Chapter 4
Sample Survey Strategies

4.1 Introduction

The goal of wildlife ecology research is to learn about wildlife populations and their use of habitats. The objective of this chapter is to provide a description of the fundamentals of sampling for wildlife and other ecological studies. We discuss a majority of sampling issues from the perspective of design-based *observational studies* where empirical data are collected according to a specific study design. We end the chapter with a discussion of several common model-based sampling approaches that combine collection of new data with parameters from the literature or data from similar studies by way of a theoretical mathematical/statistical model. This chapter draws upon and summarizes topics from several books on applied statistical sampling and wildlife monitoring and we would encourage interested readers to see Thompson and Seber (1996), Thompson (2002b), Thompson et al. (1998), Cochran (1977), and Williams et al. (2002).

Typically, the availability of resources is limited in wildlife studies, so researchers are unable to carry out a *census* of a population of plants or animals. Even in the case of fixed organisms (e.g., plants), the amount of data may make it impossible to collect and process all relevant information within the available time. Other methods of data collection may be destructive, making measurements on all individuals in the population infeasible. Thus, in most cases wildlife ecologists must study a subset of the population and use information collected from that subset to make statements about the population as a whole. This subset under study is called a *sample* and is the focus of this section. We again note that there is a significant difference between a statistical population and a biological population (Chap. 1).

All wildlife studies should involve random selection of units for study through sample surveys. This will result in data that can be used to estimate the biological parameters of interest. Studies that require a sample must focus on several different factors. What is the appropriate method to obtain a sample of the population of interest? Once the method is determined, what measurements will be taken on the characteristics of the population? Collecting the sample entails questions of sampling design, plot delineation, sample size estimation, enumeration (counting) methods, and determination of what measurements to record (Thompson 2002b).

M.L. Morrison et al., *Wildlife Study Design.*

Measurement of population characteristics allows the calculation of summary values called *parameters* that aid in describing the population or its habitat. The most common values estimated in studies of animal or plant populations are population size, density, survival, and recruitment. Each of these values is characterized by a set of parameters of interest or estimators (means, variances, and standard errors). These estimators (e.g., mean abundance per sampling plot) then allow the scientists to draw inferences about the population under study (Williams et al. 2002). For example, in the study of a deer mouse (*Peromyscus* spp.) population, the parameters of interest might be total number of mice (population size), population survival (or mortality rate) age structure and sex ratio, and mean range size. Habitat parameters of interest might include the abundance of preferred forage each season, niche parameters such as the utilization of key food items, and the standing crop of those food items.

Design-based studies are those that have a predetermined sampling and treatment structure, usually probability based. Most studies in wildlife ecology are design-based observational studies as it is frequently difficult to assign treatments and controls randomly to wildlife populations. However, design based do differ from observational studies in that under design-based studies scientists can deliberately select a sample, avoiding unrepresentativeness (Anderson 2001; Thompson 2002). In design-based studies, basic statistical inferences concerning the study areas are justified by the design of the study and data collected (Cochran 1977). However, sampling is usually distinguished from the related field of true experimental design (Kuehl 2000) where the researchers deliberately applies a specific treatment to a randomly selected portion of the population to see what impact the treatment has on the population (Thompson 2002b). Additionally, we will discuss some of the more common model-based observational sampling approaches; these approaches use assumptions to account for patterns within the populations of interest.

4.1.1 Basic Sampling Estimators

Sampling in wildlife studies is used to obtain parameter estimates for individuals within the population of interest. The goal of any ecological study is to provide estimates that are accurate as discussed in Sect. 2.5.4. If the design is appropriate and implemented correctly, wildlife ecologists can obtain estimates that satisfy these requirements with few assumptions about the underlying population.

In order to determine estimates for the population characteristics of interest, we must use an *estimator*. The most common estimators are those for means, variances, and other associated measures of central tendency and precision. The primary measure of central tendency collected in ecological studies is the sample mean ($\bar{x}$). Consider a simple random sample taken from all potential plots of a statistical population to measure some characteristic x (no. of individuals per plot) and our interest is in estimating the mean number of individuals per plot. The sample mean ($\overline{x}$) will be an unbiased estimator for the population mean (μ) or the average population size for each randomly selected sample. While the population mean is the average measurement for each of N samples (after Cochran 1977; Thompson 2002b) defined as

$$\mu = \frac{1}{N}(X_1 + X_2 + \cdots + X_N) = \frac{1}{N}\sum_{i=1}^{N} X$$

the sample mean $\overline{x}_{\mathrm{i}}$ is the average count from those surveyed plots selected under the simple random sampling design (n) estimated by

$$\overline{X} = \frac{1}{N}(X_1 + X_2 + \cdots + X_N) = \frac{1}{n}\sum_{i=1}^{n} X_i.$$

In this situation, we assumed we had a *finite* population of known size N. Thus, within a simple random sampling framework, the sample variance (s^2) is an unbiased estimator for the finite population variance σ^2. Thus,

$$s^2 = \frac{1}{n-1}\sum_{i=1}^{n}\left(X_i - \overline{X}\right)^2$$

This approach holds true for estimation of subpopulation means (mean of a statistical population based on stratification). A subpopulation mean is one where we wish to estimate the mean of a subsample of interest. For example, consider the situation where we want to estimate the abundance of mice (*Mus or Peromyscus*) across an agricultural landscape. After laying out our sampling grid, however, we determine that abundance of the two species should be estimated for both fescue (Family Poaceae) and mixed warm-season grass fields. Thus, we are interested in both the mean number of mice per sample plot and the mean number of mice per sample plot within a habitat type, e.g., a subpopulation. For habitat type h, our sample mean subpopulation estimates would be

$$\overline{X}_{\mathrm{h}} = \frac{1}{N}\sum_{i=1}^{n_{\mathrm{h}}} X_{\mathrm{h}_i}$$

with sample variance

$$s_{\mathrm{h}}^2 = \frac{1}{n_{\mathrm{h}} - 1}\sum_{i=1}^{n_{\mathrm{h}}}\left(X_{\mathrm{h}i} - \overline{X}_{\mathrm{h}}\right)^2$$

As many ecological researchers wish to estimate the total population size based on sample data, under a situation with no subpopulation estimates, our estimator for total population size (T) would be

$$\hat{T} = \frac{N}{n}\sum_{i=1}^{n} X_i.$$

Additional information on estimation of population total and means for more complex designs can be found in Cochran (1977) and Thompson (2002b).

4.1.2 Plot Construction

We use sampling designs to ensure that the data collected are as accurate as possible for a given cost. Thus, plot construction necessitates that researchers evaluate the impacts of different plot sizes and shapes have on estimator precision. Although the importance of determining optimal sizes and shape for sampling plots [for consistency within the text, we are using "plots" rather than "quadrats" as defined by Krebs (1999)] is obvious. With the exception of work by Krebs (1989, 1999) and general discussion by Thompson et al. (1998), there has been little research on plot construction in wildlife science. Wildlife tend to be nonrandomly distributed across the landscape and are influenced by inter- and intraspecific interactions (Fretwell and Lucas 1970; Block and Brennan 1993). When developing a sampling design to study a population, the researcher must decide what size of plots should be used and what shape of plots would be most appropriate based on the study question and the species life history (Thompson et al. 1998; Krebs 1999). Most frequently, plot size and shape selection is based on statistical criteria (e.g., minimum standard error), although in studies of ecological scale, the shape and size will be dependent upon the process under study (Krebs 1999). Additionally, it is important to realize that estimates of precision (variance) are dependent upon the distribution of the target organism(s) in the plots to be sampled (Wiegert 1962).

Krebs (1999) listed three approaches to determine which plot shape and size would be optimal for a given study:

1. Statistically, or the plot size which has the highest precision for a specific area or cost
2. Ecologically, or the plot sizes which are most efficient to answering the question of interest
3. Logistically, or the plot size which is the easiest to construct and use

Plot shape is directly related to both the precision of the counts taken within the plot and potential coverage of multiple habitat types (Krebs 1999). Four primary factors influence plot shape selection: (1) detectability of individuals, (2) distribution of individuals, (3) edge effects, and (4) data collection methods. Shape relates to count precision because of the *edge effect*, which causes the researcher to decide whether an individual is within the sample plot or not, even when total plot size is equal (Fig. 4.1). Given plots of equal area, long and narrow rectangular plots will have greater edge effect than square or circular plots. Thompson (1992) concluded that rectangular plots were more efficient than other plots for detecting individuals. Note that, in general, long and narrow rectangular plots will have a greater chance of intersecting species with a clumped distribution. Previous research in vegetation science has shown that rectangular plots are more efficient (higher precision) than square plots (Kalamkar 1932; Hasel 1938; Pechanec and Stewart 1940; Bormann 1953). Size is more related to efficiency in sampling (Wiegert 1962), in that we are trying to estimate population parameters as precisely as possible at the lowest cost (Schoenly et al. 2003). Generally, larger plots have a lower ratio of edge to interior,

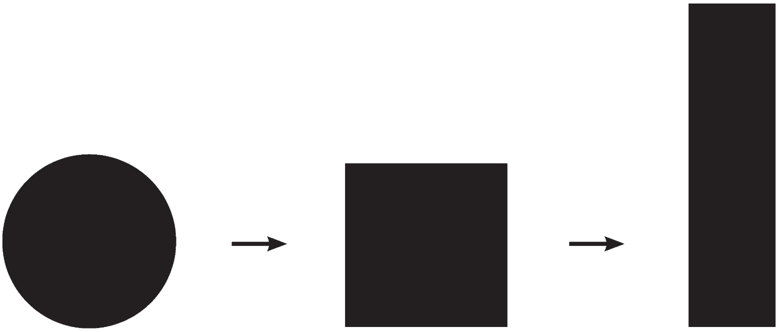

Fig. 4.1 An example of three different types of plot shapes, each with the same area, but with different perimeter to edge ratios. Reproduced from Thompson et al. (1998) with kind permission from Elsevier

limiting potential edge effects. Large plots, however, are typically more difficult to survey based on cost and logistics. Thus, under a fixed budget, there is a general trade off between plot size and number of plots to sample. A method developed by Hendricks (1956) found that as sample area increased, variance decline, but this method is less flexible as this approach had several assumptions such as proportionality of sampling cost per unit area.

4.2 Basic Sample Structure, Design, and Selection

Wildlife studies are limited by fundamental principles of inferential statistics when using sample survey data to make predictions about the population of interest. Within the population or study area boundaries, statistical inference is limited by the protocol by which study sites and/or study specimens are selected. Thus, sampling is an example of inductive logic wherein the conclusions are determined based on a limited number of events (Foreman 1991; see Sect. 1.2.3.2 and Table 1.1). A sample is a subset of the population of interest, where the population encompasses every individual located in a particular place at a particular time. Sampling entails selecting sample units (unique collection of elements; Scheaffer et al. 1990) from a sampling frame from a population and then collecting measurements on the sampling unit (Foreman 1991). Note that sampling units and elements can represent the same quantity (Thompson et al. 1998). Essentially, our purpose in sampling is to make inferences to our target population or those individuals within the population study boundaries at a specific time.

One of the primary functions of statistic and sampling is to make inductive inference and measure the degree of uncertainty around such inferences (Mood et al. 1974). Scientific progress in ecological studies is often credited to experiments that randomize and replicate treatments (Johnson 2002). However, ecologists are frequently unable to randomize treatments and must use natural experiments or descriptive studies consisting of observations of an organism's response to a perturbation.

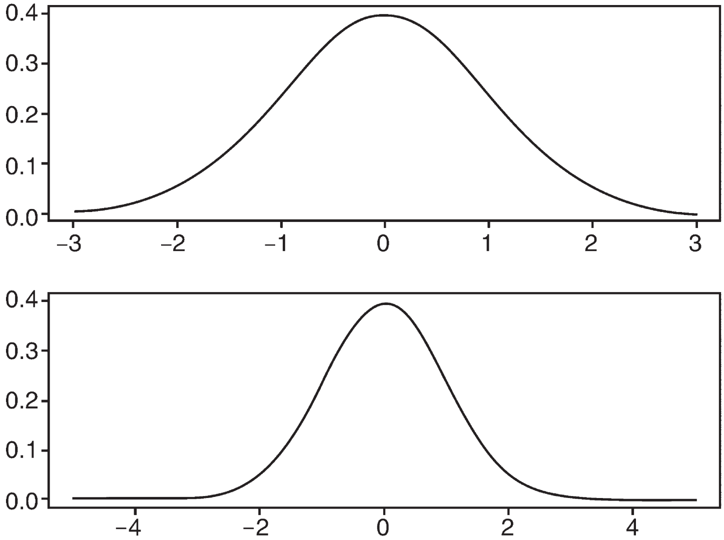

Fig. 4.2 Two normal distributions with different the same mean and different variances

Methods for sample selection typically fall into two general categories: nonrandom sampling and random sampling. In random sampling, also called probability sampling, the selection of units for inclusion in the sample has a known probability of occurring. If the sample is selected randomly, then based on sample survey theory (Cochran 1977) the sample estimates will be normally distributed. With normally distributed estimates, knowledge of the sample mean and variance specifies the shape of the normal distribution (Fig. 4.2). There is considerable literature justifying the need for probabilistic sampling designs from a standpoint of statistical inference (Cochran 1977; Thompson and Seber 1996; Thompson 2002b), but little evidence exists that nonprobabilistic samples can be inferentially justified (Cochran 1977; Anderson 2001; Thompson 2002a). In wildlife ecology, nonprobabilistic sampling designs are likely to be divided into several (overlapping) categories which we generalize as convenience/haphazard sampling (hereafter convenience) or judgment sampling/search sampling (hereafter judgment) while probabilistic sampling is the other category used in wildlife ecology. For the rest of the chapter, we will discuss these different sampling designs and their application to wildlife ecology research.

4.2.1 Nonprobability Sampling

Convenience sampling has historically been the most common approach to sampling wildlife populations. A convenience sample is one where the samples chosen are based on an arbitrary selection procedure, often based on accessibility, and justified because of constraints on time, budgets, or study logistics. Gilbert (1987, p. 19) noted in discussion of *haphazard sampling*, that:

> Haphazard sampling embodies the philosophy of "any sampling location will do." This attitude encourages taking samples at convenient locations (say near the road) or times, which can lead to biased estimates of means and other population characteristics. Haphazard sampling is appropriate if the target population is completely homogeneous. This assumption is highly suspect in most wildlife studies.

Examples of convenience sampling approaches are abundant in wildlife ecology: abundance and sex ratio estimates from spotlight surveys from roads for white-tailed deer (Collier et al. 2007), point counts along roads for birds (Peterjohn et al. 1996), surveys for mammal tracks near roads, habitat sampling in only locations where individuals were detected, to name a few. In these situations, the location of the individual(s) of interest determines the location and number of samples collected, but with no scheme to infer to the larger population (Thompson and Seber 1996). Certain kinds of surveys, such as report card harvest surveys, may have an element of convenience sampling in them if the sample is self-selected by individuals volunteering to complete the survey. One of the limitations of convenience sampling is that it cannot provide data for valid statistical inferences, because results are not repeatable. Information obtained by this type of sampling may be appropriate for preliminary inventory of an area but should not be used for formal discussion of parameter estimates.

Judgment or search sampling is another common approach used in wildlife studies. This form of sampling is based on the presumption that the wildlife scientist can select studies representative of the study area or population based on expert knowledge of the system, often requiring historical knowledge or data indicating where the resources of interest exist. Gilbert (1987) argued that judgment sampling results in subjective selection of population units by the researcher resulting in the following outcome:

> If the [researcher] is sufficiently knowledgeable, judgment can result in accurate estimates of population parameters such as means and totals even if all population units cannot be visually assessed. But, it is difficult to measure the accuracy of the estimated parameters. Thus, subjective sampling can be accurate, but the degree of accuracy is difficult to quantify.

Judgment sampling may be appropriate for preliminary inventory of an area, but is not useful for statistical inferences because results are not repeatable. Judgment sampling may have a role to play in understanding the mechanisms in force in a biological system. For example, several study areas may be selected to investigate the magnitude and duration of an environmental impact or the effect of some management action under a specific set of conditions. Judgment sampling can also be used to develop data for models of natural systems (see capture–recapture model discussion later in this chapter). However, statistical inferences from sites selected for study are strictly limited to the study sites selected and any inference beyond those sites is deductive, depending on the professional judgment of the individual making the selection and the rules by which the sites are selected.

Note that all of the above sampling approaches are based on nonprobabilistic designs and rely either on observations of the organism or expert opinion to select locations for sample data collection. Consequently, while many convenience sampling procedures are often justified based on their economics (e.g., easier to sample roads than contact landowners for access), this is often not the case as these samples do not allow for wide ranging inferences, thus limiting their applicability. Probabilistic samples allows the researcher to design a study and be confident that the results are sufficiently accurate and economical (Cochran 1977). Nonprobabilistic sampling, while common, do not lend themselves to valid statistical inference or estimation of variability and often more cost is incurred attempting to validate convenience samples than would be spent developing and applying probabilistic designs.

4.2.2 Probability Sampling

Random sampling is the process by which samples are selected from a set of n distinct sampling units, where each sample has a known likelihood of selection predetermined by the sampling methods chosen (Cochran 1977; Foreman 1991). Samples selected probabilistically provide a basis for inference (estimation of means and variances) from the data collected during the sampling process; samples from nonprobability designs do not have this characteristic.

4.2.3 Single-Level and Multilevel Probability Sampling

The simplest form of random sampling is sampling at a single level or scale. That is, the study area is divided into a set of potential units from which a sample is taken. For example, a study area could be divided into a grid of sample plots all of the same size from which a simple random sample is drawn (Fig. 4.3). The organisms of interest in each cell in the selected sample are then counted. In its simplest sense, single level sampling for a simple random sample, assume that we have $n = 100$ distinct samples, $S_1, S_2, \ldots, S_n$, where each sample S_i has a known probability of selection (π_i) or the probability that the ith sample is taken (Cochran 1977). Assuming that each sample unit (plot) is of equal size, then the probability that a single plot is chose to be sampled is 1/100 or $\pi_i = 0.01$. In the application of single-level probability sampling we assume that each unit in the population has the same chance of being selected. Although this assumption may be modified by other probabilistic sampling schemes (e.g., *stratified sampling* or *unequal probability* sampling), the decisions regarding sample selection satisfy this assumption. Sampling at more than one level, however, often is beneficial in wildlife studies. Multilevel sampling can be simple, such as selecting subsamples of the original probability sample for additional measurements as described in ranked set sampling (Sect. 4.3.5). Multilevel sampling can be more complicated, such as double sampling to estimate animal abundance (Sect. 4.3.6). In the correct circumstances, multilevel sampling can increase the quality of field data, often at a lower cost.

1	2	3	4	5	6	7	8	9	10
11	12	13	14	15	16	17	18	19	20
21	22	23	24	25	6	7	8	9	10
31	32	33	34	35	36	37	38	39	40
41	42	43	44	45	46	47	48	49	50
51	52	53	54	55	56	57	58	59	60
61	62	63	64	65	66	67	68	69	70
71	72	73	74	75	76	77	78	79	80
81	82	83	84	85	86	87	88	89	90
91	92	93	94	95	96	97	98	99	100

Fig. 4.3 A simple sampling frame of 100 sample plots that can be used for selecting a simple random sample

4.3 Sampling Designs

Although a simple random sample is the most basic method for sample selection, there are others that are relevant to wildlife ecology studies, including stratified random sampling, systematic sampling, sequential random sampling, cluster sampling, adaptive sampling, and so on. These sampling plans (and others) can be combined or extended to provide a large number of options for study designs, which can include concepts like unequal probability sampling. Many sampling designs are complicated, thus statistical guidance is suggested to select the appropriate design and analysis approaches. Below we discuss several sampling scales and then appropriate designs for each scale.

4.3.1 Simple Random Sampling

Simple random sampling is the selection of n units from a population of N units in a manner such that each of the n units has the same chance (probability) of being selected (Cochran 1977; Foreman 1991). Simple random sampling requires that the location of each sample site (unit) be selected independently of all other sites (units). Typically in ecology studies, a given unit appears at most once in the sample when sampling without replacement (Thompson 2002b). Samples can be replaced after measurements are taken so that sampling is with replacement but sampling without replacement results in a more precise estimate (Caughley 1977; Thompson 2002b).

A simple random sample may be obtained by following the basic steps in the following list (Cochran 1977; Thompson 2002b):

1. The population of sampling units is assumed to be *finite*.
2. Units (*n*) selected in the sample can be located and the measurement of the attribute of interest (e.g., count of animals) on the unit is possible. Also, the error in measuring the attribute of interest should be small compared with the differences in the attribute (counts) from unit to unit.
3. The study region, also known as the sampling frame, must be completely covered by distinct and nonoverlapping sampling units.
4. Sampling units need not be of equal size nor selected with equal probability, but differences in size and selection probability increase the complexity of those parameter estimation formulas.
5. Sample units are normally sampled without replacement.

Random sampling plans have straightforward mathematical properties (Sect. 4.1.1), but random locations are often more clumped and patchy than expected. In studies with small sample sizes, which are common in wildlife studies, entire regions of a sampling frame may be under- or overrepresented. Thus, random sampling is not always the best procedure. Random sampling should be used only if the area of interest is homogeneous with respect to the *elements* and *covariates* of interest. Because this is seldom the case, researchers should try to avoid relying solely on simple random sampling.

4.3.2 Stratified Random Sampling

In *stratified sampling*, the sampling frame is separated into different regions (*strata*) comprising the population to be surveyed and a sample of units within stratum are selected for study, usually by a random or systematic process. Ideally, strata should be homogeneous with respect to the variable of interest itself (e.g., animal density), but in practice, stratification is usually based on covariates that scientists hope are highly correlated with the variable of interest (e.g., habitat types influences animal density). Stratification may be used to increase the likelihood that the sampling effort will be spread over important subdivisions or strata of the study area, population, or study period (Fig. 4.4). Similarly, units might also be stratified for subsampling. For example, when estimating the density of forest interior birds, the wildlife biologist might stratify the study area into regions of high, medium, and low canopy cover and sample each independently, perhaps in proportion to area size.

Stratification is common in wildlife studies, as it often is used to estimate parameters within strata and for contrasting parameters among strata. This type of analysis is referred to using “strata as domains of study… in which the primary purpose is to make comparisons between different strata” (Cochran 1977, p. 140). Under

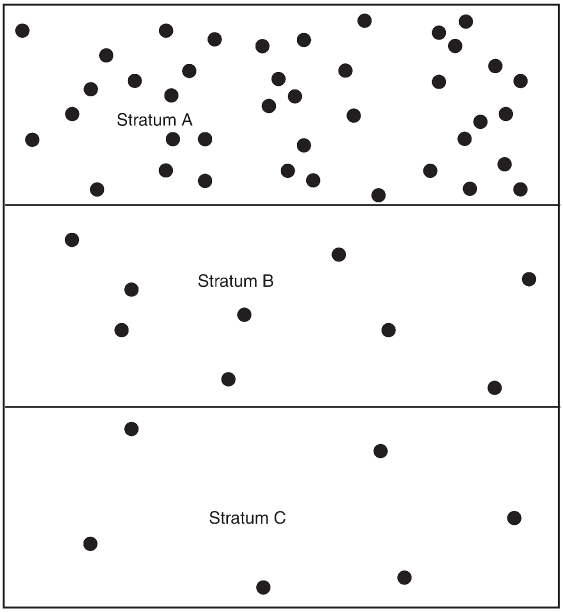

Fig. 4.4 Stratification based on the density of a population. Reproduced from Krebs (1999) with kind permission from Pearson Education

stratified designs, the formulas for analysis and for allocation of sampling effort (Cochran 1977, pp. 140–141) are quite different from formulas appearing in introductory texts such as Scheaffer et al. (1990), where the standard objective is to minimize the variance of summary statistics for all strata combined.

The primary objective of stratification is improved precision based on optimal allocation of sampling effort into more homogeneous strata. In practice, it may be possible to create homogeneous strata with respect to one or a few primary indicators, but there are often many indicators measured, and it is not likely that the units within strata will be homogeneous for all of them. For example, one could stratify a study area based on vegetative characteristics and find that the stratification works well for indicators of effect associated with trees. But, because of management (e.g., grazing), the grass understory might be completely different and make the stratification unsatisfactory for indicators of effect measured in the understory. Differences in variance among strata for the primary indicators may not occur or may not be substantially better than random sampling. Factors used to stratify an area should be based on the spatial location of regions where the population is expected to be relatively homogeneous, the size of sampling units, and the ease of identifying strata boundaries. Strata should be of obvious biological significance for the variables of interest.

A fundamental problem is that strata normally are of unequal sizes; therefore, units from different strata have different weights in any overall analysis. The formulas for computing an overall mean and its standard error based on stratified sampling are relatively complex (Cochran 1977). Formulas for the analysis of subpopulations (subunits of a study area) that belong to more than one stratum (Cochran 1977, pp. 142–144; Thompson 2002b) are even more complex for basic statistics such as means and totals. Samples can be allocated to strata in proportion to strata size or through some optimal allocation process (Thompson 2002b). When using the stratification with proportional allocation, the samples are self-weighting in that estimates of the overall mean and proportion are the same as for estimates of these parameters from simple random sample. Although proportional allocation is straightforward, it may not make the most efficient use of time and budget. If it is known that within strata variances differ, samples can be allocated to optimize sample size. Detailed methods for optimizing sample size are described in Cochran (1977) and Thompson (2002b).

Stratification has some inherent problems. In any stratification scheme, some potential study sites will be misclassified in the original classification (e.g., a dark area classified as a pond on the aerial photo was actually a parking lot). Stratification is often based on maps that are inaccurate, resulting in misclassification of sites that have no chance of selection. Misclassified portions of the study area can be adjusted once errors are found, but data analysis becomes much more complicated, primarily because of differences in the probability of selecting study units in the misclassified portions of the study area. Short-term studies usually lead to additional research questions requiring longer term research and a more complicated analysis of subpopulations (Cochran 1977, pp. 142–144) that cross strata boundaries. However, strata may change over the course of a study. Typical strata for wildlife studies include physiography/topography, vegetative community, land use, temporal frame, or management action of interest. Note, however, that the temporal aspect of a study is of particular significance when stratifying on a variable that will likely change with time (e.g., land use). Stratified sampling works best when applied to short-term studies, thus reducing the likelihood that strata boundaries will change. In long-term studies, initial stratification procedures at the beginning of the study are likely to be the most beneficial to the investigators.

4.3.3 Systematic and Cluster Sampling

In *systematic sampling*, the sampling frame is partitioned into primary units where each primary unit consists of a set of secondary units (Thompson 2002b). Sampling then entails selecting units spaced in some systematic fashion throughout the population based on a random start (Foreman 1991). A systematic sample from an ordered list would consist of sampling every *k*th item in the list. A spatial sample typically utilizes a systematic grid of points. Systematic sampling distributes the locations of samples (units) uniformly through the list or over the area (site). Mathematical properties of systematic samples are not as straightforward as for random sampling, but the statistical precision generally is better (Scheaffer et al. 1990).

Systematic sampling has been criticized for two basic reasons. First, the arrangement of points may follow some unknown cyclic pattern in the response variable. Theoretically, this problem is addressed a great deal, but is seldom a problem in practice. If there are known cyclic patterns in the area of interest, the patterns should be used to advantage to design a better systematic sampling plan. For example, in a study of the cumulative effects of proposed wind energy development on passerines and shore birds in the Buffalo Ridge area of southwestern Minnesota, Strickland et al. (1996) implemented a grid of sampling points resulting in observations at varying distances from the intersection of roads laid out on section lines.

Second, in classical finite sampling theory (Cochran 1977), variation is assessed in terms of how much the result might change if a different random starting point could be selected for the uniform pattern. For a single uniform grid of sampling points (or a single set of parallel lines) this is impossible, and thus variation cannot be estimated in the classical sense. Various model-based approximations have been proposed for the elusive measure of variation in systematic sampling (Wolter 1984). Sampling variance can be estimated by replicating the systematic sample. For example, in a study requiring a 10% sample it would be possible to take multiple smaller samples (say a 1% sample repeated ten times), each with a random starting point. Inference to the population mean and total can be made in the usual manner for simple random sampling.

Systematic sampling works very well in the following situations:

1. Analyses of observational data conducted as if random sampling had been conducted (effectively ignoring the potential correlation between neighboring locations in the uniform pattern of a systematic sample)
2. Encounter sampling with unequal probability (Overton et al. 1991; Otis et al. 1993)
3. The model-based analysis commonly known as spatial statistics, wherein models are proposed to estimate treatment effects using the correlation between neighboring units in the systematic grid (kriging)

The design and analysis in case 1 above is often used in evaluation of indicators of a treatment response (e.g., change in density) in relatively small, homogeneous study areas or small study areas where a gradient is expected in measured values of the indicator across the area. Ignoring the potential correlation and continuing the analysis as if it is justified by random sampling can be defended (Gilbert and Simpson 1992), especially in situations where a conservative statistical analysis is desired (e.g., impact assessment). Estimates of variance treating the systematic sample as a random sample will tend to overestimate the true variance of the sample (Hurlbert 1984; Scheaffer et al. 1990; Thompson 2002). Thus, systematic sampling in relatively small impact assessment study areas following Gilbert and Simpson's (1992) formulas for analysis makes a great deal of sense. This applies whether systematic sampling is applied to compare two areas (assessment and reference), the same area before and following the incident, or between strata of a stratified sample.

In wildlife studies, populations tend to be aggregated or clustered, thus sample units closer to each other will be more likely to be similar. For this reason, systematic sampling tends to overestimate the variance of parameter estimates. A uniform grid of points or parallel lines may not encounter rare units. To increase the likelihood of capturing some of these rare units, scientists may stratify the sample such that all units of each distinct type are joined together into strata and simple random samples are drawn from each stratum. Nevertheless, stratification works best if the study is short term, no units are misclassified and no units change strata during the study. In longer term studies, such as the US Environmental Protection Agency's (EPA's) long-term Environmental Monitoring and Assessment Program (EMAP), as described by Overton et al. (1991), systematic sampling has been proposed to counter these problems.

Cluster sampling is closely related to systematic sampling. A cluster sample is a probabilistic sample in which each sampling unit is a collection, or cluster, of elements such as groups of animals or plants (Scheaffer et al. 1990; Thompson 2002b). One of the most common uses of cluster sampling is the two-stage cluster sample. First, the researcher selects a probabilistic sample of plots, each of the primary plots having eight secondary plots. Then, within those primary plots, we either select another probability sample of plots from the eight secondary plots, or consider the cluster of eight secondary plots of our sample and conduct our enumeration method within each of those plots (Fig. 4.5). The selection of progressively smaller subsets of elements within the original set of sample clusters leads to a multistage cluster sample. Cluster sampling methods can become considerably complex, depending on sampling design, study question, and phenology of the species under study (Christman 2000). For example, consider an ecologist interested in estimating Greater Prairie-chicken (*Tympanuchus cupido*) lek numbers in the

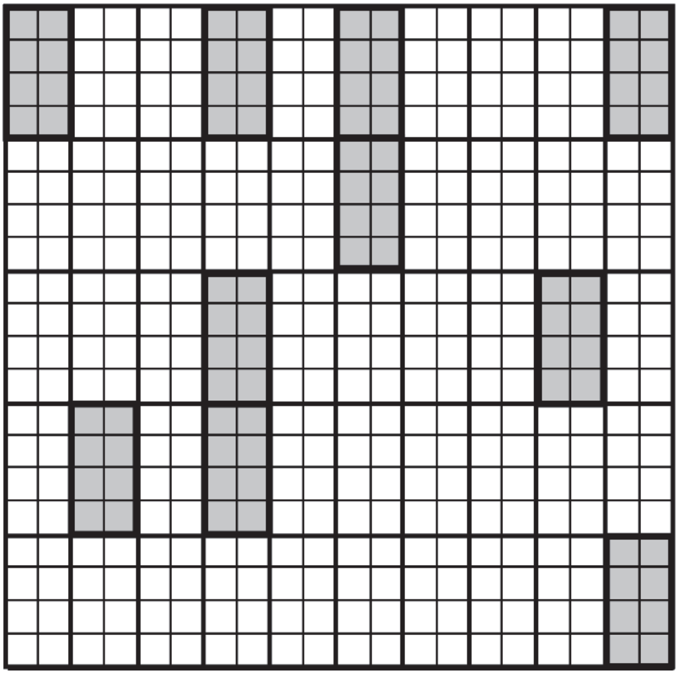

Fig. 4.5 (**a**) Cluster sample of ten primary units with each primary unit consisting of eight secondary units; (**b**) systematic sample with two starting points. Reproduced from Thompson (2002) with kind permission from Wiley

plains during the breeding season. Lek sites are typically close spatially, relative to the size of grasslands matrix these birds inhabit, thus we would expect that if a lek is located within a primary sample plot, there are other leks in the vicinity. For this reason, the researcher would randomly sample primary plots across a landscape of Greater Prairie-chicken habitat, then, within those large plots, conduct enumeration of lek numbers within the secondary plots.

Thompson (2002b, pp. 129–130) lists several features that systematic and cluster sampling that make these designs worth evaluating for ecological studies:

- In systematic sampling, it is not uncommon to have a sample size of 1, that is, a single primary unit (see Fig. 4.5).
- In cluster sampling, the size of the cluster may serve as auxiliary information that may be used either in selecting clusters with unequal probabilities or in forming ratio estimators.
- The size and shape of clusters may affect efficiency.

4.3.4 Adaptive Sampling

Numerous sampling designs integrate stratified, systematic, and cluster sampling – commonly under a framework called *adaptive sampling* – where, following an initial probabilistic sample of units, additional units are added to the sample in the neighborhood of original units that satisfy a specified condition (Thompson and Seber 1996). Thus, methods for adaptive sampling differ from most other sampling designs as the sample selection procedure is not determined before sampling, but is fluid and changes as successive samples are taken. Given the wide range of adaptive techniques available, we refer the interested readers to Thompson and Seber (1996), Christman (2000), and Thompson (2002).

Wildlife biologists are often bothered by probability sampling plans because sampling is limited to a set of previously selected units to the exclusion of units adjacent to, but not in, the sample. Adaptive sampling offers biologists a way to augment the probability sample with samples from adjacent units without losing the benefits of the original probabilistic design. Because animal populations usually are aggregated, adaptive methods take advantage of this tendency and uses information on these aggregations to direct future sampling. Adaptive sampling may yield more precise estimates of population abundance or density for given sample size or cost and may increase the yield of interesting observations resulting in better estimates of population parameters of interest (Thompson and Seber 1996).

Under a general adaptive sampling framework, a sample of units is first selected by any probabilistic sampling design. Rules for selection of additional samples are established based on some characteristic of the variable of interest (e.g., presence/absence, age, sex, and height). The values of the variables of interest are then noted on the original probabilistic sample of units and rules for selection of additional samples are applied (Thompson and Seber 1996). In a sense, adaptive sampling is a method for systematically directing biologists' tendency toward search sampling.

4.3.4.1 Definitions

We provide a brief and general description of the theory of adaptive sampling; a comprehensive discussion of the mathematics and theory is beyond the scope of this book. See Thompson and Seber (1996) for a complete discussion of this subject. We adopted the notations used by Thompson (2002b) for this discussion. To understand adaptive sampling it is useful to label sampling units and aggregations of units. The following definitions assume a simple random sample of units from a study area.

A neighborhood is a cluster of units grouped together based on some common characteristic. Typical definitions of a neighborhood include spatially contiguous units or a systematic pattern of surrounding units. For example, a neighborhood of 1-m^2 units in a grid might include each unit and the eight adjacent units (i.e., units at the four sides and corners). However, neighborhoods of units may be defined in many other ways including social or institutional relationships among units. For every unit, if unit i (u_i) is in the neighborhood of unit k (u_k) then u_k is in the neighborhood of u_i. Likewise, if neighborhood u_{ij} belongs to the neighborhood of u_{kl} then u_{kl} belongs to the neighborhood of u_{ij}.

The condition of interest (C) is the characteristic of the variable of interest (y) that determines if a unit is added to the neighborhood of units in the sample. Thus, u_i satisfies the condition and is added to the neighborhood if $y_i \in C$ where C is a specified interval or set of y_i. For example, C might be a carcass search plot containing ≥1 carcass. When a selected unit satisfies the condition, then all units within its neighborhood are added to the sample.

All the units added to the sample as the result of the selection of u_i are considered a cluster. A cluster may combine several neighborhoods. All the units within a cluster that satisfy the condition are considered to be in the same network. A population can be uniquely partitioned into K networks. An originally selected unit that does not satisfy the condition forms a unique network by itself. Units in the neighborhood that do not satisfy the condition are defined to be edge units and are not included in networks.

4.3.4.2 Adaptive Cluster Sampling Example

Adaptive sampling refers to those designs where selection of sample plots is dependent upon variables of interest observed (or not observed) within the sample during the survey. Adaptive sampling provides a method for using the clustering tendencies of a population when locations and shapes of clusters can generally be predicted (i.e., they are not known in the physical landscape but can be predicted based on existing information). Therefore, adaptive designs allow the researchers to add nearby plots under the assumption that if the species of interest is located in a plot, then it is likely that there are more members of the species within the immediate vicinity. Probably the most frequently used adaptive approach in wildlife ecology is that of adaptive cluster sampling (Smith et al. 1995, 2004, Noon et al. 2006). For example, consider a survey of mule deer across a range that is divided into 400 study units (Fig. 4.6a). In an effort to estimate the number of dead deer

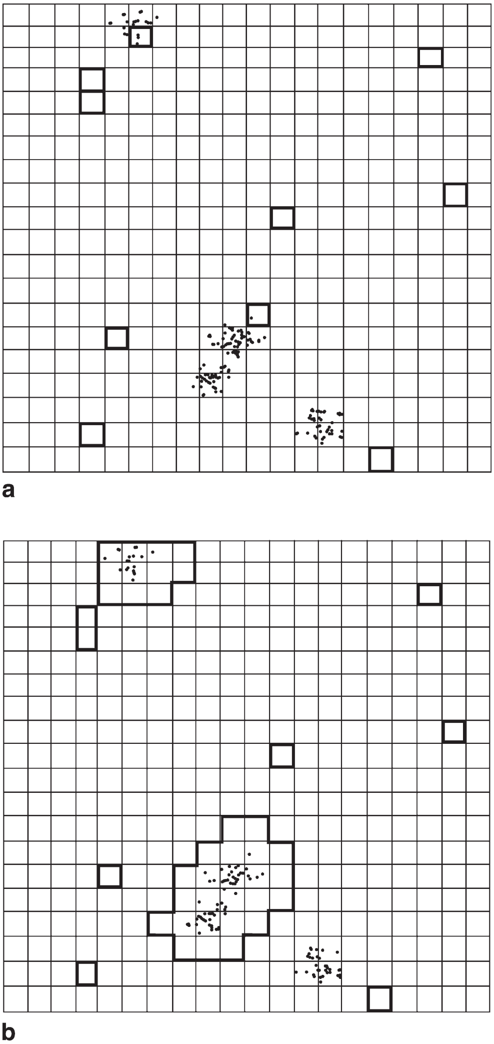

Fig. 4.6 A hypothetical example of adaptive sampling, illustrating a mule deer winter range that is divided into 400 study units (*small squares*) with simple random sample of ten units selected (*dark squares* in (**a**)) potentially containing deer carcasses (*black dots*). Each study unit and all adjacent units are considered a neighborhood of units. The condition of including adjacent units in the adaptive sample is the presence of one or more carcasses (*black dots*) in the unit. Additional searches result in the discovery of additional carcasses in a sample of 45 units in ten clusters (*dark squares* in (**b**)). (Thompson 1990. Reprinted with permission from the Journal of the American Statistical Association, Copyright 1990 by the American Statistical Association. All rights reserved)

following a severe winter, a survey for deer carcasses is conducted. An initial simple random sample of ten units is selected (see Fig. 4.6a). Each study unit and all adjacent units are considered a neighborhood of units. The condition of including adjacent units is the presence of one or more carcasses in the sampled unit. With the adaptive design, additional searches are conducted in those units in the same neighborhood of a unit containing a carcass in the first survey. Additional searches are conducted until no further carcasses are discovered, resulting in a sample of 45 units in ten clusters (see Fig. 4.6b).

The potential benefits of adaptive sampling are obvious in the mule deer example. The number of carcasses (point-objects in Fig. 4.6) is relatively small in the initial sample. The addition of four or five more randomly selected sample units probably would not have resulted in the detection of the number of carcasses contained in the ten clusters of units. Thus, the precision of the estimates obtained from the cluster sample of 45 units is greater than from a random sample of 45 units. This increase in precision could translate into cost savings by reducing required samples for a given level of precision. Cost savings also could result from reduced cost and time for data collection given the logistics of sampling clusters of sampled units vs. potentially a more widely spread random sample of units. This cost saving, however, is partially offset by increased record keeping and increased training costs. Although there are numerous adaptive sampling options, design efficiency depends upon several factors, including initial sample size, population distribution, plot shape, and selection conditions (Smith et al. 1995; Thompson 2002b). Thus we recommend that adaptive designs be pilot tested before implementation to ensure that estimate precision and sampling efficiency is increased over alternate designs.

4.3.4.3 Unbiased Estimators for Simple Random Samples

The potential efficiencies of precision and cost associated with adaptive sampling come with a price. Computational complexities are added because of sample size uncertainty and unequal probability associated with the sample unit selection. Units within the neighborhood of units meeting the condition enter the sample at a much higher probability than the probability of any one unit when sampled at random, resulting in potentially biased estimates of the variable of interest. For example, u_i is included if selected during the initial sample, if it is in the network of any unit selected, or if it is an edge unit to a selected network. In sampling with replacement, repeat observations in the data may occur either due to repeat selections in the initial sample or due to initial selection of more than one unit in a cluster.

> The Horvitz–Thompson (H–T) estimator (Horvitz and Thompson 1952) provides an unbiased estimate of the parameter of interest when the probability α_i that unit i is included in the sample is known. The value for each unit in the sample is divided by the probability that the unit is included in the sample. Inclusion probabilities are seldom known in field studies, and modifying the Horvitz–Thompson estimator, where estimates of inclusion probabilities are obtained from the data, as described by Thompson and Seber (1996) forms an unbiased estimator (modified H–T).

Implementing the adaptive sampling procedure described above results in an initial sample of n_1 primary units selected by a systematic or random procedure (without replacement). If a secondary unit satisfies the condition, then all units in the neighborhood are added to the sample. If any of the new units satisfies the condition, then their neighbors also are added. In the modified H–T estimator, the final sample consists of all units in the initial primary units and all units in the neighborhood of any sample unit satisfying the condition. Edge units must be surveyed, but are used in the modified H–T estimator only if they belong to the initial primary units. Thus, an edge unit in the initial sample of primary units is weighted more than individual units in networks and edge units within a cluster are given a weight of 0. Formulas for the modified H–T estimator may be found in Thompson and Seber (1996).

4.3.4.4 Other Adaptive Designs

Thompson and Seber (1996) and Thompson (2002b) summarized a variety of other adaptive sampling designs. Strip adaptive cluster sampling includes sampling an initial strip(s) of a given width divided into units of equal lengths. Systematic adaptive cluster sampling may be used when the initial sampling procedure is based on a systematic sample of secondary plots within a primary plot. Stratified adaptive cluster sampling may be useful when the population is highly aggregated with different expectations of densities between strata. In this case, follow-up adaptive sampling may cross strata boundaries (Thompson 2002b). Thompson and Seber (1996) also discuss sample size determination based on initial observations within primary units, strata, or observed values in neighboring primary units or strata. Adaptive sampling has considerable potential in ecological research, particularly in studies of rare organisms and organisms occurring in clumped distributions.

In Fig. 4.7, the initial sample consists of five randomly selected strips or primary units. The secondary units are small, square plots. Whenever a target element is located, adjacent plots are added to the sample, which effectively expands the width of the primary strip. As depicted in the figure, because this is a probabilistic sampling procedure not all target elements are located (in fact, you might not know they exist). For systematic adaptive cluster sampling (Fig. 4.8) the initial sample is a spatial systematic sample with two randomly selected starting points. Adjacent plots are added to the initial sample whenever a target element is located. The choice of the systematic or strip adaptive cluster design depends primarily on the a priori decision to use a specific conventional sampling design to gather the initial sample, such as the preceding example using aerial or line transects.

Stratified adaptive cluster sampling essentially works like the previous adaptive designs, and is most often implemented when some existing information on how an initial stratification is available. In conventional (nonadaptive) stratified sampling, units that are thought to be similar are grouped a priori into stratum based on prior information. For example, in Fig. 4.9a, the initial stratified random sample of five units in two strata is established. Then, whenever a sampling unit containing the

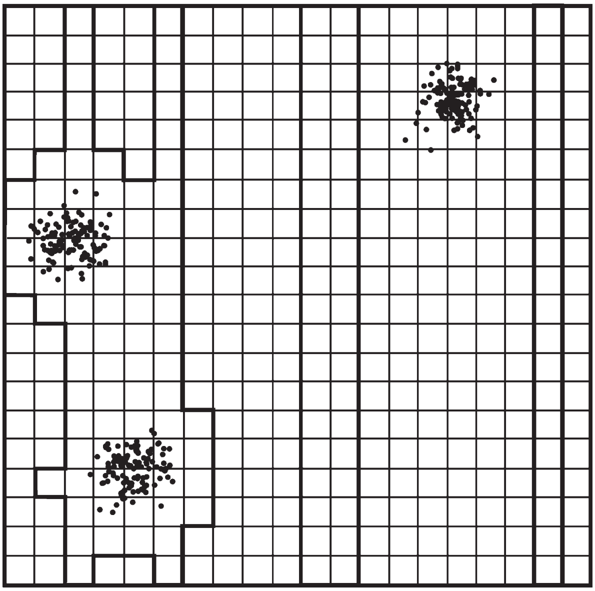

Fig. 4.7 An example of an adaptive cluster sample with initial random selection of five strip plots with the final sample outlined. Reproduced from Thompson (1991a) with kind permission from the International Biometric Society

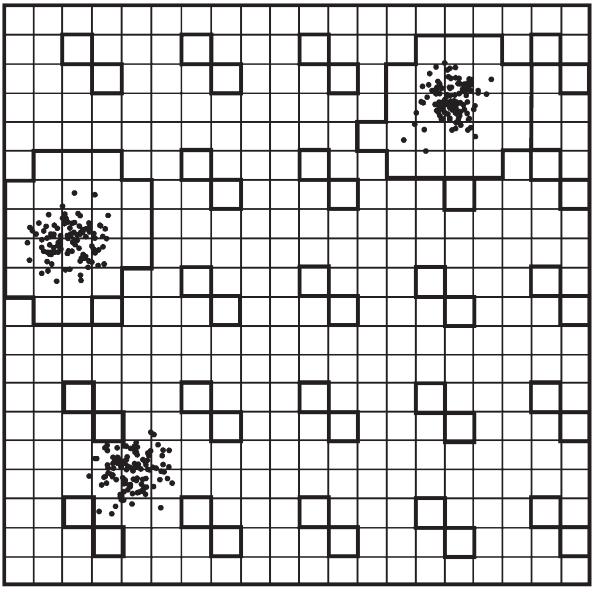

Fig. 4.8 An example of an adaptive cluster sample with initial random selection of two systematic samples with the final sample outlined. Reproduced from Thompson (1991a) with kind permission from the International Biometric Society

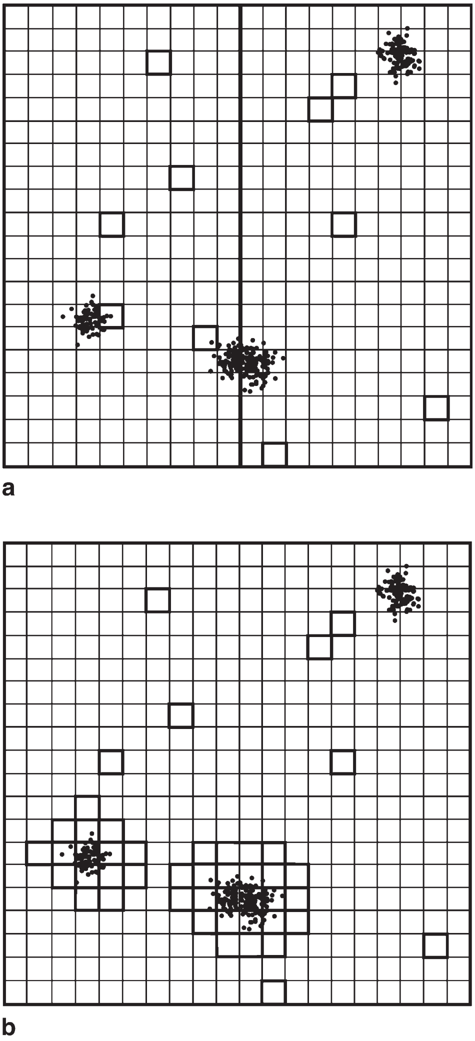

Fig. 4.9 (**a**) Stratified random sample of five units per strata. (**b**) The final sample, which results from the initial sample shown in (**a**). Reproduced from Thompson et al. (1991b) with kind permission from Oxford University Press

desired element is encountered, the adjacent units are added. The final sample in this example (Fig. 4.9b) shows how elements from one strata can be included in a cluster initiated in the other stratum (some units in the right-side stratum were included in the cluster [sample] as a result of an initial selection in the left-side stratum). Thompson (2002b, pp. 332–334) provides a comparison of this example with conventional stratified sampling.

There are four challenges you will encounter when considering implementing an adaptive cluster design (Smith et al. 2004, pp. 86–87):

1. Should I apply adaptive cluster sampling to this population?
2. How large should I expect the final sample size to be?
3. How do I implement adaptive sampling under my field conditions?
4. How can I modify adaptive sampling to account for the biology, behavior, and habitat use of the elements?

Although most biological populations are clustered, adaptive cluster sampling is not necessarily the most appropriate method for all populations. Estimators for adaptive cluster sampling are more complicated and less well understood than those associated with nonadaptive (classical) methods. Adaptive methods should only be used when the benefits of their use clearly outweigh the additional complications.

A difficulty with adaptive sampling is that the final sample size is not known when initiating the study. Although "stopping rules" are available, they can potentially bias results. If the study area is reasonable and well defined, then sampling will "stop" on its own when no additional elements are located. However, if the study area is extremely large and not readily defined (e.g., "the Sierra Nevada," "eastern Texas"), then adaptive sampling becomes difficult to stop once initiated. Perhaps one of the simplest means of stopping, given an appropriate initial sample, is to frequently examine the mean and variances associated with the parameter(s) being sampled and watch for stability of those parameter estimates. These parameter estimates can also be used in conventional power analysis to help guide the stopping decision. Conventional systematic sampling is an effective sampling design for clustered populations, and can be used as a surrogate for designing adaptive sampling.

The suitability of the adaptive design vs. nonadaptive designs depends on the characteristics of the population being sampled. Adaptive cluster sampling is most practical when units are easily located, the condition for selecting units is relatively constant and set at a reasonable level, and the distribution of elements of interest is truly clumped. Adaptive designs are most practical for ground-based surveys for things such as contaminants, plant(s) growing in scattered clumps, wildlife species that exhibit a general seasonal phenology which cause aggregations (e.g., breeding grounds). Adaptive sampling is not recommended for aerial surveys where locating sampling units is difficult at best and locating borders of a neighborhood of units would be extraordinarily difficult and time consuming. Adaptive sampling is also not recommended for situations where the condition is temporary. If the condition causing a unit to be included in a network is likely to change, e.g., presence or absence of a bird in a study plot, then a survey once started would need to be completed as quickly as possible, making planning for surveys difficult. If the conditions were too sensitive or the distribution of the elements of interest not sufficiently clumped (e.g., broadly distributed species like deer) the survey requirements would quickly become overwhelming.

4.3.5 Double Sampling

In double sampling, easy-to-measure or economical indicators are measured on a relatively large subset or census of sampling units in the treatment and reference areas and expensive or time-consuming indicators are measured on a subset of units from each area. As always, easily obtainable ancillary data should be collected. Analysis formulas are available in Cochran (1977). The principles for double sampling are straightforward and the method is easy to implement.

Consider the following examples where y is the primary variable of interest that is relatively expensive to measure on each experimental unit compared with an indicator variable x:

1. y = the number of pairs of breeding ducks present in a certain strip transect measured by ground crews, X = the number of breeding pairs seen during an aerial survey of the same strip
2. y = number of moose seen in a strip transect during an intensive aerial survey, X= number of moose seen in the same strip during a regular aerial survey (e.g., Gasaway et al. 1986)
3. y = the amount of vegetative biomass present on a sample plot, X = ocular estimate of the vegetative biomass on the same plot

In some cases the total (or mean) of the indicator variable may be known for the entire study area while the more expensive variable is known for only a portion of the area. If x and y are positively correlated then double sampling may be useful for improving the precision of estimates over the precision achieved from an initial, small, and expensive sample of both x and y (Eberhardt and Simmons 1987).

4.3.5.1 Double Sampling with Independent Samples

Double sampling would normally be used with independent samples where an initial (relatively small) sample of size n_1 is taken where both y and x are measured. The means for the two variables are calculated or, if the mean is known, the value of the variable is estimated as

$$\bar{y}_I = \sum\nolimits_i y_i/n_i \quad \text{or} \quad \hat{Y}\ \ N\bar{y}_I \text{ and}$$

$$\bar{x}_1 = \sum\nolimits_i x_i/n_i \quad \text{or} \quad \hat{X}_i = N\bar{x}_i.$$

In a relatively large sample of size n_2 (or a census) only the variable x is measured. Its mean is

$$\bar{x}_2 = \sum\nolimits_i x_i/n_2 \quad \text{or} \quad \hat{X}_2 = N\bar{x}_2.$$

In some situations, the mean for X_2 or $(\bar{X}_2)$ is known from census data, thus the standard error is zero ($X_2 = 0.0$). As an example, suppose X_2 = total production for a farmer's native hay field and Y = potential production without deer as measured in n_1 = 10 deer proof exclosures randomly located in a field. Two variables (X_i,y_i) are measured on the ith enclosure, where y_i is the biomass present on a plot inside the enclosure and X_i is the biomass present on a paired plot outside the enclosure.

The *ratio* of production inside the exclosures to production outside the exclosures is

$$R = \frac{\bar{y}_i}{\bar{x}_1} = \frac{\hat{y}_1}{\hat{x}_1} = \frac{\sum y_i}{\sum x_i}.$$

The ratio estimator for the total production without deer is

$$\hat{Y}_{\mathrm{R}} = \left[\frac{\bar{y}_1}{\bar{x}_1}\right] \cdot \hat{x}_2 = \hat{R}\hat{X}_2,$$

and the estimate of the mean production per plot ($\bar{Y}$) without deer is

$$\bar{y}_{\mathrm{R}} = \left[\frac{\bar{y}_1}{\bar{x}_1}\right] \cdot \bar{x}_2 = \hat{R}\bar{x}_2.$$

There is the tendency to obtain as small a sample as possible of the first more expensive sample. As with any form of probability sampling, the smaller the sample size the greater the likelihood of bias. However, using the ratio estimator, the effect of this bias is reduced. Consider the following example. Suppose the size of the field (N) is 100,000 m^2, the mean production outside the exclosure is 60 gm m^{-2}, the mean production inside the exclosure is 75 gm m^{-2}, and the total production for the field is (X_2) = 100,000 m^2 (50 gm m^{-2}) = 5,000,000 gm outside exclosures. The ratio of the estimates of production is 60 gm m^{-2}/75 gm m^{-2} = 1.25. Thus, there is an additional 0.25 gm of production per m^2 of production inside exclosures for every gm of production outside the exclosures. The estimated production without deer is (50 gm m^{-2}) (1.25) = 62.5 gm m^{-2} and total production of the entire field (Y_2) = 100,000 m^2 (62.5 gm m^{-2}) = 6,250,000 gm if the field could have been protected from deer. Note that the estimate of 75 gm m^{-2} for sample plots inside exclosures is adjusted *down* since the total production ($\bar{X}_2$ = 50 gm m^{-2}) is below the average of paired sample plots outside the exclosures ($\bar{X}_1$ = 60 gm m^{-2}). In our example, the small sample of exclosures apparently landed on higher production areas of the field by *chance*. We assume that the ratio R is adequately estimated by the initial, small but expensive sample. The large, inexpensive, second sample (i.e., total production by the farmer) adjusts for the fact that the initial sample may not truly represent the entire field.

Computation of the variances and standard errors is tedious because a ratio and a product are involved. The variance of the product with independent samples is estimated by the unbiased formula proposed by Reed et al. (1989).

4.3.5.2 Applications of Double Sampling

Smith's (1979) two-stage sampling procedure is a variation of the general double-sampling method for use in environmental impact studies. Smith suggests oversampling in an initial survey, when knowledge concerning impacts is most limited, and recording economical easy-to-measure indicators. For example, animal use (an index to abundance sampled according to a probability sample) might be taken during a pilot study, allowing one to identify species most likely affected by a treatment or impact. In the second stage and with pilot information gained, the more expensive and time-consuming indicators (e.g., the actual number of individuals) might be measured on a subset of the units. If the correlation between the indicators measured on the double-sampled units is sufficiently high, precision of statistical analyses of the expensive and/or time-consuming indicator is improved.

Application of double sampling has grown in recent years, particularly for correcting for visibility bias. Eberhardt and Simmons (1987) suggested double sampling as a way to calibrate aerial observations. Pollock and Kendall (1987) included double sampling in their review of the methods for estimating visibility bias in aerial surveys. Graham and Bell (1969) reported an analysis of double counts made during aerial surveys of feral livestock in the Northern Territory of Australia using a similar method to Caughley and Grice (1982) and Cook and Jacobson (1979). Several studies have used radiotelemetered animals to measure visibility bias, including Packard et al. (1985) for manatees (*Trichechus manatus*), Samuel et al. (1987) for elk, and Flowy et al. (1979) for white-tailed deer (*Odocoileus virginianus*). McDonald et al. (1990) estimated the visibility bias of sheep groups in an aerial survey of Dall sheep (*Ovus dalli*) in the Arctic National Wildlife Refuge (ANWR), Alaska using this technique. Strickland et al. (1994) compared population estimates of Dall sheep in the Kenai Wildlife Refuge in Alaska using double sampling following the Gasaway et al. (1986) ratio technique and double sampling combined with logistic regression. Recently, Bart and Earnst (2002) outlined applications of double sampling to estimate bird population trends. Double sampling shows great promise in field sampling where visibility bias is considered a major issue.

4.3.6 Additional Designs

First, wildlife studies are usually plagued with the need for a large sample size in the face of budgetary and logistical constraints. Ranked set sampling provides an opportunity to make the best of available resources through what Patil et al. (1994) referred to as observational economy. Ranked set sampling can be used with any sampling scheme resulting in a probabilistic sample. A relatively large probabilistic sample of units (N) is selected containing one or more elements (n_i) of interest. The elements then are ranked within each unit based on some obvious and easily discernible characteristic (e.g., patch size, % cover type). The ranked elements are then selected in ascending or descending order of rank – one per unit – for further analysis. The resulting rank-ordered sample provides an unbiased estimator of the population mean superior in efficiency to a simple random sample of the same size (Dell and Clutter 1972).

Ranked set sampling is a technique originally developed for estimating vegetation biomass during studies of terrestrial vegetation; however, the procedure deserves much broader application (Muttlak and McDonald 1992). The technique is best explained by a simple illustration. Assume 60 uniformly spaced sampling units are arranged in a rectangular grid on a big game winter range. Measure a quick, economical indicator of plant forage production (e.g., plant crown diameter) on each of the first three units, rank order the three units according to this indicator, and measure an expensive indicator (e.g., weight of current annual growth from a sample of twigs) on the highest ranked unit. Continue by measuring shrub crown diameter on the next three units (numbers 4, 5, and 6), rank order them, and estimate the weight of current annual growth on the second-ranked unit. Finally, rank order units 7, 8, and 9 by plant crown diameter and estimate the weight of current annual growth on the lowest-ranked unit; then start the process over on the next nine units. After, completion of all 60 units, a ranked set sample of 20 units will be available for estimates of the weight of current annual growth. This sample is not as good as a sample of size 60 for estimating the weight of current annual growth, but should have considerably better precision than a simple random sample of size 20. Ranked set sampling is most advantageous when the quick, economical indicator is highly correlated with the expensive indicator, and ranked set sampling can increase precision and lower costs over simple random sampling (Mode et al. 2002). These relationships need to be confirmed through additional research. Also, the methodology for estimation of standard errors and allocation of sampling effort is not straightforward.

One of the primary functions of sampling design it to draw a sample that we hope provides good coverage of the area of interest and allows for precise estimates of the parameter of interest. The simple Latin square sampling +1 design can provide better sample coverage than systematic or simple random sampling, especially when the distribution of the target species exhibits spatial autocorrelation (Munholland and Borkowski 1996). A simple Latin square +1 design is fairly straightforward; a sampling frame is developed first (note that a Latin square +1 is irrespective of plot shape or size), then a random sample of plots is selected from each row–column combination (Fig. 4.10a), and then a single plot (the +1) is selected at random from the remaining plots (6 showing in Fig. 4.10a). Simple Latin square +1 sampling frames need not be square; they could also be linear (Fig. 4.10b) or any other a range of various shapes (Thompson et al. 1998) so long as the sampling frame can be fully specified.

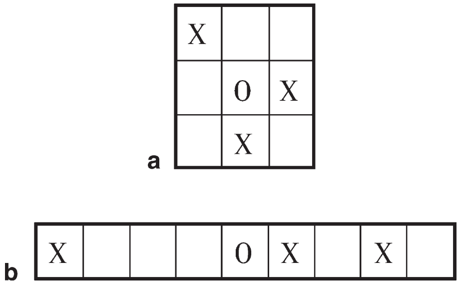

Fig. 4.10 (**a**) A simple Latin square sample of +1 drawn from a sampling frame consisting of nine square plots. Those plots having an "X" were the initial randomly selected plots based for each row–column; the plot having an "O" is the +1 plot, which was randomly selected from the remaining plots. (**b**) The same sampling frame adapted to a population tied to a linear resource. Reproduced from Thompson et al. (1998) with kind permission from Elsevier

Another approach to sampling natural resources, called generalized random-tessellation stratified designs (GRTS; Stevens and Olsen 1999, 2004), was developed to assist with spatial sampling of natural resources and ensure that the samples are evenly dispersed across the resource. Stratified sampling designs tend to spread out sample plots evenly across a landscape, simple random sampling tends to give patterns that are more spatially clumped. Under GRTS designs, the assumption is that segments of a population tend to be more similar the closer they are in space. So, in order to gather a sample of the resource in question, it is desirable to attempt to spread the points fairly evenly across the study frame. For each sampling procedure, a reverse hierarchical ordering is applied and generalized random-tessellation samples are designed such that for a given sample size (N) the first n units will be spatially balanced across a landscape (Stevens and Olsen 2004). GRTS designs have been used for large-scale environmental monitoring studies although they could potentially be used for smaller scale studies.

4.4 Point and Line Sampling

In the application of probability sampling, as seen above, one assumes each unit in the population has equal chance of being selected. Although this assumption may be modified by some sampling schemes (e.g., stratified sampling), the decisions regarding sample selection satisfy this assumption. In the cases where the probability of selection is influenced in some predictable way by some characteristic of the object or organism, this bias must be considered in calculating means and totals. Examples include line intercept sampling of vegetation (McDonald 1980; Kaiser 1983), plotless techniques such as the Bitterlich plotless technique for the estimation of forest cover (Grosenbaugh 1952), aerial transect methods for estimating big game numbers (Steinhorst and Samuel 1989; Trenkel et al. 1997), and the variable circular plot method for estimating bird numbers (Reynolds et al. 1980). If the probability of selection is proportional to some variable, then equations for estimating the magnitude and mean for population characteristics can be modified by an estimate of the bias caused by this variable. *Size bias* estimation procedures are illustrated where appropriate in the following discussion of sample selection methods.

4.4.1 Fixed Area Plot

Sampling a population is usually accomplished through a survey of organisms in a collection of known size sample units. The survey is assumed complete (e.g., a census), so the only concern is plot-to-plot variation. Estimating the variance of these counts uses standard statistical theory (Cochran 1977). Results from the counts of organisms on sample units are extrapolated to area of interest based on the proportion of area sampled. For example, the number of organisms (N) in the area of interest is estimated as

$$\hat{N} = \frac{N'}{\alpha},$$

where the numerator (N') equals the number of organisms counted and the denominator (α) equals the proportion of the area sampled. In the case of a simple random sample, the variance is estimated as

$$\hat{\text{var}}(x_i) = \sum_{i=1}^{n} \frac{(x_i - \bar{x})^2}{(n-1)},$$

where n = the number of plots, x_i = the number of organisms counted on plot i, and $\bar{x}$ = the mean number of organisms counted per sample plot.

Sampling by fixed plot is best done when organisms are sessile (e.g., plants) or when sampling occurs in a short time frame such that movements from plots has no effect (e.g., aerial photography). We assume, under this design, that counts are made without bias and no organisms are missed. If counts have a consistent bias and/or organisms are missed, then estimation of total abundance may be inappropriate (Anderson 2001). Aerial surveys are often completed under the assumption that few animals are missed and counts are made without bias. However, as a rule, total counts of organisms, especially when counts are made remotely such as with aerial surveys, should be considered conservative. Biases are also seldom consistent. For example, aerial counts are likely to vary depending on the observer, the weather, ground cover, pilot, and type of aircraft.

4.4.2 Line Intercept Sampling

The objective in line intercept sampling is estimation of parameters of two-dimensional objects in a two-dimensional study area. The basic sampling unit is a line randomly or systematically located perpendicular to a baseline and extended across the study area. In wildlife studies, the objects (e.g., habitat patches, fecal pellets groups) will vary in size and shape and thus will be encountered with a bias toward larger objects relative to the baseline. This *size bias* does not affect the estimate of aerial coverage of the objects but may bias estimates of other parameters. For example, estimates of age or height of individual plants would be biased toward the larger plants in the study area. Estimates of these parameters for the study area must be corrected for this source of bias.

Parameters in line intercept sampling are illustrated in Fig. 4.11. The study region (R) can be defined by its area (A). Within the study area there is a population (N) of individual objects ($N = 5$ in Fig. 4.11) with each defined by an area (a_i). Each object may also have an attribute (Y_i) (e.g., biomass, height, or production of shrubs) and a total of the attribute (Y) over all objects. A mean of the attribute ($\bar{Y}$) can also be calculated (Y/N). Finally, the aerial coverage (C) of N objects can be calculated where the percentage cover is the total area of individual plants divided by the area of the study area ($C = \Sigma_{ai}/A$).

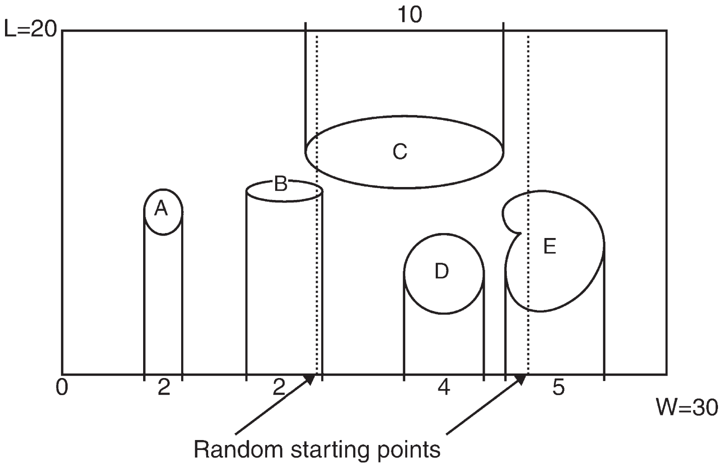

Fig. 4.11 Parameters in line intercept sampling, including the area ($A = L \times W$) of the study area, the objects of interest (1–5), aerial coverage ($a_1,\ldots,a_n$) of the objects, the intercept lines and their random starting point and spacing interval. Reproduced from McDonald (1991) with kind permission from Lyman McDonald

Here we define the following statistics for the line transect:

1. L = length of the randomly located line
2. v_i = length of the intersection of the line and the ith object
3. w_i = width of the projection of the ith object on the baseline
4. m = number of replications of the basic sampling unit (e.g., the number of lines randomly selected)
5. n = number of individual objects intercepted by the line

The primary application of line intercept sampling has been to estimate coverage by the objects of interest (Canfield 1941). The procedure also has been used to record data on attributes of encountered objects (Lucas and Seber 1977; Eberhardt 1978; McDonald 1980; Kaiser 1983), to estimate a variety of parameters including the aerial coverage of clumps of vegetation, coverage and density (number per unit area) of a particular species of plant, number of prairie dog burrows, and the coverage by different habitat types on a map.

4.4.3 *Size-biased Sampling*

Even though biologists often do not recognize that items have been sampled with unequal probability and that these data are size biased, care should be taken to recognize and correct for this source of bias. Size bias can be accounted for by calculating the probability of encountering the ith object with a given length (L) and width (W) with a line perpendicular to the baseline from a single randomly selected point

$$P_i = w_i / W;\ i = 1,2,3,\ldots,\ N,$$

where w_i is the width of the object in relation to the baseline. The estimate of the number of objects N is

$$\hat{N} = \sum_{i=1}^{n} (1/p_i) = W \sum_{i=1}^{n} (1/w_i),$$

and the density of objects, $D = D/A$, is estimated by

$$\hat{D} = W \sum_{i=1}^{n} (1/w_i)/(LW) = (1/L) \sum_{i=1}^{n} (1/w_i)$$

where n is the number of objects intercepted by the single line of length L.

The total of the attribute, $\hat{Y} = \sum_{i=1}^{n} Y_1$; over all objects in the area sampled is estimated by

$$\hat{Y} = W \sum_{i=1}^{n} (y_i / w_i)$$

and the mean of the attribute per object is estimated by

$$\hat{u}_y = \left(\sum_{i=1}^{n} (y_i / w_i) \right) \Big/ \left(\sum_{i=1}^{n} (1/w_i) \right).$$

Means and standard errors for statistical inference can be calculated from independent (m) replications of the line-intercept sample. Lines of unequal length result in means weighted by the lengths of the replicated lines.

4.4.4 Considerations for Study Design

Since the probability of encountering an object is typically a divisor in estimators, it is desirable to design sampling to maximize p_i, minimizing the variance of the estimates. The width of objects ($w_1, w_2, \ldots, w_n$) is in the denominator of the formula for calculating the probability of encountering the objects. Thus, the baseline should be established so that the projections of the objects on the baseline are maximized, increasing the probability that lines extending perpendicular to the baseline will encounter the objects. Lines of unequal length require that weighted means be used for making estimates of parameters when combining the results of independent replicate lines. As an example,

$$\hat{D} = \sum_{j=1}^{m} L_j / D_j / \sum_{j=1}^{m} L_j .$$

4.4.5 Estimation of Coverage by Objects

Estimation of coverage of objects, such as clumps of vegetation, is a common use of line-intercept sampling in wildlife studies (Canfield 1941). The estimate of percent cover of objects is unbiased and can be estimated by the percentage of the line that is intersected by the objects (Lucas and Seber 1977) using the formula

$$\hat{C} = \sum_{i=1}^{n} v_i / L,$$

where v_i is the length of the intersection of the ith object with a single replicate line of length L. Again, replication of lines of intercept m times allows the estimate of a standard error for use in making statistical inferences. Equal length lines can be combined in the above formula to equal L. Weighted means are calculated when lines are of unequal length.

4.4.6 Systematic Sampling

Line intercept methodologies often employ systematic sampling designs. In the systematic placement of lines, the correct determination of the replication unit and thus the correct sample size for statistical inferences is an issue. If sufficient distance between lines exists to justify an assumption of independence, then the proper sample size is the number of individual lines and the data are analyzed as if the individual lines are independent replications. However, if the assumption of independence is not justified (i.e., data from individual lines are correlated) then the set of correlated lines is considered the replication unit. The set of m lines could be replicated m' times using a new random starting point each time, yielding an independent estimate of parameters of interest with $L' = m(L)$ as the combined length of the transects to yield m' independent replications. Statistical inferences would follow the standard procedures.

The general objectives in systematic location of lines are to:

1. Provide uniform coverage over the study region, R
2. Generate a relatively large variance within the replication unit vs. a relatively small variance from replication to replication

For example, the total biomass and cover by large invertebrates on tidal influenced beaches may be estimated by line intercept sampling with lines perpendicular to the tidal flow. Standard errors computed for systematically located lines should be conservative (too large) if densities of the invertebrates are more similar at the same tidal elevation on all transects vs. different tidal elevations on the same transect (condition 2 above is satisfied). Even if individual lines cannot be considered independent, when condition 2 is satisfied then standard computational procedures for standard errors can be used (i.e., compute standard errors as if the data were independent) to produce conservative estimates.

4.4.7 One Line with No Replication

Often one or more long lines are possible but the number is not sufficient to provide an acceptable estimate of the standard error. Standard errors can be estimated by breaking the lines into subsets, which are then used in a jackknife or bootstrap procedure. A good example might be surveys along linear features such as rivers or highways. Skinner et al. (1997) used bootstrapping for calculating confidence intervals around estimates of moose density along a long transect zigzagging along the Innoko River in Alaska. Each zigzag is treated as an independent transect. While there may be some lack of independence where the segments join, it is ignored in favor of acquiring an estimate variance for moose density along the line. This works best with a relatively large sample size that fairly represents the area of interest. Skinner et al. (1997) reported satisfactory results with 40–60 segments per stratum.

Generally, the jackknife procedure estimates a population parameter by repeatedly estimating the parameter after one of the sample values is eliminated from the calculation resulting in several pseudoestimates of the parameter. The pseudoestimates of the parameter are treated as a random sample of independent estimates of the parameter, allowing an estimate of variance and confidence intervals. The bootstrap is the selection of a random sample of n values $X_1, X_2, \ldots, X_n$ from a population and using the sample to estimate some population parameter. Then a large number of random samples (usually >1,000) of size n are taken from the original sample. The large number of bootstrap samples is used to estimate the parameter of interest, its variance, and a confidence interval. Both methods require a large number of calculations and require a computer. For details on jack-knife, bootstrap, and other computer-intensive methods, see Manly (1991).

4.5 Line Transects

Line transects are similar to line intercept sampling in that the basic sampling unit is a line randomly or systematically located on a baseline, perpendicular to the baseline, and extended across the study region. Unlike line intercept sampling, objects are recorded on either side of the line according to some rule of inclusion. When a total count of objects is attempted within a fixed distance of the line, transect sampling is analogous to sampling on fixed plot (see Sect. 4.4.1). This form of line transect, also known as a belt (strip) transect, has been used by the US Fish and Wildlife Service (Conroy et al. 1988) in aerial counts of black ducks. As with most attempts at total counts, belt transect surveys usually do not detect 100% of the animals or other objects within the strip. When surveys are completed according to a standard protocol, the counts can be considered an index. Conroy et al. (1988) recognized ducks were missed and suggested that survey results should be considered an index to population size.

Line-transect sampling wherein the counts are considered incomplete has been widely applied for estimation of density of animal populations (Laake et al. 1979, 1993). Burnham et al. (1980) comprehensively reviewed the theory and applications of this form of line-transect sampling. Buckland et al. (1993) updated the developments in line-transect sampling through the decade of the 1980s. Alpizar-Jara and Pollock (1996), Beavers and Ramsey (1998), Manly et al. (1996), Quang and Becker (1996, 1997), and Southwell (1994) developed additional theory and application. The notation in this section follows Burnham et al. (1980).

Line-transect studies have used two basic designs and analytic methods depending on the type of data recorded (1) perpendicular distances (x) or sighting distances (r) and (2) angles (θ) (Fig. 4.12). Studies based on sighting distances and angles are generally subject to more severe biases and are not emphasized in this discussion.

There are several assumptions required in the use of line-transect surveys (Buckland et al. 2001), including:

1. Objects on the line are detected with 100% probability.
2. Objects do not move in response to the observer before detection (e.g., animal movements are independent of observers).
3. Objects are not counted twice.
4. Objects are fixed at the point of initial detection.
5. Distances are measured without errors.
6. Transect lines are probabilistically located in the study area.

4.5.1 Detection Function

The probability of detecting an object at a perpendicular distance of x from the transect line is known as the object's detection function $g(x)$ illustrated in Fig. 4.12. Assumption 1, above, that $g(0) = 1$ (i.e., the probability is 1.0 that an object with $x = 0$ will be detected) is key and allows estimation of the necessary parameter for correcting for visibility bias away from the line (i.e., $g < 1.0$). The detection function can be made up of a mixture of more simple functions which depend on factors

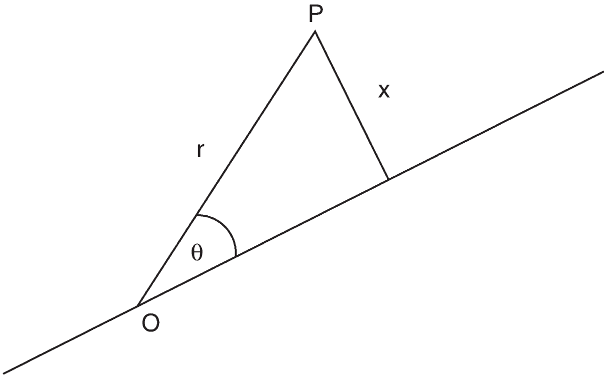

Fig. 4.12 The types of data recorded for the two basic types of line-transect study designs including perpendicular distances (x) or sighting distances (r) and angles (θ). The probability of detecting an object at a perpendicular distance of x from the transect line is known as the object's detection function $g(x)$. Reproduced from Burnham et al. (1980) with kind permission from The Wildlife Society

such as weather, observer training, vegetation type, etc., so long as all such functions satisfy the condition that probability of detection is 100% at the origin $x = 0$ (Burnham et al. 1980).

The average probability of detection for an object in the strip of width $2w$ is estimated by

$$\hat{P}_w = 1/\hat{w}f(0)$$

where $f(x)$ denotes the relative probability density function of the observed right angle distances, x_i, $i = 1, 2,\ldots,n$. The function $f(x)$ is estimated by a curve fitted to the (relative) frequency histogram of the right angle distances to the observed objects and $\hat{f}(0)$ is estimated by the intersection of $f(x)$ with the vertical axis at $x = 0$. Given $\hat{P}_w = 1/\hat{w}f(0)$, and detection of n objects in the strip of width $2w$ and length L, the observed density is computed by

$$\hat{D} = n/2Lw.$$

The observed density is corrected for visibility bias by dividing by the average probability of detection of objects to obtain

$$\begin{aligned}\hat{D} &= (n/2Lw)/(1/w\hat{f}(0)) \\ &= n\hat{f}(0)/2L\end{aligned}.$$

The width of the strip drops out of the formula for estimation of density of objects allowing line-transect surveys with no bound on w (i.e., $w = \infty$). However, at large distances from the line, the probability of detection becomes very low and it is desirable to set an upper limit on w such that 1–3% of the most extreme observations are truncated as *outliers*. Decisions on dropping outliers from the data set can be made after data are collected.

4.5.2 Replication

Estimates of the variances and standard errors associated with line-transect sampling are usually made under the assumption that the sightings are independent events and the number of objects detected is a Poisson random variable. If there are enough data (i.e., ≥40 detected objects) on independent replications of transect lines or systematic sets of lines, then a better estimate of these statistics can be made. Replications must be physically distinct and be located in the study area according to a true probability sampling procedure providing equal chance of detection for all individuals. Given independent lines, the density should be estimated on each line and the standard error of density estimated by the usual standard error of the mean density (weighted by line length if lines vary appreciably in length).

If there are not enough detections on independent replications, then jackknifing the lines should be considered (Manly 1991). For example, to jackknife the lines, repeatedly leave one line out of the data set and obtain the pseudoestimate of density by biasing estimates on the remaining lines. The mean of the pseudoestimates and the standard error of the pseudoestimates would then be computed. While jackknifing small samples will allow the estimation of variance, sample sizes are not increased and the pseudovalues are likely to be correlated to some extent, resulting in a biased estimate of variance. The significance of this bias is hard to predict and should be evaluated by conducting numerous studies of a range of situations before reliance is placed on the variance estimator (Manly 1991).

4.5.3 Line-transect Theory and Application

Size bias is an issue when the probability of detecting subjects is influenced by size (e.g., the subject's width, area, etc.). In particular, animals typically occur in groups, and the probability of detecting an individual increases with group size. Estimates of group density and mean group size are required to estimate the density of individuals and an overestimate of mean group size will lead to an overestimate of true density. Drummer and McDonald (1987) proposed bivariate detection functions incorporating both perpendicular distance and group size. Drummer (1991) offered the software package SIZETRAN for fitting size-biased data. Quang (1989) presented nonparametric estimation procedures for size-biased line-transect surveys.

Distance-based methods have been combined with aerial surveys (Guenzel 1997) to become a staple for some big game biologists in estimating animal abundance. As pointed our earlier (Sect. 4.5.1), the probability of detecting objects during line-transect surveys can influence parameter estimates. Quang and Becker (1996) offered an approach for incorporating any appropriate covariate influencing detection into aerial surveys using line-transect methodology by modeling scale parameters as log-linear functions of covariates. Manly et al. (1996) used a double-sample protocol during aerial transect surveys of polar bear. Observations by two observers were analyzed using maximum likelihood methods combined with an information criterion (AIC) to provide estimates of the abundance of polar bears. Beavers and Ramsey (1998) illustrated the use of ordinary least-squares regression analyses to adjust line-transect data for the influence of variables (covariates).

The line-transect method is also proposed for use with aerial surveys and other methods of estimating animal abundance such as a form of capture–recapture (Alpizar-Jara and Pollock 1996) and double sampling (Quang and Becker 1997; Manly et al. 1996). Lukacs et al. (2005) investigated the efficiency of trapping web designs, which can be combined with distance sampling to estimate density or abundance (Lukacs et al. 2004) and provided software for survey design (Lukacs 2002). In addition, line-transect methods have been developed which incorporate covariates (Marques and Buckland 2004), combine capture–mark–recapture data (Burnham et al. 2004), and a host of other potential topics (Buckland et al. 2004). The field of abundance and density estimation from transect-based sampling schemes is active, so additional methodologies are sure to be forthcoming.

4.6 Plotless Point Sampling

The concept of plotless or distance methods was introduced earlier in our discussion of the line intercept method (see Sect. 4.4.2). Plotless methods from sample points using some probability sampling procedure are considered more efficient than fixed area plots when organisms of interest are sparse and counting of individuals within plots is time consuming (Ludwig and Reynolds 1988).

4.6.1 *T-square Procedure*

In the *T*-square procedure, sampling points are at random, or systematically selected locations, and two distances are taken at each point (Fig. 4.13). For example, this method has been used in the selection individual plants and animals for study. McDonald et al. (1995) used the method for selection of invertebrates in the study of the impacts of the Exxon Valdez oil spill. The two measurements include:

1. The distance (x_i) from the random point (O) to the nearest organism (P)
2. The distance (z_i) from the organism (P) to its nearest neighbor (Q) with the restriction that the angle OPQ must be more than 90° (the *T*-square distance).

The most robust population density estimator from *T*-square data is the compound estimate using both measures x_i and z_i (Byth 1982), computed as

$$\hat{N}_{\mathrm{T}} = \frac{n^2}{2\sum(x_i)\sqrt{2}\sum(z_i)},$$

where n represents the number of random points (the sample size). The somewhat complicated standard error is calculated on the reciprocal of the compound density given by Diggle (1983) as

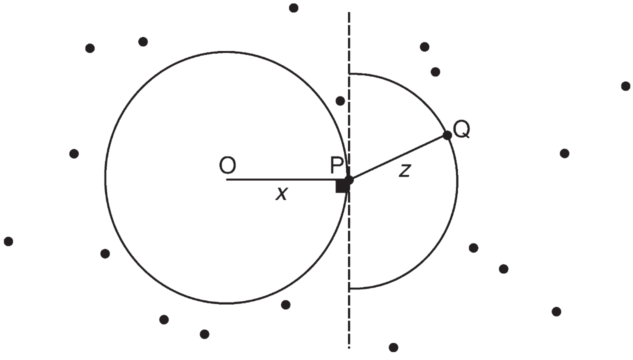

Fig. 4.13 The two *T*-square sampling points and the two distances measured at each point. Reproduced from Morrison et al. (2001) with kind permission from Springer Science + Business Media

$$\text{Standard error of } (1/\hat{N}_{\mathrm{T}}) = \sqrt{\frac{8(\overline{z}^2 S_x^2 + 2\overline{xz}s_{xz} + \overline{x}^2 s_z^2)}{n}},$$

where S_x^2 is the variance of point-to-organism distances, S_z^2 is the variance of T-square organism-to-neighbor distances, and S_{xz} is the covariance of x and z distances.

4.6.2 Variable Area Circular Plots

The variable circular plot is often applied as a variation of line-transect sampling for estimating the number of birds in an area (Reynolds et al. 1980). Counts of organisms along a transect is a standard sampling procedure, particularly when the organisms of interest are relatively rare. The variable circular plot is recommended, however, in dense vegetation and rough terrain where attention may be diverted from the survey and toward simply negotiating the transect line. An added advantage of the circular plot is that the observer can allow the surveyed animals to settle down. For example, in breeding bird surveys, observers wait several minutes to allow the songbirds disturbed by their arrival to settle down before counts begin and sound as well as visual observation can be used to detect birds.

While the plot is perceived as circular, the procedure is plotless since all observations made from a point, in any direction, are recorded. Plot size is a function of the observer's ability to detect the organism of interest and not the design (Ramsey and Scott 1979). As with a line transect, estimation of the number of organisms within the area surveyed is based on a detection function $g(x)$ that represents the distance at which the observer can detect organisms of interest. Density is estimated as

$$\hat{D} = \frac{n}{\pi P^2},$$

where n is the number of birds detected and the denominator is the area of a circle with a radius of ρ, the distance from the plot center within which we would expect n birds to be located (Lancia et al. 2005).

Program DISTANCE (Buckland et al. 1993, 2001) can be used to estimate bird densities from variable circular plot data. The theoretical models and estimation methods used in DISTANCE work best when at least 40 independent observations exist for the area of interest. Data may be pooled across time periods or species to estimate detection functions resulting in an average detection probability.

Distance estimates are usually recorded as continuous data. Buckland (1987) proposed binomial models for variable circular plots where subjects are categorized as being within or beyond a specified distance. Estimates of distances to detected subjects may also be assigned to intervals with the frequency of observations analyzed in the intervals. Placing detected subjects in intervals of distance should be more accurate for subjects close to the observer so we recommend that intervals near the center of the plot be smaller than intervals farthest from the observer. The critical point estimate is the intersection of the detection function at the origin. Burnham et al. (1980) suggested trimming data so that roughly 95% of the observed distances are used in the analysis. The assumption is that the outer 5% of observations are outliers that may negatively affect density estimates.

The assumption that counts are independent may be difficult, as subjects being counted are seldom marked or obviously unique. Biologists may consider estimating use per unit area per unit time as an index to abundance. When subjects are relatively uncommon, the amount of time spent within distance intervals can be recorded. In areas with a relatively high density of subjects, surveys can be conducted as instantaneous counts of animals at predetermined intervals of time during survey periods.

4.7 Model-based Sampling

The major advantage of classic probability sampling is that assumptions regarding the underlying population are unnecessary. Using this approach, the population of interest is considered fixed in time and space. Randomness is present only because of the sample-selection process and variation within the population must be dealt with in the course of data analysis. Model-based sampling uses assumptions to account for patterns of variability within the population and uses these patterns in sampling schemes.

As a note of caution, literature dealing with strictly model-based studies often focuses on the analysis of data. Model-based approaches are often promoted as a less costly and logistically easier alternative to large design-based field studies. The assumption sometimes seems to be that design deficiencies in model-based studies can be overcome by modeling. Data analysis can improve the quality of the information produced by these studies; however, fundamentally flawed design issues should not be ignored. It is worth repeating the philosophy of model selection and data analysis advice on modeling in science as offered by McCullagh and Nelder (1983, p. 6) and Lebreton et al. (1992):

> Modeling in science remains, partly at least, an art. Some principles exist, however, to guide the modeler. The first is that all models are wrong; some, though, are better than others and we can search for the better ones. At the same time we must recognize that eternal truth is not within our grasp. The second principle (which applies also to artists!) is not to fall in love with one model, to the exclusion of alternatives. Data will often point with almost equal emphasis at several possible models and it is important that the analyst accepts this. A third principle involves checking thoroughly the fit of the model to the data, for example by using residuals and other quantities derived from the fit to look for outlying observations, and so on. Such procedures are not yet fully formalized (and perhaps never will be), so that imagination is required of the analyst here, as well as in the original choice of models to fit.

Our distinction between model-based and design-based sampling is somewhat artificial. Modeling is defined as the mathematical and statistical processes involved in fitting mathematical functions to data. Given this definition, models are included in all study designs. The importance of models and assumptions in the analysis of empirical data ranges from little effect in design-based studies to being a critical part of data analysis in model-based studies. Design-based studies result in predicted values and estimates of precision as a function of the study design. Model-based studies lead to predicted values and estimates of precision based on a combination of study design and model assumptions often open to criticism. The following discussion focuses on the most prevalent model-based studies that are heavily dependent on assumptions and estimation procedures involving linear and logistic regression for data analysis. These study methods are only slightly more model-based than some previously discussed (e.g., plotless and line intercept) involving estimates of *nuisance parameters* such as detection probabilities, probabilities of inclusion, and encounter probabilities.

4.7.1 Capture–Recapture Studies

When observational characteristics make a census of organisms difficult, capture–recapture methods may be more appropriate for estimating population abundance, survival, recruitment, and other demographic parameters (e.g., breeding probabilities, local extinction, and recolonization rates). In capture–recapture studies, the population of interest is sampled two or more times and each captured animal is uniquely marked. Depending upon study objectives, captures may be by live trapping, harvest, passive integrated transponder (PIT) tags, radioactive markers, radio-telemetry, observing marks such as neck or leg bands, or repeated counts. Some individual animals may carry unique markings such as color patterns (e.g., stripes on a tiger), vocal patterns (e.g., unique bird sonograms), and even genetic markers. With capture–recapture studies, there is a concern with variation from both the sampling procedure and detectability (capture probability) issues related to the individuals under study (Lancia et al. 2005; Williams et al. 2002). Some detectability issues can be solved through study design, as described by our discussion of line intercept and double sampling (see Sects. 4.3.5 and 4.5). Capture–recapture studies, and the extensive theory dealing with models for the analysis of these data, combine issues related to the sampling process and those issues related to the uncertainty regarding the appropriate model to be used to explain the data (Williams et al. 2002).

In general, sample plans should allow the study to meet the assumptions of the model being used to analyze the resulting data and allow the desired statistical inference. We consider a range of models including the relatively simple Petersen–Lincoln model (Lincoln 1930), the closed and open population capture–recapture Cormack–Jolly–Seber and Jolly–Seber model (Otis et al. 1978; Seber 1982; Pollock et al. 1990; Williams et al. 2002), models for survival of radio-tagged individuals (Pollock et al. 1989; Venables and Ripley 2002), and models for presence–absence data (MacKenzie et al. 2002). For a general review of modeling of capture–recapture statistics we refer you to Pollock (1991) and Williams et al. (2002).

4.7.2 Petersen–Lincoln Model

The Petersen–Lincoln model has been used for years by wildlife biologists to estimate animal abundance and is considered a closed population model. The Petersen–Lincoln model should be considered an index to abundance when a systematic bias prevents of one or more of the assumptions described below from being satisfied. In a Petersen–Lincoln study, a sample n_1 of the population is taken at time t_1 and all organisms are uniquely marked. A second sample n_2 is taken at time t_2 and the organisms captured are examined for a mark and a count is made of the recaptures (m_2). Population size (N) is estimated as

$$\hat{N} = n_1 n_2 / m_2.$$

The assumptions for the Petersen–Lincoln model are:

1. The population is closed (i.e., N does not change between time t_1 and time t_2).
2. All animals have equal probability of capture in each sample.
3. There are no errors of measurement.

The assumption of closure is fundamental to the Petersen–Lincoln and other closed population models. Populations can increase or decrease through reproduction or immigration and mortality or emigration, respectively. The elimination of immigration and emigration is difficult in large and relatively mobile species. The success of mark–recapture studies with mobile populations often depends on the selection of study area boundaries grounded in this assumption. Lebreton et al. (1992 [from Gaillard 1988]) provided an example of studies of roe deer (*Capreolus capreolus*) in a large fenced enclosure, essentially creating an artificially closed population. Numerous studies of larger and more mobile species have attempted to document and account for immigration and emigration through the use of radiotelemetry (e.g., Miller et al. 1997). The assumption can best be met for small and relatively immobile species by keeping the interval between samples short. Lancia et al. (2005) reported 5–10 days as the typical interval, although the appropriate period between samples will be taxon-specific.

The assumption of closure can be relaxed in some situations (Seber 1982). Losses from the population are allowed if the rate of loss is the same for marked and unmarked individuals, which is a difficult assumption to justify. If there are deaths at the time of marking the first sample, then the Petersen–Lincoln estimate applies to the number of animals alive in the population after time t_1. If there is natural mortality of animals between the two samples and it applies equally to marked and unmarked animals, then the estimate applies to the population size at the time of the release of the first sample. Kendall (1999) suggested that if animals are moving in and out of the study area in a completely random fashion, then the Petersen–Lincoln estimator (and closed population methods in general) is unbiased for the larger estimate of abundance. The jackknife estimator of Burnham and Overton (1978) is a good general tool for dealing with heterogeneity of capture probabilities. When heterogeneity is not severe, turning multiple samples into two, as in Menkins and Anderson (1988), works reasonably well. Kendall (1999) also discussed the implications of these and other types of closure violations for studies involving greater than two samples of the population.

The second assumption is related to the first and implies that each sample is a simple random sample from a closed population and that marked individuals have the same probability of capture as the unmarked animals. If the probability of capture is different for different classes of animals (say young vs. adults) or for different locations, then the sampling could follow the stratified random sampling plan. It is common in studies of large populations that a portion of the animal's range may be inaccessible due to topography or land ownership. The estimate of abundance is thus limited to the area of accessibility. This can be a problem for animals that have large ranges, as there is no provision for animals being unavailable during either of the sampling periods. The probability of capture can also be influenced by the conduct of the study such that animals become trap happy (attracted to traps) or trap shy (repulsed from traps). The fact that study design seldom completely satisfies this assumption has led to the development of models (discussed below) that allow the relaxation of this requirement.

The third assumption depends on an appropriate marking technique. Marks must be recognizable without influencing the probability of resighting or recapture. Thus, marks must not make the animal more or less visible to the observer or more or less susceptible to mortality. Marks should not be easily lost. If the loss of marks is a problem, double marking (Caughley 1977; Seber 1982) can be used for corrections to the recapture data. New methods of marking animals are likely to help refine the design of mark–recapture observational studies and experiments (Lebreton et al. 1992). This assumption illustrates the need for standardized methods and good standard operating procedures so that study plans are easy to follow and data are properly recorded.

An appropriate study design can help meet the assumptions of the Petersen–Lincoln model, but the two trapping occasions do not allow a test of the assumptions upon which the estimates are based. Lancia et al. (2005) suggested that in two-sample studies, the recapture method be different and independent of the initial sample method. For example, one might trap and neckband mule deer and then use observation as the *recapture* method. This recommendation seems reasonable and should eliminate the concern over trap response and heterogeneous capture probabilities.

4.7.3 Closed Population Mark–Recapture

Otis et al. (1978) and White et al. (1982) offered a modeling strategy for making density and population size estimates using capture data on closed animal populations. With a complete capture history of every animal caught, these models allow relaxation of the equal catchability assumption (Pollock 1974; Otis et al. 1978; Burnham and Overton 1978; White et al. 1982; Pollock and Otto 1983; Chao 1987, 1988, 1989; Menkins and Anderson 1998; Huggins 1989, 1991; Brownie et al. 1993;

Lee and Chao 1994). A set of eight models is selected to provide the appropriate estimator of the population size. The models are M_0, M_t, M_b, M_h, M_{tb}, M_{th}, M_{bh}, and M_{tbh}, where the subscript “0” indicates the null case, and t, b, and h, are as follows:

- 0 – All individuals have the same probability of capture throughout the entire study
- t – Time-specific changes in capture probabilities (i.e., the Darroch 1958 model where probability of capture is the same for all individuals on a given occasion)
- b – Capture probabilities change due to behavioral response from first capture (i.e., probability of capture remains constant until first capture, can change once, and then remains constant for the remainder of the study)
- h – Heterogeneity of capture probabilities in the population (i.e., different subsets of the individuals have different probability of capture but, probability of capture does not change during the course of the study)

This series of eight models includes all possible combinations of the three factors, including none and all of them (Table 4.1 and Fig. 4.14). Population estimates from removal data can also be obtained because the estimators for the removal model of Zippen (1958) are the same as the estimators under the behavioral model M_b.

Estimators for the eight models can be found in Rexstad and Burnham (1991). We suggest you also check the US Geological Survey Patuxent Wildlife Research Center’s software archive (http://www.pwrc.usgs.gov) for additional information and updated software for mark–recapture data. Since explicit formulas do not exist for the estimators, they must be solved by iterative procedures requiring a computer. The design issues are essentially identical to the two-sample Petersen–Lincoln study with the condition of assumption 2 met through the repeated trapping events and modeling.

4.7.4 Population Parameter Estimation

When studying animal populations, survival and recruitment may be of equal or greater interest than density or absolute abundance. Capture–recapture models

Table 4.1 The eight models summarized by symbol, sources of variation in capture probability, and the associated estimator, if any

Model	Sources of variation in capture possibilities	Appropriate estimator
M_0	None	Null
M_t	Time	Darroch
M_b	Behavior	Zippin
M_h	Heterogeneity	Jacknife
M_{tb}	Time, behavior	None
M_{th}	Time, heterogeneity	None
M_{bh}	Behavior, heterogeneity	Generalized removal
M_{tbh}	Time, behavior, heterogeneity	None

The names provided are those used by program Capture and MARK for these estimators

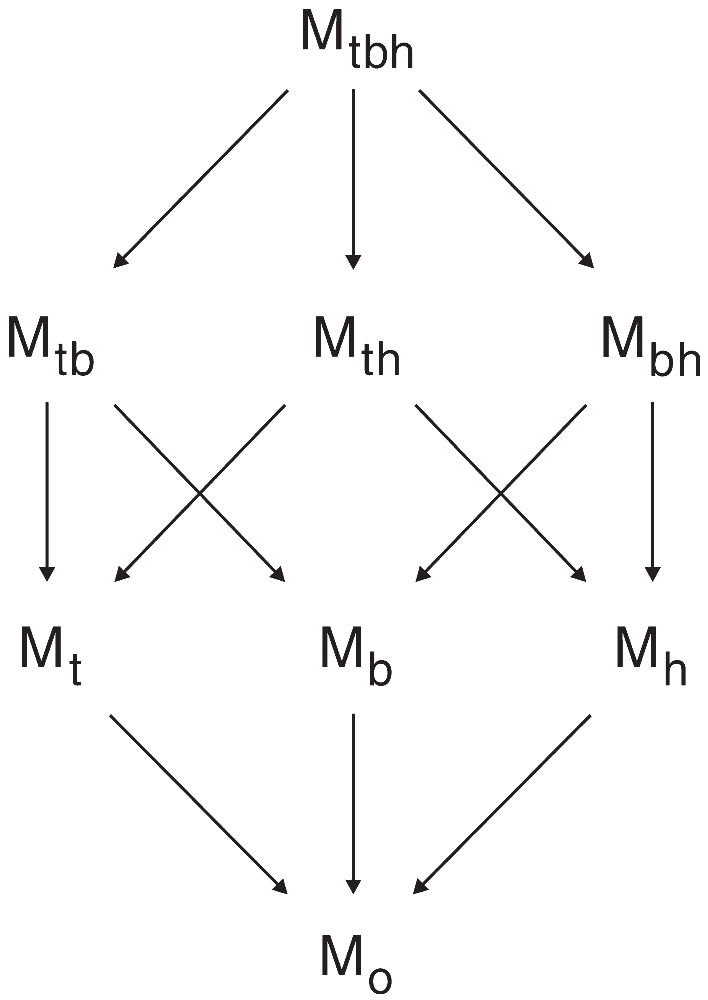

Fig. 4.14 The series of eight closed population models proposed includes all possible combinations of three factors, including none and all of them. Reproduced from Otis et al. (1978) with kind permission from The Wildlife Society

focused on estimation of survival originally treated survival as a nuisance parameter to estimation of abundance (Williams et al. 2002). Beginning around the 1980s, however, survival estimation became a primary state variable of interest in wildlife population ecology (Lebreton et al. 1992). Here we provide a brief overview of several related topics with respect to parameter estimation, but refer readers to Seber (1982), Williams et al. (2002), and Amstrup et al. (2005) for a detailed discussion as the literature and methods for estimating population parameters are continually being reevaluated and refined. Additionally, see Chap. 2 for a list of statistical programs that can be used for estimation procedures.

4.7.4.1 Open Population Mark–Recapture

The Cormack–Jolly–Seber and Jolly–Seber methods (Seber 1982; Williams et al. 2002) allow for estimates of abundance, survival, recruitment, and account for nuisance parameters (e.g., detectability). These models are referred to as open population models because they allow for gain or loss in animal numbers during the study. Note that the rate of gain, sometimes called the birth rate, could be recruitment and immigration and the rate of loss, sometimes called the death rate, could be death and permanent emigration. Estimates of population size follow the Petersen–Lincoln estimator previously discussed (see Sect. 4.7.2). The estimate of survival is the ratio of the number of marked animals in the $i+1$ sample to the number of marked animals in the ith sample. Recruitment from time period i to time period $i+1$ is estimated as the difference between the size of the population at time i and the expected number of survivors from i to $i+1$. Formulas for these estimators are presented with examples in Williams et al. (2002) and Lancia et al. (2005).

Assumptions required by the models and possible sampling implications include:

1. The probability of capture in the ith sample is the same for all animals (marked and unmarked).
2. The probability of survival from t_i to t_{i-1} is the same for all marked animals.
3. The probability that an animal in the ith sample is returned alive is the same for all animals.
4. Marks are not lost or overlooked.
5. The sampling is instantaneous and fates of marked individuals are independent.
6. Emigration from the sample area is permanent.

If the probability of capture varies by characteristics such as age and sex of animal then the data can be stratified during analysis. Similarly, if capture probabilities vary depending on habitat or other environmental variables, then stratification of the study area during sampling may be attempted with separate estimates made for each habitat. The assumption of equal probability of survival (and its reciprocal, the probability of death) of marked animals is not required for either method. For example, young and adult marked animals can have different survival probabilities, a common occurrence in wildlife populations. Using a classic design of one capture occasion per period, survival–immigration and death–permanent emigration are completely confounded in capture–recapture data. However, for the models to be useful, one must accept the assumption that survival probability is the same for marked and unmarked animals. In many situations, one can assume that immigration and emigration offset and thus have little impact on the assumption that estimates of the rate of gain and loss equal birth rate and death rate. If a segregation of these rates is desired, however, then study boundaries should minimize this interchange or interchange must be estimated (e.g., Miller et al. 1997). Emigration and immigration could be significant problems in short-term studies of highly mobile animals with large home ranges (e.g., bears) or in source populations where emigration far exceeds immigration (e.g., dispersal of young mountain lions as described by Hornocker 1970). The confounding mentioned above can be partially avoided by using more complex applications of these models. If the study is being done at multiple sites then multistate models (e.g., Brownie et al. 1993; Williams et al. 2002) can be used to estimate probabilities of movement between areas. Supplemental telemetry could be used to estimate some of the movement. Band recoveries can be combined with recapture information to separate philopatry from survival (Burnham 1993). In age-dependent models, recruitment from a lower age class can be separate from immigration (Nichols and Pollock 1983). There are many different types of capture–recapture models including approaches outlined by Burnham (1993), the super-population approach of Schwarz and Arnason (1996), a host of models by Pradel (1996) which focus on survival and recruitment, as well as the Link and Barker (2005) reparameterization of the Pradel (1996) model to better estimate those recruitment parameters.

4.7.4.2 Pollock's Robust Design

Lancia et al. (2005) pointed out that the distinction between open and closed populations is made to simplify models used to estimate population parameters of interest. The simplifications are expressed as assumptions and study design must take these simplifying assumptions into account. Pollock (1982) noted that long-term studies often consist of multiple capture occasions for each period of interest. He showed that the extra information from the individual capture occasions could be exploited to reduce bias in Jolly–Seber estimates of abundance and recruitment when there is heterogeneity in detection probabilities.

Under Pollock's robust design, each sampling period consists of at least two subsamples, ideally spaced closely together so that the population can be considered closed to additions and deletions during that period. Kendall and Pollock (1992) summarized other advantages of this basic design, in that abundance, survival rate, and recruitment can be estimated for all time periods in the study, whereas with the classic design one cannot estimate abundance for the first and last periods, survival rate to the last period, and the first and last recruitment values; recruitment can be separated into immigration and recruitment from a lower age class within the population when there are at least two age classes, whereas the classic design requires three age classes (Nichols and Pollock 1990); abundance and survival can be estimated with less dependence, thereby lessening some of the statistical problems with density-dependent modeling (Pollock et al. 1990); and study designs for individual periods can be customized to meet specific objectives, due to the second level of sampling. For instance, adding more sampling effort in period i (e.g., more trapping days) should increase precision of the abundance estimate for period i. However, adding more sampling effort after period i should increase precision of survival rate from i to $i + 1$.

The additional information from the subsamples in the robust design allows one to estimate the probability that a member of the population is unavailable for detection (i.e., a temporary emigrant) in a given period (Kendall et al. 1997). Depending on the context of the analysis, this could be equivalent to an animal being a nonbreeder or an animal in torpor. Based on the advantages listed above, we recommend that Pollock's robust design be used for most capture–recapture studies. There are no apparent disadvantages in doing so. Even the assumption of closure across subsamples within a period is not necessarily a hindrance (Schwarz and Stobo 1997; Kendall 1999). Even where it turns out that it is not possible to apply sufficient effort to each subsample to employ the robust design, the data still can be pooled and traditional methods used. The advantages of the robust design derive from the second source of capture information provided by the subsamples. Obviously, the overall study design must recognize the desired comparisons using the open models, even though the distribution of the samples for the closed model (as long as it is a probabilistic sample) is of relatively little consequence.

4.7.4.3 Time-to-event Models

Survival analysis is a set of statistical procedures for which the outcome variable is the time until an event occurs (Kleinbaum 1996). As such, survival analysis is concerned with the distribution of lifetimes (Venables and Ripley 2002). In wildlife research, survival analysis is used to estimate survival ($\hat{S}$), or the probability that an individual survives a specified period (days, weeks, years). Because estimates of survival are used in population models, evaluations of changing population demography, and as justification for altering management practices, approaches to survival analysis have becoming increasingly common in wildlife research. Probably the most common approach to survival analysis in wildlife science is estimation using known fate data based on radio-telemetry where individuals are relocated on some regular basis. Another common application of time to event models has been recent work focused on estimating survival of nests where the event of interest is the success or failure of a nest (Stanley 2000; Dinsmore et al. 2002; Rotella et al. 2004; Shaffer 2004).

Generally, estimation of survival is focused on the amount of time until some event occurs. Time-to-event models are not constrained to evaluating only survival, as the event of interest could include not only death, but also recovery (e.g., regrowth after a burn), return to a location (e.g., site fidelity), incidence (e.g., disease transmission or relapse), or any experience of interest that happens to an individual (Kleinbaum 1996). Typically, the time in time-to-event models refers to an anthropomorphic specification set by the researchers (e.g., days, months, seasons) based on knowledge of the species of interest. In wildlife studies, the event of interest is usually death (failure).

One key point that must be addressed is censoring, both right and interval censoring and left truncation. Censoring occurs when the information on the individual(s) survival is incomplete, thus we do not know the survival times exactly. There are three types of censoring which influence survival modeling:

- Right censoring – when the dataset becomes incomplete on the right size of the follow-up period
- Middle censoring – when during the study, the probability of detecting an individual is <1
- Left truncation – when the dataset is incomplete at the left side of the follow-up period

Censoring of individuals in wildlife studies can be caused by several factors, including loss or failure of the radio-tag, detection probabilities <1, topography, or observer search image as well as emigration, which we break into two classes, temporary, or when a radio tagged individual leaves the study area for 1 sampling occasion and then returns (e.g., middle censoring), and permanent emigration, or when an individual leaves the study area and does not return. One primary difficulty in radio-telemetry studies is distinguishing radio failure from permanent emigration. Additionally, nonrelocation due to temporary emigration during an encounter (sampling) occasion also causes censoring. For example, temporary emigration can be a problem when attempting to evaluate effects of some factor on survival, but this factor differs on and off the study area (e.g., hunting on public lands [study area], but no hunting off the study area on adjacent private lands).

There are three basic survivorship functions using for analysis of time to event data. First, consider that T is a random variable that indicated the length of time before a specific event occurs, e.g., the event typically is "failure", i.e., death of a study individual, but it could be "success," such as returning to an area.

The three potential survivorship functions (from Venables and Ripley 2002; Hosmer and Lemeshow 1999) are

- $S(t) = \Pr(T>t)$, which is the survivorship function which described the probability than an individual animal survives longer than time T. This is frequently estimated as the proportion of animals surviving longer than t, $\hat{S}(t)$
- $f(t) = 1 - S(t)$ or $f(t) = \mathrm{d}F(t)/\mathrm{d}t = -\,\mathrm{d}S(t)/\mathrm{d}t$, which is the probability density function for the time until event. $f(t)$ is most often called the life distribution or the failure time distribution
- $h(t) = f(t)/S(t)$ is the hazard function and is interpreted as a conditional probability of failure rate

Perhaps the most common estimator for survival is the Kaplan–Meier product limit estimator (Kaplan and Meier 1958; Pollock et al. 1989). The Kaplan–Meier estimator does not make any underlying assumptions about the function being estimated and is basically an extension of the binomial estimator (Williams et al. 2002). In its simplest form, the Kaplan–Meier estimator is

$$\hat{S}(t) = \prod_{a=1}^{J} \left(1 - \frac{d_j}{r_j}\right),$$

where the product of all j terms for which $a_j <$ time t given that a_j are the discrete time points (j) when death occurs, d_j is the number of deaths at the jth time point, and r_j is the number of animals at risk at the jth time point. Thus, the probability of surviving from time 0 to a_1 (interval during which first death occurs) is estimated as

$$\hat{S}(a_1) = 1 - \frac{d_1}{r_1}$$

and the probability of surviving from time a_1 to a_2 is $1 - d_2/r_2$, so $\hat{S}(a_2)$ is the product of the first 2 is given by

$$\hat{S}(a_2) = \left(1 - \frac{d_1}{r_1}\right)\left(1 - \frac{d_2}{r_2}\right), \quad \text{and so on.}$$

There are several general assumptions for time to event studies (see Pollock et al. 1989; Williams et al. 2002). First, we assume that radio-tagged individuals are a random sample from the population of interest. This assumption can be satisfied by using random location of trapping sites or perhaps stratifying trapping effort by perceived density of the population. We also assume that survival times are independent among different animals; violating this assumption leads to *overdispersion*. For example, you catch a brood of quail (say 6 young) and radio-tag each, but a predator finds the brood and predates the hen and all the young – thus survival time between individuals was not independent. Additionally, we assume that radio transmitters (or other marks) do not affect the survival of marked individuals and that the censoring mechanism in random or that censoring is not related to fate of the individual (e.g., a radio destroyed during predation or harvest event). For staggered entry studies, newly marked individuals have the same survival function as previously marked individuals.

4.7.4 Occupancy Modeling

Occupancy modeling is a recent entry into the field of capture–recapture analysis (MacKenzie et al. 2002; MacKenzie 2005). This approach stems from historical work done to confirm presence of a species in a particular location at a particular time, and as such relates data on site-specific features (e.g., canopy cover) to the presence of a species. Thus, the presence or absence of the feature can be used as a surrogate for abundance in monitoring temporal and spatial changes in species distributions (MacKenzie et al. 2006). Research on animal detectability has focused primarily on density or abundance estimation (e.g., Buckland et al. 2001; Borchers et al. 2002; Williams et al. 2002), but more limited efforts have been expended on presence–absence approaches (Vojta 2005). Occupancy modeling focuses on estimating the proportion of an area of suitable habitat that is occupied by an individual of the species of interest (MacKenzie et al. 2004).

Occupancy surveys make the same general assumptions as most capture–mark–recapture studies and several specific assumptions (MacKenzie et al. 2006) including (1) survey sites are closed to changes in occupancy over the survey season, (2) occupancy probabilities and detection probabilities are either constant across sites or a function of survey covariates, and (3) detections at each location are independent. Surveys for occupancy are usually less labor intensive than surveys for estimation of abundance in that both active (e.g., point counts during breeding season) and passive approaches (e.g., track counts or hair snares) can be used to survey for presence. However, the difficulty becomes determining when a species is truly absent from the study plot, because failing to locate an individual during a survey does not imply absence (MacKenzie et al. 2006).

From a survey design standpoint, the percentage of sampling units occupied by a species of interest across a landscape is important for population management and monitoring (MacKenzie and Royle 2005). Occupancy surveys are developed to estimate this quantity (fraction of sampling units occupied), while accounting for incomplete detectability and those factors, which influence detectability. Consider the hypothetical situation where we conduct bird point counts to evaluate presence–absence of an endangered passerine across a physiographic region. We are unable to sample every potential area the birds might inhabit, but we know that the birds select a specific habitat type (e.g., closed canopy forest). Thus, our sampling frame will be all potential bird habitat within this ecoregion, and we will sample, according to some probabilistic design, a subset of the total number of sampling units (sites). For each site, we will conduct several visits; the number of visits depends upon bird phenology and survey effort necessary, although MacKenzie and Royle (2005) suggest 3 visits. On each visit, presence or absence is noted, with our intent being to estimate occupancy (ψ_i) as well as detection probability (p_i) for the *i*th sampling unit for the species of interest (MacKenzie and Royle 2005; MacKenzie et al. 2006). Currently, occupancy models are available for single or multiple season surveys, and considerable research is continuing on combining occupancy surveys with count data or marked individuals to estimate population size (MacKenzie et al. 2006).

Occupancy modeling provides an alternative to managers for monitoring species trends (proportion of plots with the species) as well as evaluating colonization and extinction from study sites. Occupancy approaches require less data and effort. More precise abundance estimation for a rare species across a landscape may not be implementable due to costs associated with capture and marking animals over a broad spatial and temporal frame, while collection of presence–absence data can demonstrate whether the population is expanding or contracting over time. This might be all the information required for sound management.

Species detectability frequently hinders the ability of managers to make appropriate management decisions. Detectability becomes extremely important when dealing with species that are rare either functionally or operationally (McDonald 2004). Work by Royle and Nichols (2003), Royle (2004a,b), Kery et al. (2005), Royle and Link (2005), and Royle et al. (2005) focused on estimating species abundance by combining repeated survey counts and mixture models (beta-binomial mixtures) to estimate both detectability and abundance. We see occupancy modeling as a considerable improvement over uncorrected surveys (e.g., bird point counts) and these approaches should be evaluated for applicability across wildlife science.

4.8 Resource Selection

A primary concern of the biologist is the identification, availability, and relative importance of resources (e.g., food, cover, or water) used by animals (i.e., habitat). Habitat or *resource selection* by animals is of interest when evaluating habitat management and the impact of perturbations on wildlife populations. These studies have far reaching importance to wildlife management, particularly as they relate to federally protected species. For example, results of habitat use studies were central to the debate over the importance of old-growth timber to the spotted owl (*Strix occidentalis*) and instream flows in the central Platte River in Nebraska to the whooping crane (*Grus americana*).

In resource selection studies, the availability of a resource is the quantity accessible to the animal (or population of animals) and the use of a resource is that quantity utilized during the time period of interest (Manly et al. 1993). When use of a resource is disproportionate to availability, then the use is selective (i.e., the animal is showing a preference or avoidance for the resource). Manly et al. (1993) provide a unified statistical theory for the analysis of selection studies. The theory and application of resource selection studies were updated (Johnson 1998). We recommend a thorough review of both of these references for anyone considering this type of study.

Biologists often identify resources used by animals and document their availability (usually expressed as abundance or presence/absence). Resource selection models can be developed using most of the designs previously discussed. In most observational studies, it will be impossible to identify unique animals. However, using observations of animals seen from randomly or systematically chosen points, it is possible to use resource variables with known availability (e.g., vegetation) as predictor variables. For example, assume that a certain vegetation type is preferentially selected as feeding sites for elk within a certain distance of conifer cover (Thomas 1979). For example, if the distance was 0.5 km, then one could predict that the impact of timber harvest on elk forage would increase if logging occurs <0.5 km from this vegetation type. Alternatively, the study area could be classified into available units characterized on the basis of a set of predictor variables, such as vegetation type, distance to water, distance to cover, and distance to roads. If use is defined as the presence or absence of feeding elk, resource selection could be used to evaluate the effect of a set of predictor variables on available forage.

4.8.1 Sampling Designs

Alldredge et al. (1998) reviewed the multitude of methods used in the study of resource selection. Resource selection occurs in a hierarchical fashion from the geographic range of a species, to individual animal ranges within a geographic range, to use of general features (habitats) within the individual's range, to the selection of particular elements (food items) within the feeding site (Manly et al. 1993). The first design decision in a resource selection study is the scale of study (Johnson 1980). Manly et al. (1993) suggested conducting studies at multiple scales. Additional important decisions affecting the outcome of these studies include the selection of the study area boundary and study techniques (Manly et al. 1993).

Resource selection probability functions give probabilities of use for resource units of different types. This approach may be used when the resource being studied can be classified as a universe of N available units, some of which are used and the remainder not used. Also, every unit can be classified by the values that it possesses for certain important variables ($X = X_1, X_2, \ldots, X_p$) thought to affect use. Examples include prey items selected by predators based on color, size, and age, or plots of land selected by ungulates based on distance to water, vegetation type, distance to disturbance, and so on. Sampling of used and unused units must consider the same issues as discussed previously for any probability sample.

Thomas and Taylor (1990) described three general study designs for evaluating resource selection. In design I, measurements are made at the population level. Units available to all animals in the population are sampled or censused and classified into used and unused. Individual animals are not identified. In design II, individual animals are identified and the use of resources is measured for each while availability is measured at the level available to the entire population. In design III, individuals are identified or collected as in design II and at least two of the sets of resource units (used resource units, unused resource units, available resource units) are sampled or censused for each animal.

Manly et al. (1993) also offered three sampling protocols for resource selection studies. First, one outlines random sampling or complete counts on available units and randomly samples used resource units. Next, one = outlines randomly samples or census subjects within available units and randomly samples unused units. Finally, one takes an independent sample of both used and unused units. Also, it is possible in some situations to census both used and unused units. Erickson et al. (1998) described a moose (*Alces alces*) study on the Innoko National Wildlife Refuge in Alaska that evaluated habitat selection following Design I and sampling protocol A (Fig. 4.15).

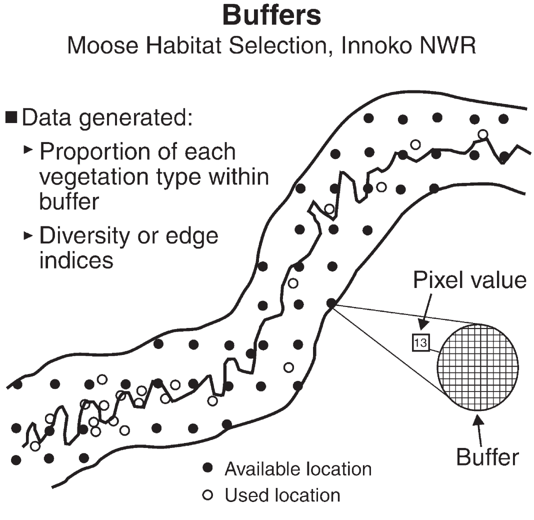

Fig. 4.15 Schematic of design I and sampling protocol A (from Manly et al. 1993) as used in a survey of potential moose use sites in a river corridor in Innoko National Wildlife Refuge in Alaska. Reproduced from Erickson et al. (1998) with kind permission from American Statistical Society

The selection of a particular design and sampling protocol must consider the study area, the habitats or characteristics of interest, the practical sample size, and the anticipated method of analysis. The design of studies should also consider the relationship between resource selection and the anticipated benefits of the selection of good resources, such as increased survival rate, increased productivity, and/or increased fitness (Alldredge et al. 1998).

4.9 Spatial Statistics

Wildlife studies frequently are interested in describing the spatial pattern of resources or contaminants. The application of spatial statistics offers an opportunity to evaluate the precision of spatial data as well as improve the efficiency of spatial sampling efforts. Spatial statistics combine the geostatistical prediction techniques of kriging (Krige 1951) and simulation procedures such as conditional and unconditional simulation (Borgman et al. 1984, 1994). Both kriging and simulation procedures are used to estimate random variables at unsampled locations. Kriging produces best linear unbiased predictions using available known data, while the simulation procedures give a variety of estimates usually based on the data's statistical distribution. Kriging results in a smoothed version of the distribution of estimates, while simulation procedures result in predicted variance and correlation structure, and natural variability of the original process are preserved (Kern 1997). If the spatial characterization of the mean of the variable in the mean in each cell of a grid, for example, then kriging procedures are satisfactory. However, if the spatial variability of the process is of importance, simulation procedures are more appropriate. For a more complete treatment of simulation techniques see Borgman et al. (1994) or Deutsch and Journel (1992). Cressie (1991) gave a complete theoretical development of kriging procedures, while Isaaks and Srivastava (1989) provided a more applied treatment appropriate for the practitioner. For the original developments in geostatistics, we refer you to Krige (1951), Matheron (1962, 1971), and Journel and Huigbregts (1978).

In a study using spatial statistics, data generally are gathered from a grid of points and the spatial covariance structure of variables is used to estimate the variable of interest at points not sampled. The data on the variable of interest at the sample locations could be used to predict the distribution of the variable for management or conservation purposes. For example, suppose a wind plant is planned for a particular area and there is concern regarding the potential for the development to create risk to birds. If bird counts are used as an index of local use, then estimates of local mean bird use could be used to design the wind plant to avoid high bird use areas. Preservation of local variability would not be necessary, and kriging would provide a reasonable method to predict locations where bird use is low and hence wind turbines should be located. Using this sort of linear prediction requires sampling in all areas of interest.

Geostatistical modeling, which considers both linear trends and correlated random variables, can be more valuable in predicting the spatial distribution of a variable of interest. These geostatistical simulation models are stochastic, and

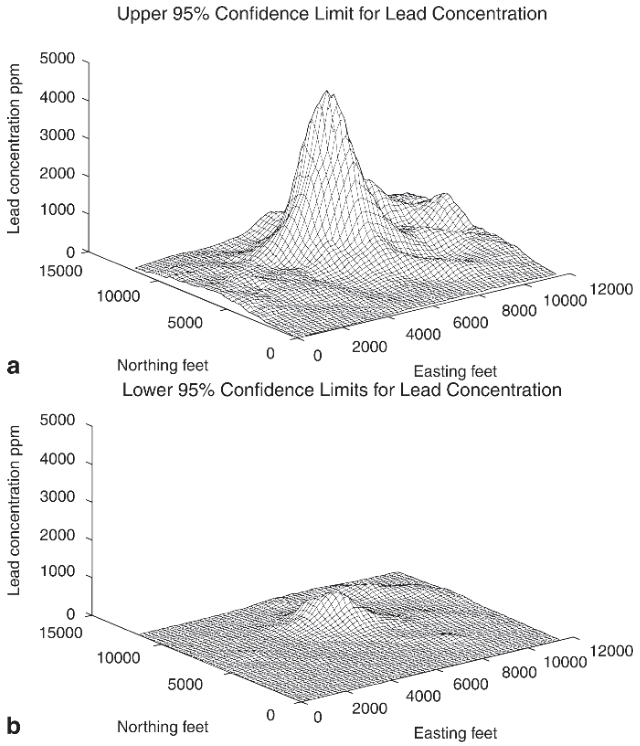

Fig. 4.16 A hypothetical three-dimensional map generated by geostatistical modeling illustrating an upper (**a**) and lower (**b**) 95% confidence limit for lead concentration (from Kern 1997)

predict a degree of randomness in spatial perception of the parameter (Borgman et al. 1994). For example, if one is interested in the spatial distribution of a contaminant for the purposes of cleanup, then a fairly high degree of interest would exist in the location of high concentrations of the contaminant as well as the degree of confidence one could place in the predicted distribution. This confidence in the predicted distribution of contaminates would lead to decisions about where cleanup is required and where more sampling effort is needed. Figure 4.16 illustrates a hypothetical upper and lower confidence limit for lead concentration. These kinds of maps could be valuable in impact evaluation, as well as management situations such as contaminant clean up.

4.10 Summary

The goal of wildlife ecology research is to learn about wildlife populations and the habitats that they use. Thus, the objective of Chap. 4 was to provide a description of the fundamental methods for sampling and making inferences in wildlife studies.

We began with a discussion of the basics of sample survey design, plot shape and size, random and nonrandom sample survey selection as well as a description of common definitions used in wildlife sample survey design. Within Sect. 4.1, we detail the necessity to define clearly study objectives, the area of inference, and the sampling unit(s) of importance. Additionally, we discuss the need for clear definition of the parameters to measure. In Sects. 4.2 and 4.3, we discussed numerous methods for probability sampling, ranging from simple random sampling to strip adaptive cluster sampling. Under this framework, we outline the need for probabilistic sampling procedures and how their use lead to strong inference. We outlined several methods to sample populations, ranging from simple fixed area plots to more complicated distance-based estimators under design-based inference.

Next, we focused on model-based sampling (Sect. 4.7). We outlined the rationale for using model-based techniques and discussed the differences between model-based and design-based studies (also see Chap 2). Often, as each wildlife study is unique, decisions regarding the sampling plan will require use of a variety of methods. With this in mind, we discussed several variant of capture–mark–recapture techniques, analysis of presence–absence data, and time to event models; all of which are used for model-based inferences. We conclude this chapter with a discussion on resource selection and spatial statistics and their application to wildlife conservation.

References

Alldredge, J. R., D. L. Thomas, and L. McDonald. 1998. Survey and comparison of methods for study of resource selection. J. Agric. Biol. Environ. Stat. 3: 237–253.

Alpizar-Jara, R., and K. H. Pollock. 1996. A combination line transect and capture re-capture sampling model for multiple observers in aerial surveys. J. Environ. Stat. 3: 311–327.

Amstrup, S. C., T. L. McDonald, and B. F. J. Manly. 2005. Handbook of Capture–Recapture Analysis. Princeton University Press, Princeton.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildl. Soc. Bull. 29: 1294–1297.

Bart, J. and S. Earnst. 2002. Double sampling to estimate density and population trends in birds. Auk 119: 36–45.

Beavers, S. C., and F. L. Ramsey. 1998. Detectability analysis in transect surveys. J. Wildl. Manage. 62(3): 948–957.

Block, W. M., and L. A. Brennan. 1992. The habitat concept in ornithology: Theory and applications. Curr. Ornithol. 11: 35–91.

Borchers, D. L., S. T. Buckland, and W. Zucchini. 2002. Estimating Animal Abundance. Springer, Berlin Heidelberg New York.

Borgman, L. E., M. Taheri, and R. Hagan. 1984. Three-dimensional, frequency-domain simulations of geologic variables, in G. Verly, M. David, A. G. Journel, and A. Marechal, Eds. Geostatistics for Natural Resources Characterization, Part I. Reidel, Dordrecht.

Borgman, L. E., C. D. Miler, S. R. Signerini, and R. C. Faucette. 1994. Stochastic interpolation as a means to estimate oceanic fields. Atmos.-Ocean. 32(2): 395–419.

Bormann, F. H. 1953. The statistical efficiency of sample plot size and shape in forest ecology. Ecology 34: 474–487.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49: 1173–1187.

Buckland, S. T. 1987. On the variable circular plot method of estimating animal density. Biometrics 43: 363–384.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling. Oxford University Press, Oxford.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced Distance Sampling. Oxford University Press, Oxford.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data, in J. D. Lebreton and P. M. North, Eds. Marked Individuals in the Study of Bird Population, pp. 199–214. Birkhäuser-Verlag, Basel, Switzerland.

Burnham, K. P., and W. S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Bometrika 65: 625–633.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72: 1–202.

Burnham, K. P., S. T. Buckland, J. L. Laake, D.L. Borchers, T. A. Marques, J. R. B. Bishop, and L. Thomas. 2004. In S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, Eds. Advanced Distance Sampling, pp. 307–392. Oxford University Press, Oxford.

Byth, K. 1982. On robust distance-based intensity estimators. Biometrics 38: 127–135.

Canfield, R. H. 1941. Application of the line intercept method in sampling range vegetation. J. Forest. 39: 388–394.

Caughley, G. 1977. Sampling in aerial survey. J. Wildl. Manage. 41: 605–615.

Caughley, G., and D. Grice. 1982. A correction factor for counting emus from the air and its application to counts in western Australia. Aust. Wildl. Res. 9: 253–259.

Chao, A. 1987. Estimating the population size for capture–recapture data with unequal catchability. Biometrics 43: 783–791.

Chao, A. 1988. Estimating animal abundance with capture frequency data. J. Wildl. Manage. 52: 295–300.

Chao, A. 1989. Estimating population size for sparse data in capture–recapture experiments. Biometrics 45: 427–438.

Christman, M. C. 2000. A review of quadrat-based sampling of rare, geographically clustered populations. J. Agric. Biol. Environ. Stat. 5: 168–201.

Cochran, W. G. 1977. Sampling Techniques, 3rd Edition. Wiley, New York.

Collier, B. A., S. S. Ditchkoff, J. B. Raglin, and J. M. Smith. 2007. Detection probability and sources of variation in white-tailed deer spotlight surveys. J. Wildl. Manage. 71: 277–281.

Conroy, M. J., J. R. Goldsberry, J. E. Hines, and D. B. Stotts. 1988. Evaluation of aerial transect surveys for wintering American black ducks. J. Wildl. Manage. 52: 694–703.

Cook, R. D., and J. O. Jacobson. 1979. A design for estimating visibility bias in aerial surveys. Biometrics 35: 735–742.

Cressie, N. A. C. 1991. Statistics for Spatial Data. Wiley, New York.

Darroch, J. N. 1958. The multiple recapture census: I. Estimation of a closed population. Biometrika 45: 343–359.

Dell, T. R., and J. L. Clutter. 1972. Ranked set sampling theory with order statistics background. Biometrics 28: 545–553.

Deutsch, C. V., and A. G. Journel. 1992. GSLIB Geostatistical Software Library and User's Guide. Oxford University Press, New York.

Diggle, P. J. 1983. Statistical Analysis of Spatial Point Patterns. Academic, London.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83: 3476–3488.

Drummer, T. D. 1991. SIZETRAN: Analysis of size-biased line transect data. Wildl. Soc. Bull. 19(1): 117–118.

Drummer, T. D., and L. L. McDonald. 1987. Size bias in line transect sampling. Biometrics 43: 13–21.

Eberhardt, L. L. 1978. Transect methods for populations studies. J. Wildl. Manage. 42: 1–31.

Eberhardt, L. L., and M. A. Simmons. 1987. Calibrating population indices by double sampling. J. Wildl. Manage. 51: 665–675.

Erickson, W. P., T. L. McDonald, and R. Skinner. 1998. Habitat selection using GIS data: A case study. J. Agric. Biol. Environ. Stat. 3: 296–310.

Flowy, T. J., L. D. Mech, and M. E. Nelson. 1979. An improved method of censusing deer in deciduous–coniferous forests. J. Wildl. Manage. 43: 258–261.

Foreman. K. 1991. Survey Sampling Principles. Marcel Dekker, New York.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Acta Biotheoret. 19: 16–36.

Gaillard, J. M. 1988. Contribution a la Dynamique des Populations de Grands Mammiferes: l'Exemple du Chevreuil (*Capreolus capreolus*). Dissertation. Universite Lyon I, Villeurbanne, France.

Gasaway, W. C., S. D. DuBois, D. J. Reed, and S. J. Harbo. 1986. Estimating Moose Population Parameters from Aerial Surveys. Institute of Arctic Biology, Biological Papers of the University of Alaska, Fairbanks, AK 99775, No. 22.

Gilbert, R. O. 1987. Statistical Methods for Environmental Pollution Monitoring. Van Nostrand Reinhold, New York.

Gilbert, R. O., and J. C. Simpson. 1992. Statistical methods for evaluating the attainment of cleanup standards. Vol. 3, Reference-Based Standards for Soils and Solid Media. Prepared by Pacific Northwest Laboratory, Battelle Memorial Institute, Richland, WA, for U.S. Environmental Protection Agency under a Related Services Agreement with U.S. Department of Energy, Washington, DC. PNL-7409 Vol. 3, Rev. 1/UC-600.

Graham, A., and R. Bell. 1969. Factors influencing the countability of animals. East Afr. Agric. For. J. 34: 38–43.

Grosenbaugh, L. R. 1952. Plotless timber estimates – new, fast, easy. J. For. 50: 532–537.

Guenzel, R. J. 1997. Estimating Pronghorn Abundance Using Aerial Line Transect Sampling. Wyoming Game and Fish Department, Cheyenne, WY.

Hasel, A. A. 1938. Sampling error in timber surveys. J. Agric. Res. 57: 713–736.

Hendricks, W. A. 1956. The Mathematical Theory of Sampling. The Scarecrow Press, New Brunswick.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deor and elk in the Idaho Primitive Area. Wildl. Monogr. 21.

Horvitz, D. G., and D. J. Thompson. 1952. A generalization of sampling without replacement from a finite universe. J. Am. Stat. Assoc. 47: 663–685.

Hosmer Jr., D. W., and S. Lemeshow. 1999. Applied Survival Analysis. Wiley, New York.

Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76: 133–140.

Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47: 725–732.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187–211.

Isaaks, E. H., and R. M. Srivastava. 1989. An Introduction to Applied Geostatistics, Oxford University Press, New York.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71.

Johnson, D. H., Ed. 1998. J. Agric. Biol. Environ. Stat. 3(3) Special Issue: Resource Selection Using Data from Geographical Information Systems (GIS).

Johnson, D. H. 2002. The importance of replication in wildlife research. J. Wildl. Manage. 66: 919–932.

Journel, A. G., and C. J. Huijbregts. 1978. Mining Geostatistics. Academic, London.

Kaiser, L. 1983. Unbiased estimation in line-intercept sampling. Biometrics 39: 965–976.

Kalamkar, R. J. 1932. Experimental error and the field plot technique with potatoes. J. Agric. Sci. 22: 373–383.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53: 457–481.

Kendall, W. L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. Ecology 80: 2517–2525.

Kendall, W. L., and K. H. Pollock. 1992. The robust design in capture–recapture studies: A review and evaluation by Monte Carlo simulation, in D. R. McCullough, and R. H. Barrett, Eds. Wildlife 2001: Populations, pp. 31–43. Elsevier, London.

Kendall, W. L., J. D. Nichols, and J. E. Hines, 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78: 563–578.

Kern, J. W. 1997. Data analysis techniques for point prediction and estimation of spatial means. Technical Research Work Order Dan Goodman, Department of Biology, Montana State University, Bozeman, MT. Contract 290801.

Kery, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecol. Appl. 15: 1450–1461.

Kleinbaum, D. G. 1996. Survival Analysis: A self-learning text. Springer, New York.

Krebs, C. J. 1989. Ecological Methodology. Harper Collins, New York.

Krebs, C. J. 1999. Ecological Methodology, 2nd Edition. Addison-Welsey, Menlo Park.

Krige, D. G. 1951. A Statistical Approach to Some Mine Valuation and Allied Problems at the Witwaterstrand. Unpublished Masters Thesis, University of Witwaterstrand.

Kuehl, R. O. 2000. Design of Experiments: Statistical Principles of Research Design and Analysis, 2nd Edition. Brooks/Cole, Pacific Grove.

Laake, J. L., K. P. Burnham, and D. R. Anderson. 1979. User's Manual for Program TRANSECT, 26 pp. Utah State University Press, Logan, Utah.

Laake, J. L., S. T. Buckland, D. R. Anderson, and K. P. Burnham. 1993. DISTANCE User's Guide. Version 2.0. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.

Lancia, R. A., W. L. Kendall, K. H. Pollock, and J. D. Nichols. 2005. Estimating the number of animals in wildlife populations, in C. E. Braun, Ed. Research and Management Techniques for Wildlife and Habitats, pp. 106–153. Wildlife Society, Bethesda, MD.

Lebreton, J. -D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol. Monogr. 62: 67–118.

Lee, S. -M., and A. Chao. 1994. Estimating population size via sample coverage for closed capture–recapture models. Biometrics 50: 88–97.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. US Dept. Agric. Circ. No. 118: 1–4.

Link, W. A., and R. J. Barker. 2005. Modeling association among demographic parameters in analysis of open population capture–recapture data. Biometrics 61: 46–54.

Lucas, H. A., and G. A. F. Seber. 1977. Estimating coverage and particle density using the line intercept method. Biometrika 64: 618–622.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical Ecology. Wiley, New York.

Lukacs, P. M. 2002. WebSim: Simulation software to assist in trapping web design. Wildl. Soc. Bull. 30: 1259–1261.

Lukacs, P. M., A. B. Franklin, D. R. Anderson. 2004. In S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, Eds. Advanced Distance Sampling, pp. 260–278. Oxford University Press, Oxford.

Lukacs, P. M., D. R. Anderson, and K. P. Burnham. 2005. Evaluation of trapping-web design. Wildl. Res. 32: 103–110.

MacKenzie, D. I. 2005. What are the issues with presence–absence data for wildlife managers? J. Wildl. Manage. 69: 849–860.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: General advice and allocating survey effort. J. Appl. Ecol. 42: 1105–1114.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83: 2248–2255.

MacKenzie, D. I., J. A. Royle, J. A. Brown, and J. D. Nichols. 2004. Occupancy estimation and modeling for rare and elusive species. In W. L. Thompson, Ed. Sampling Rare or Elusive Species, pp. 149–172. Island Press,Washington.

MacKenzie, D. I., J. D. Nichols, J. Andrew Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy Estimation and Modeling. Academic Press, London.

Manly, B. F. J. 1991. Randomization and Monte Carlo Methods in Biology. Chapman and Hall, London.

Manly, B. F. J., L. McDonald, and D. Thomas. 1993. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Chapman and Hall, London.

Manly, B. F. J., L. McDonald, and G. W. Garner. 1996. Maximum likelihood estimation for the double-count method with independent observers. J. Agric. Biol. Environ. Stat. 1(2): 170–189.

Marques, F. C. C., and S. T. Buckland. 2004. In S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, Eds. Advanced Distance Sampling, pp. 31–47. Oxford University Press, Oxford.

Matheron, G. 1962. Traite de Geostatistique Appliquee, Tome I. Memoires du Bureau de Recherches Geologiques et Minieres, No. 14. Editions Technip, Paris.

Matheron, G. 1971. The theory of regionized variables and its applications. Cahiers du Centre de Morphologie Mathematique, No. 5. Fontaine-bleau, France.

McCullagh, P., and J. A. Nelder. 1983. Generalized Linear Models. Chapman and Hall, London.

McDonald, L. L. 1980. Line-intercept sampling for attributes other than cover and density. J. Wildl. Manage. 44: 530–533.

McDonald, L. L. 1991. Workshop Notes on Statistics for Field Ecology. Western Ecosystems Technology, Inc. Cheyenne, WY.

McDonald, L. L. 2004. Sampling rare populations, in W. L. Thompson, Ed. Sampling Rare or Elusive Species, pp. 11–42. Island Press, Washington.

McDonald, L. L., H. B. Harvey, F. J. Mauer, and A. W. Brackney. 1990. Design of aerial surveys for Dall sheep in the Arctic National Wildlife Refuge, Alaska. Seventh Biennial Northern Wild Sheep and Goat Symposium. May 14–17, 1990, Clarkston, Washington.

McDonald, L. L., W. P. Erickson, and M. D. Strickland. 1995. Survey design, statistical analysis, and basis for statistical inferences in Coastal Habitat Injury Assessment: *Exxon Valdez* Oil Spill, in P. G. Wells, J. N. Buther, and J. S. Hughes, Eds. *Exxon Valdez* Oil Spill: Fate and Effects in Alaskan Waters. ASTM STP 1219. American Society for Testing and Materials, Philadelphia, PA.

Menkins Jr., G. E., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology 69: 1952–1959.

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alsaka using radiotelemetry and replicated mark-resight techniques. Wildl. Monogr. 133.

Mode, N. A., L. L. Conquest, and D. A. Marker. 2002. Incorporating prior knowledge in environmental sampling: ranked set sampling and other double sampling procedures. Environmetrics 13: 513–521.

Mood, A. M., F. A. Graybill, and D. C. Boes. 1974. Introduction to the Theory of Statistics, 3rd Edition. McGraw-Hill, Boston.

Morrison, M. L., W. M. Block, M. D. Strickland, and W. L. Kendall. 2001. Wildlife Study Design. Springer.

Munholland, P. L., and J. J. Borkowski. 1996. Simple latin square sampling +1: A spatial design using quadrats. Biometrics 52: 125–136.

Muttlak, H. A., and L. L.McDonald. 1992. Ranked set sampling and the line intercept method: a more efficient procedure Biometrical J. 34: 329–346.

Nichols, J. D., and K. H. Pollock. 1983. Estimation methodology in contemporary small mammal capture–recapture studies. J. Mammal. 64: 253–260.

Nichols, J. D., and K. H. Pollock. 1990. Estimation of recruitment from immigration versus in situ reproduction using Pollocks robust design. Ecology 71: 21–26.

Noon, B. R., N. M. Ishwar, and K. Vasudevan. 2006. Efficiency of adaptive cluster sampling and random sampling in detecting terrestrial herptofauna in a tropical rainforest. J. Wildl. Manage. 34: 59–68.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62.

Otis, D. L., L. L. McDonald, and M. Evans. 1993. Parameter estimation in encounter sampling surveys. J. Wildl. Manage. 57: 543–548.

Overton, W. S., D. White, and D. L. Stevens. 1991. Design Report for EMAP: Environmental Monitoring and Assessment Program. Environmental Research Laboratory, U.S. Environmental Protection Agency, Corvallis, OR. EPA/600/3–91/053.

Packard, J. M., R. C. Summers, and L. B. Barnes. 1985. Variation of visibility bias during aerial surveys of manatees. J. Wildl. Manage. 49: 347–351.

Patil, G. P., A. K. Sinha, and C. Taillie. 1994. Ranked set sampling, in G. P. Patil and C. R. Rao, Eds. Handbook of Statistics, Environmental Statistics, Vol. 12. North-Holland, Amsterdam.

Pechanec, J. F., and G. Stewart. 1940. Sage brush-grass range sampling studies: size and structure of sampling unit. Am. Soc. Agron. J. 32: 669–682.

Peterjohn, B. G., J. R. Sauer, and W. A. Link. 1996. The 1994 and 1995 summary of the North American Breeding Bird Survey. Bird Popul. 3: 48–66.

Pollock, K. H. 1974. The Assumption of Equal Catchability of Animals in Tag-Recapture Experiments. Ph.D. Thesis, Cornell University, Ithaca, NY.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. J. Wildl. Manage. 46: 752–757.

Pollock, K. H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. J. Am. Stat. Assoc. 86: 225–238.

Pollock, K. H., and M. C. Otto. 1983. Robust estimation of population size in closed animal populations from capture–recapture experiments. Biometrics 39: 1035–1049.

Pollock, K. H., and W. L. Kendall. 1987. Visibility bias in aerial surveys: A review of estimation procedures. J. Wildl. Manage. 51: 502–520.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: The staggered entry design. J. Wildl. Manage. 53: 7–15.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inferences for capture–recapture experiments. Wildl. Monogr. 107.

Pradel, R. 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. Biometrics 52: 703–709.

Quang, P. X. 1989. A nonparametric approach to size-biased line transect sampling. Draft Report. Department of Mathematical Sciences, University of Alaska, Fairbanks, AK 99775. Biometrics 47(1): 269–279.

Quang, P. X., and E. F. Becker. 1996. Line transect sampling under varying conditions with application to aerial surveys. Ecology 77: 1297–1302.

Quang, P. X., and E. F. Becker. 1997. Combining line transect and double count sampling techniques for aerial surveys. J. Agric. Biol. Environ. Stat. 2: 230–242.

Ramsey, F. L., and J. M. Scott. 1979. Estimating population densities from variable circular plot surveys, in R. M. Cormack, G. P. Patil and D. S. Robson, Eds. Sampling Biological Populations, pp. 155–181. International Co-operative Publishing House, Fairland, MD.

Reed, D. J., L. L. McDonald, and J. R. Gilbert. 1989. Variance of the product of estimates. Draft report. Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701.

Rexstad, E., and K. Burnham. 1991. Users Guide for Interactive Program CAPTURE, Abundance Estimation for Closed Populations. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, CO.

Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82(3): 309–313.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. Anim. Biodivers. Conserv. 27: 187–205.

Royle, J. A. 2004a. Generalized estimators of avian abundance from count survey data. Anim. Biodivers. Conserv. 27: 375–386.

Royle, J. A. 2004b. Modeling abundance index data from anuran calling surveys. Conserv. Biol. 18: 1378–1385.

Royle, J. A., and W. A. Link. 2005. A general class of multinomial mixture models for anuran calling survey data. Ecology 86: 2505–2512.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84: 777–790.

Royle, J. A., J. D. Nichols, and M. Kery. 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos 110: 353–359.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. J. Wildl. Manage. 51: 622–630.

Scheaffer, R. L., W. Mendenhall, and L. Ott. 1990. Elementary Survey Sampling. PWS-Kent, Boston, MA.

Schoenly, K. G., I. T. Domingo, and A. T. Barrion. 2003. Determining optimal quadrat sizes for invertebrate communities in agrobiodiversity studies: A case study from tropical irrigated rice. Environ. Entomol. 32: 929–938.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. Biometrics 52: 860–873.

Schwarz, C. J., and W. T. Stobo. 1997. Estimating temporary migration using the robust design. Biometrics 53: 178–194.

Seber, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters, 2nd Edition. Griffin, London.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121: 526–540.

Skinner, R., W. Erickson, G. Minick, and L. L. McDonald. 1997. Estimating Moose Populations and Trends Using Line Transect Sampling. Technical Report Prepared for the USFWS, Innoko National Wildlife Refuge, McGrath, AK.

Smith, W. 1979. An oil spill sampling strategy, in R. M. Cormack, G. P. Patil, and D. S. Robson, Eds. Sampling Biological Populations, pp. 355–363. International Co-operative Publishing House, Fairland, MD.

Smith, D. R., M. J. Conroy, and D. H. Brakhage. 1995. Efficiency of adaptive cluster sampling for estimating density of wintering waterfowl. Biometrics 51: 777–788.

Smith, D. R., J. A. Brown, and N. C. H. Lo. 2004. Application of adaptive sampling to biological populations, in W. L. Thompson, Ed. Sampling Rare or Elusive Species, pp. 77–122. Island Press, Washington.

Southwell, C. 1994. Evaluation of walked line transect counts for estimating macropod density. J. Wildl. Manage. 58: 348–356.

Stanley, T. R. 2000. Modeling and estimation of stage-specific daily survival probabilities of nests. Ecology 81: 2048–2053.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45: 415–425.

Stevens, D. L., and A. R. Olsen. 1999. Spatially restricted surveys over time for aquatic resources. J. Agric. Biol. Environ. Stat. 4: 415–428.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. J. Am. Stat. Assoc. 99: 262–278.

Strickland, M. D., L. McDonald, J. W. Kern, T. Spraker, and A. Loranger. 1994. Analysis of 1992 Dall's sheep and mountain goal survey data, Kenai National Wildlife Refuge. Bienn. Symp. Northern Wild Sheep and Mountain Goat Council.

Strickland, M. D., W. P. Erickson, and L. L. McDonald. 1996. Avian Monitoring Studies: Buffalo Ridge Wind Resource Area, Minnesota. Prepared for Northern States Power, Minneapolis, MN.

Thomas, J. W. Ed. 1979. Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. US Forest Service, Agriculture Handbook 553.

Thompson, S. K. 1990. Adaptive cluster sampling. J. Am Stat. Assoc. 85: 1050–1059.

Thompson, S. K. 1991a. Adaptive cluster sampling: designs with primary and secondary units. Biometrics 47: 1103–1115.

Thompson, S. K. 1991b. Stratified adaptive cluster sampling. Biometrika 78: 389–397.

Thompson, S. K. 1992. Sampling. Wiley, New York.

Thompson, W. L. 2002a. Towards reliable bird surveys: Accounting for individuals present but not detected. Auk 119: 18–25.

Thompson, S. K. 2002b. Sampling, 2nd Edition. Wiley, New York.

Thompson, S. K., and G. A. F. Seber. 1996. Adaptive Sampling. Wiley, New York.

Thomas, D., and E. Taylor. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manage. 54: 322–330.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic, London.

Trenkel, V. M., S. T. Buckland, C. McLean, and D. A. Elston. 1997. Evaluation of aerial line transect methodology for estimating red deer (*Cervus elaphus*) abundance in Scotland. J. Environ. Manage. 50: 39–50.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Springer, New York.

Vojta, C. D. 2005. Old dog, new tricks: Innovations with presence–absence information. J. Wildl. Manage. 69: 845–848.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis, 1982. Capture–Recapture and Removal Methods for Sampling, Closed Populations. Rpt. LA-8787-NERP. Los Alamos National Laboratory, Los Alamos, NM.

Wiegert, R. G. 1962. The selection of an optimum quadrat size for sampling the standing crop of grasses and forbs. Ecology 43: 125–129.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Population. Academic, London.

Wolter, K. M. 1984. Investigation of some estimators of variance for systematic sampling. J. Am. Stat. Assoc. 79: 781–790.

Zippen, C. 1958. The removal method of population estimation. J. Wildl. Manage. 22: 82–90.