\psi_i = 1 - \Pr(N_i = 0). \qquad (3.51)$$

Occupancy probability is therefore the probability that there is *at least* one individual present at a site. It is also seems reasonable to suspect there may be a positive relationship between the probability of detecting a species and local abundance. In other words, sites with higher local densities may be more likely to be detected as occupied simply because there are more individuals available for detection. One may describe heterogeneity in detection probability that is induced by variability in abundance among sites by placing a mixture distribution on the unknown abundance at each site. Under certain conditions, use of mixtures may allow inference about abundance (or density) from detection/nondetection data. Royle and Nichols (2003) proposed that the detection probability for site i at sampling occasion t (p_{it}) is determined by its local population size (N_i) and the detection probability of an individual in the population (r_{it}):

$$p_{it} = 1 - (1 - r_{it})^{N_i}. \qquad (3.52)$$

In other words, the probability of detection for site i is the probability that *at least* one of the N_i individuals is detected.

Similar to models of local abundance described in Section 3.2, a model for N_i must also be specified, such as Poisson or negative binomial. The model for N_i provides an estimate of mean density (λ_i) of animals for equal-sized plots under the following four assumptions: (i) every individual in the population has the same probability of detection; (ii) individual detections must be independent; (iii) each local population is closed and N_i must be constant across all surveys of a plot; and (iv) any other sources of variability in detection can be adequately explained by measurable covariates.

In practice, these strong and largely untestable assumptions are unlikely to be valid, and violation of any of these assumptions may lead to questionable inferences about abundance (or density). For discussions on the interpretability of local abundance parameters using this approach, see Royle and Nichols (2003), MacKenzie et al. (2006, pp. 140–141), and Royle and Dorazio (2008, pp.139–140). Regardless, this formulation can still be a useful model for generic site-level heterogeneity in detection probability (Royle 2006).

3.3.3.3 Multistate and Multiscale Occupancy Models

In previous sections, we focused on two states of species occurrence, whether the site is occupied or not occupied, and at a single spatial scale of the site. However, extensions of the single- and multiple-season occupancy models can accommodate additional states and scales of occupancy. *Multistate occupancy models* allow occupied sites to be characterized by additional attributes (or

categories of occupancy), such as occupied sites where reproduction occurred (Nichols et al. 2007; MacKenzie et al. 2009), or occupied sites containing diseased or parasitized individuals (Kendall 2009; McClintock et al. 2010c). For example, suppose that anurans were repeatedly sampled at ponds and swabbed for a pathogenic fungus suspected in recent global amphibian declines. Each visit to a pond could fall under one of three possible states: (i) unoccupied by the host anuran species; (ii) occupied by the host with no infected individuals; or (iii) occupied by the host with infected individuals. If we assume no false positive host or pathogen detections, then there is no uncertainty about the state of a site when an infected individual is detected. However, due to nondetection, there remains uncertainty about the disease state of occupied ponds if the pathogen was not detected, and also about the occupancy state of ponds if the host was not detected.

Royle and Link (2005) and Nichols et al. (2007) proposed a multiple-state extension of the single-season occupancy model for this type of situation. These models may be considered a special case of *species co-occurrence models* (not covered here; see MacKenzie et al. 2006, pp. 225–247; Richmond et al. 2010). As with standard occupancy estimators, these approaches allow the estimation of occupancy and detection probability, but they also provide a means to estimate the probability that an occupied site has particular attributes such as infected or not infected, while still accounting for imperfect detection of such attributes such as infected but not detected. MacKenzie et al. (2009) further extended these methods to multiple-season models, thereby allowing investigation of species occurrence dynamics with multiple states. Many interesting ecological hypotheses about the patterns and dynamics of species occurrence may therefore be addressed using multistate occupancy modeling. For example, MacKenzie et al. (2009) showed that California Spotted Owls (*Strix occidentalis occidentalis*) did not tend to colonize a new territory and successfully reproduce within the same season.

Multistate models can also be used to investigate relationships among local abundance, occupancy, and detection probability. For example, it can be difficult to count individuals during calling anuran surveys, but calling intensity is often used as an index of breeding population size. In their analysis of calling survey data for green frogs (*Rana clamitans*), Royle and Link (2005) used a multistate occupancy model with four types of observations that were imperfectly detected: nondetection ($h_{it} = 0$), nonoverlapping calls ($h_{it} = 1$), discrete overlapping calls ($h_{it} = 2$), and a full chorus of continuous overlapping calls ($h_{it} = 3$). Each site was assumed to have a maximum potential calling index that could be observed given the underlying (latent) breeding population size. They authors found that ca. 47%

of sites were unoccupied, 33% were capable of generating nonoverlapping calls (corresponding to the lowest abundance level), 15% were capable of generating discrete overlapping calls (intermediate abundance level), and only 4% of sites had abundance levels capable of generating a full chorus of continuous overlapping calls. In an investigation of an assemblage of threatened stream fishes, Falke et al. (2010) used a similar approach that incorporated two relative abundance states (high or low), and modeled detection probability as a function of time, relative abundance, and depth of spawning habitat. They found spawning habitat area, depth, or type were important predictors of occupancy, with spawning habitat size being an important predictor of both larval occurrence and relative abundance.

By incorporating additional levels of repeated sampling, occupancy models can also be extended to multiple spatial scales (Nichols et al. 2008; Kendall 2009). For example, suppose interest is in occupancy across M geographic regions of interest, and each of these regions contains R_i sites for $i = 1, \ldots, M$. Nichols et al. (2008) developed a model for this scenario that allows occupancy estimation at both the region and site level while accounting for imperfect detection. Motivated by large-scale wildlife disease monitoring, McClintock et al. (2010c) extended the multi-state, multiple-season model of MacKenzie et al. (2009) to accommodate multiple spatial scales, and the model awaits further testing with empirical data.

3.3.3.4 Metapopulation Occupancy Models

The occupancy models described thus far have not explicitly accounted for the relative spatial locations of sites. However, the relative locations of sites could be an important factor driving patterns and dynamics of site occupancy. For example, one might expect similarity in the occupancy status of neighboring sites as a function of distance or connectivity; dispersal from an occupied site could lead to the colonization of neighboring sites, or the spread of a disease could lead to local extinction in neighboring sites. Less mechanistic approaches could utilize spatially correlated random effects (Magoun et al. 2007), but spatial models for binary response data or *autologistic models* (Besag 1972) can be used to model correlations in the occupancy status of neighboring sites.

Sargeant et al. (2005) used an autologistic model to estimate the spatial distribution of swift foxes (*Vulpes velox*) under imperfect detection. By dividing the study area into a spatial lattice of Q sites (R of which were surveyed for foxes), each site was assigned a set of s_i neighboring sites (G_i) that shared a boundary with site i. The occupancy status of each site, z_i, was then assumed to have a conditional Bernoulli distribution

$$z_i \mid \mathbf{z}_{-i} \sim \text{Bernoulli}(\psi_i), \tag{3.53}$$

where z_{-i} is a vector indicating the occupancy status (1 = occupied, 0 = unoccupied) of all sites except site i. Inclusion of spatial structure allowed site occupancy to be modeled as a function of the number of occupied neighbors for site i:

$$\text{logit}(\psi_i) = \alpha + x_i\beta, \tag{3.54}$$

where the auto-covariate

$$x_i = \frac{1}{s_i}\sum\nolimits_{j\in G_i}z_j. \tag{3.55}$$

Hoeting et al. (2000) and Royle and Dorazio (2008, pp. 314–321) describe some alternative autologistic formulations under imperfect detection. McClintock et al. (2010c) describe the use of autologistic methods in multi-state occupancy models to explain correlations in the disease infection state of neighboring sites. Bled et al. (2011) and Yackulic et al. (2012b) extended the multiple-season occupancy model to accommodate spatiotemporal autologistic models. Using a different approach, Sutherland et al. (2014) extended classical stochastic patch occupancy models (Hanski 1999) to investigate metapopulation dynamics and persistence of water voles (*Arvicola amphibius*), while accounting for imperfect detection and missing data.

3.3.3.5 False Positive Occupancy Models

It is now widely acknowledged that false negatives or nondetections are an important source of observation error that must be accounted for when making inferences about occupancy from detection/nondetection data. The false negative detection process can be adequately explained using the occupancy models described thus far, and the assumption of no false positive detections, that unoccupied sites are never falsely detected as occupied, is likely reasonable in many cases. For example, it seems reasonable to assume that studies relying on the physical capture of individuals for species identification would have low false positive error rates. However, studies relying on visual or auditory detections for species identification may be more susceptible to *false positive errors* where misidentification can lead to apparent detection of a species that is actually absent (Simons et al. 2007; McClintock et al. 2010b; Miller et al. 2012b; McClintock et al. 2015). Until recently, little attention has been focused on accounting for false positive errors in the estimation of species occurrence (but see Royle and Link 2006). If not accounted for, false positive detections can lead to overestimation of occupancy probability (Royle and Link 2006) and subsequently bias estimators for both local extinction and local colonization (McClintock et al. 2010a). Even when false positive detections are thought to be relatively rare, they are an important issue to consider.

For example, McClintock et al. (2010a) demonstrated that false positive errors constituting ≤1% of all detections in calling anuran surveys can cause severe overestimation of site occupancy, colonization, and extinction probabilities.

Miller et al. (2011) extended occupancy models to accommodate both false negative and false positive detections by utilizing additional information about the false positive detection process. The approach relies on study designs that enable occupancy status of some sites to be determined with certainty. Some species detections are known to be true positive detections, but all other (less certain) detections are susceptible to false positive errors. One way this can be accomplished is by adopting sampling protocols where observers categorize species detections as certain or uncertain. For example, calling intensities of anurans are often recorded during auditory surveys, and it may be reasonable to assume that detections of many calling individuals in a "chorus" at a site may be more reliable than a single individual detection. Another study design that can inform the false positive detection process utilizes two detection methods at each site. One sampling method may be intensive and not susceptible to false positive errors such as physical capture of individuals, whereas the second sampling method may be less intensive, but susceptible to false positive errors, such as auditory or visual surveys. Using either study design, the true underlying state for each site is either occupied or not occupied, but the observations can fall under three categories: (i) species not detected; (ii) species detected, but not with certainty; and (iii) species detected with certainty. The approach of Miller et al. (2011) uses these three types of observations to simultaneously estimate occupancy, false negative detection, and false positive detection probabilities.

Sutherland et al. (2013) extended the approach of Royle and Link (2006) to accommodate multiple seasons and transients moving through the study area. In this case, *false positives* were attributed to transient movements through otherwise unoccupied sites. Based on detections of highly distinctive latrines used to mark territories of established colonies, Sutherland et al. (2013) used their approach to separate *true occupancy* of residents from *apparent occupancy* of transients in a highly dispersive population of water voles (*Arvicola amphibious*).

3.4 Software Tools

A growing number of software tools are available for implementing the methods described in this chapter. One of the most useful and versatile is the R package `unmarked` (Fiske and Chandler, 2011). For abundance

and related demographic parameters, `unmarked` includes the distance sampling models of Royle et al. (2004) and Chandler et al. (2011), replicated count models of local abundance and open population extensions (Royle 2004a; Kéry et al. 2005; Chandler et al. 2011; Dail and Madsen 2011), and removal (or multiple-observer) sampling models (Royle 2004b). For species occurrence, the `unmarked` package includes the single- and multiple-season models of MacKenzie et al. (2002, 2003), the Royle-Nichols model relating detection probability and abundance (Royle and Nichols 2003), and single-season models accounting for both false negative and false positive detections (Royle and Link 2006; Miller et al. 2011). Kéry and Royle (2015) include examples of the use of `unmarked` as well as equivalent Bayesian models implemented in the `BUGS` language.

Program `Distance` (Thomas et al. 2009) is the most popular and comprehensive stand-alone software for the design and analysis of distance sampling data, including a built-in GIS for survey design, the classical analysis methods described above, and the model-based two-stage approach of Hedley and Buckland (2004). There are also `R` packages dedicated to distance sampling analyses, including `Distance` (Miller 2013), `mrds` (Laake et al. 2012), and `dsm` (Miller et al. 2013a). The `dsm` package implements the two-stage model-based approach of Hedley and Buckland (2004), with some extensions. Johnson et al. (2010) implemented a one-stage approach in the `R` package `DSpat` (Johnson et al. 2014). Conn et al. (2012, 2013) developed other promising model-based extensions for multiple-observer distance sampling surveys that can accommodate species misidentification and are available in the `R` package `hierarchicalDS` (Conn 2014). An `R`-based simulation package, `wisp`, is also available (www.ruwpa.st-and.ac.uk/estimating.abundance/WiSP), and was designed primarily as a teaching aid to accompany the text of Borchers et al. (2002), but covers many methods other than distance sampling. However, `wisp` is no longer under active development; instead we recommend the `R`-package `DSsim` for simulation studies to examine optimal survey design, test the effect of assumption violations, and so forth.

Programs `PRESENCE` (MacKenzie et al. 2006) and `MARK` (White and Burnham 1999) are popular stand-alone software for detection/nondetection and replicated count data. Both `PRESENCE` and `MARK` include local abundance models for spatially replicated counts (Royle 2004a), single- and multiple-season occupancy models (MacKenzie et al. 2002, 2003) and multiple-state extensions (Royle and Link 2005; Nichols et al. 2007; MacKenzie et al. 2009), finite mixture occupancy models for site heterogeneity in detection probability (Royle 2005), the Royle-Nichols occupancy model relating detection probability and abundance (Royle and Nichols 2003), the

multiscale occupancy model of Nichols et al. (2008), single-and multiple-season occupancy models accounting for both false negatives and false positives (Miller et al. 2011, 2013b), and single-season species co-occurrence models (MacKenzie et al., 2006). `PRESENCE` also includes the autologistic occupancy model of Yackulic et al. (2012b), and several other species occurrence models not described here. Program `MARK` also includes removal models (White et al. 1982; Pledger 2000), multiple-season species co-occurrence models (Richmond et al. 2010; Miller et al. 2012a), and many different capture-recapture models (Chapters 5 and 7). We note that `R` users can implement most of the models featured in Program `MARK` using the package `RMark` (Laake 2013).

Most of the approaches described in this chapter are implemented in some form in stand-alone software or `R` packages. However, the objectives underlying the design and analysis of unmarked population studies often necessitate custom computer code or model-fitting algorithms. Loaded with fully worked examples and custom code, Royle and Dorazio (2008) and Kéry and Royle (2015) provide an excellent foundation for motivated ecologists whose analysis needs are not covered by existing software.

3.5 Online Exercises

The online `R` exercises for chapter 3 include four exercises intended to acquaint the reader with several different types of analyses using unmarked population data. Exercises 1 and 2 utilize the dolphin data from Miller et al. (2013a) to provide comparative examples of classical and model-based distance sampling analyses, respectively. The goal of Exercise 3 is to recreate the analysis of spatially replicated counts of Mallards from Kéry et al. (2005) as described in Box 3.3. Exercise 4 uses the same dataset from Mallards to fit the single-season occupancy models as described in Box 3.4.

3.6 Future Directions

Over the past two decades, we have witnessed an explosion of new methods for the analysis of unmarked population data to make inferences about population abundance and species occurrence under imperfect detection. Classical distance sampling methods continue to be extended, and the more recent model-based distance sampling methods continue to be refined. Spatially replicated count and removal methods have been developed further and are regularly applied by population ecologists. Fortunately, user-friendly software is helping to facilitate increased use of these abundance estimation

methods by practitioners (Section 3.5). A recent review by Dénes et al. (2015) covers some of the recent "bleeding edge" developments in the estimation of abundance from unmarked individuals that we were unable to cover in detail here, including open population and spatially explicit models.

Classical distance sampling is partly model-based with detection function modeling, and partly design-based by using design properties to extrapolate beyond the surveyed area. Recent developments in detection function modeling have been aimed at increasing robustness through using different classes of flexible models (Miller and Thomas 2015) or relaxing assumptions such as perfect detectability (Borchers and Cox 2016) or no animal movements (Glennie et al. 2015). One particularly interesting development has been a move to unify distance sampling and capture-recapture in a common conceptual framework (Borchers et al. 2015). For model-based distance sampling, one ongoing research thrust is to embed detection function estimation within the well-established framework of point process modeling (Yuan et al. 2017), thereby leveraging that extensive literature. Another development has been to include distance sampling within the general framework of hierarchical modeling (chapters 7–8 of Kèry and Royle 2015; chapter 24 of Kèry and Royle 2016).

Developments in occupancy estimation are appearing so regularly that it can sometimes be difficult to keep up. Bailey et al. (2014) provide a review of recent advances in occupancy estimation, including many approaches not covered here. As with abundance estimation, the continued development of freely available occupancy estimation software is helping practitioners track and apply these developments as they become available. Metapopulation occupancy modeling approaches have not yet received a great deal of attention, but we anticipate the use and development of autologistic and related spatial models to rapidly increase in the future (Bled et al. 2011; Yackulic et al. 2012b; Sutherland et al. 2014). Most occupancy models are for a single species, but species co-occurrence models (MacKenzie et al. 2006; Richmond et al. 2010) have the potential to accommodate a variety of different trophic interactions and may have broad utility for questions in ecology. Species richness and community composition can also be investigated using data collected from unmarked populations in ways that are similar to the occupancy models described above. MacKenzie et al. (2006, pp. 249–264) and Royle and Dorazio (2008, pp. 379–400) provide accessible introductions to these methods, and community-level occupancy modeling is becoming more commonplace (Zipkin et al. 2009; Dorazio et al. 2010). Further development and application of methods for inferring species richness, interactions, and community dynamics from unmarked population data remains a very promising avenue for future research.

Despite mostly separate treatment of the topics in this chapter, there are clear relationships between abundance and species occurrence. We touched on some of these relationships in Sections 3.2.2.1 and 3.3.3.2. In an interesting "marriage" of the two concepts, Wenger and Freeman (2008) combined the spatially replicated count model of Royle (2004a) with the occupancy model of MacKenzie et al. (2002) for the simultaneous estimation of occupancy probability and abundance while accounting for imperfect detection. We anticipate the joint modeling of abundance and species occurrence will continue to be a focus of much future research (Royle et al. 2005).

Much of the material we have covered attempts to account for imperfect detection. One source of variability in detection probability is attributable to differences among individual animals due to behavior or appearance, and among sites due to size or habitat characteristics. Distance sampling methods are typically robust to such heterogeneity, a property of the estimators that is generally referred to as *pooling robustness* (Section 11.12 of Buckland et al. 2004). However, accommodating additional covariates that affect detectability can sometimes be useful (Section 3.2.1). By contrast, many of the other methods covered in this chapter are highly nonrobust to unmodelled heterogeneity. If not properly accounted for, individual heterogeneity can result in biased estimators of abundance because only the "most detectable" individuals are encountered. Unmarked population data contain little, if any information about individual heterogeneity in detection probability. We recommend using capture-recapture methods or other approaches for estimating abundance (Chapter 5), when individual heterogeneity is non-negligible and distance sampling methods cannot be used.

Similarly, unmarked population data contain little information about the vital rates driving population dynamics. If interest lies in estimation of demographic parameters such as fecundity, survival, or movement, then one should consider using capture-recapture or other methods that can directly examine these processes (Chapters 5, 7, and 9). If more informative methods based on marked individuals are not an option, Dail and Madsen (2011) and Zipkin et al. (2014) describe open population models for estimating demographic parameters from data on unmarked individuals. Although this may seem like squeezing juice from a turnip, these new and relatively untested approaches could be reasonable under certain conditions (but see Knape and Korner-Nievergelt 2016), particularly when used in an integrated population model. Integrated population models perhaps hold the most promise for extracting more reliable

inferences from unmarked population data (Chapter 9), and we anticipate much development in this area in the coming years (Chandler and Clark 2014).

Besides individual heterogeneity in detection probability, other issues can make reliable inference about abundance difficult to obtain from unmarked populations. Distance sampling methods are not always feasible when a species of interest is highly mobile or when it is difficult to obtain accurate distance measurements to detected individuals. Spatially replicated counts or removal methods that do not involve physical capture are not always feasible with highly mobile species because it can be difficult to avoid double counting of previously detected individuals. Similarly, removal methods involving physical removal are not always feasible for large animals or species of concern. In these circumstances, capture-recapture, or less-invasive methods, may be necessary to reliably estimate abundance (Chapter 5).

When the abundance estimation methods described in this chapter are not feasible or satisfactory, mark-recapture distance sampling (Borchers et al. 1998) and mark-resight models (White and Shenk 2001) are two examples of methodologies that can often be less expensive and less invasive alternatives to conventional capture-recapture (Chapters 5 and 7). Mark-recapture distance sampling can be particularly useful when detection at distance zero is not perfect, and mark-resight can be useful when individual heterogeneity or other sources of variability in detection probability make it difficult to reliably estimate abundance based solely on counts of unmarked individuals. By utilizing encounter data from both marked and unmarked individuals, mark-recapture distance sampling and mark-resight constitute hybridizations of capture-recapture and the unmarked population abundance estimation methods described in this chapter. Borchers et al. (1998) and Laake and Borchers (2004) describe mark-recapture distance sampling, and these methods have seen increased use since their implementation in Program `Distance` (Thomas et al. 2009) and the R package `mrds` (Laake et al. 2012). White and Shenk (2001) review mark-resight methods for estimating abundance, and McClintock and White (2012) describe some more recent approaches to estimating abundance and other demographic parameters from mark-resight data that are implemented in Program `MARK` (White and Burnham 1999). Chandler and Royle (2013) and Sollmann et al. (2013) have developed spatial models of abundance that accommodate this hybrid study design. In our chapter, we have focused on estimation of occupancy and abundance from unmarked individuals, and other book chapters address estimation of abundance and related demographic parameters from data consisting entirely of marked individual encounter (Chapters 5–7). In the future, we predict more development of hybrid models that can exploit the potentially advantageous trade-off between "inexpensive" unmarked versus "expensive" marked population data.

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