CHAPTER 5

ESTIMATING ABUNDANCE: LINE TRANSECTS AND DISTANCE METHODS

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Page

Sampling plants or animals with quadrats is not the only alternative to mark-recapture estimation of abundance. Quadrats are not natural sampling units and one must always decide what size and shape of quadrat to use. One alternative is to use "plotless" sampling procedures. These techniques have been developed by plant ecologists and have been applied recently by animal ecologists. They are useful for plants or animals that move little or can be located before they move. Plotless methods provide a third general class of methods for estimating abundance in plant and animal populations, and in addition to mark-recapture and quadrat counts provide an important tool for the field ecologist.

5.1 LINE TRANSECTS

The line intercept method discussed in Chapter 4 is one example of a family of methods for estimating abundance from transects. Another important method for estimating populations with transect lines is *line transect* sampling. Much of the material on line transect sampling has been brought together in Buckland *et al.* (2001) and Thomas et al. (2010) which provide a detailed reference for these methods. Here I will summarize the general procedures of line transect sampling and highlight the assumptions you must make to use these methods to estimate abundance.

Figure 5.1 illustrates how line transect sampling is done. A transect line is searched and each animal seen provide one measurement of the perpendicular distance to the transect line. Since in practice animals are often seen along the line, three measurements can be taken for each individual sighted (Figure 5.2):

1. Sighting distance (r_i)
2. Sighting angle (Θ_i)
3. Perpendicular distance (x_i)[a]

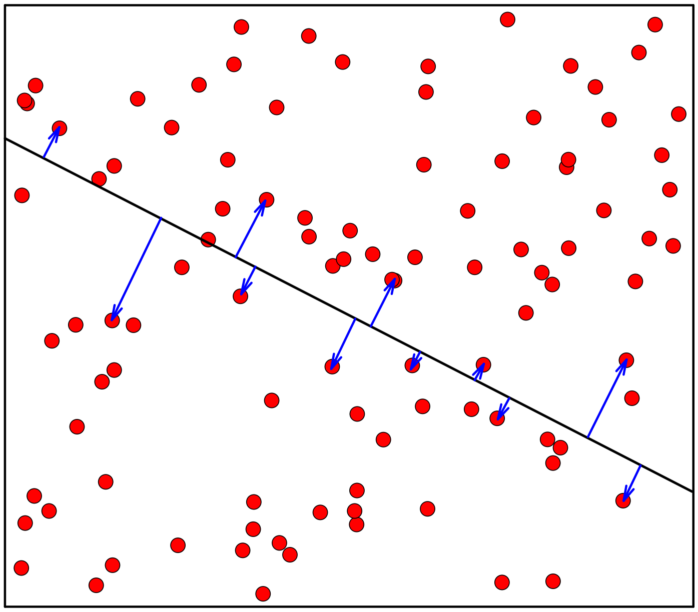

Figure 5.1 Schematic view of the method of line transect sampling. The census zone is the whole area of the square. Only one transect is shown for illustration. The observer moves along the transect line and the distances indicated by the blue arrows are measured to the animals seen. In this example 13 animals were seen (including two right on the transect line). Note that many individuals were not seen and that detection falls of with distance from the transect line

Transect lines may be traversed on foot, on horseback, in a vehicle, or in a helicopter or airplane.

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[a] The perpendicular distance can be calculated from the other two by $x = r \sin \theta$

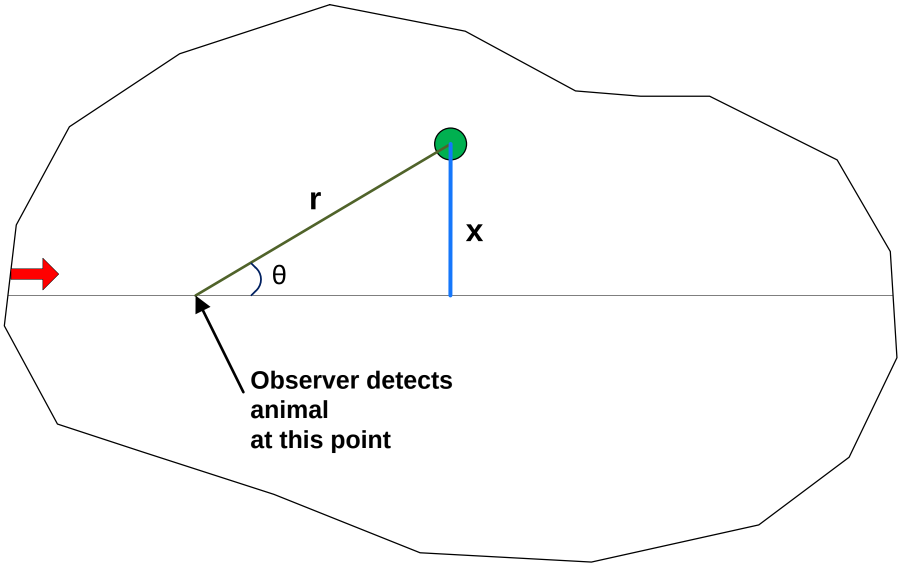

Figure 5.2 Illustration of the basic measurements that can be taken for each individual (green dot) sighted along a line transect. The key measurement is the perpendicular distance (x_i, blue line). If the sighting distance (r_i , green line) is easier to record in the field, the sighting angle (θ)must also be measured. The perpendicular distance $x = r \sin(\theta)$.

If a fixed width of strip is counted, and if all organisms in the strip are seen, estimates of population size are simple, because strips are just long thin quadrats. All the principles of quadrat sampling discussed in Chapter 4 can apply to this situation. Plant ecologists sometimes use *line transects* to mean these long, thin quadrats which are completely censused.

In practice some organisms are undetected as one moves along a transect and in these cases it is best not to limit observations to a fixed strip width. Because individuals are missed, an undercounting bias occurs. In these cases estimation of population density is more difficult because we need to estimate the *detection function* (Figure 5.3). Figure 5.3 shows that in general the detectability will fall off with distance from the center line of the transect. If we can make 4 assumptions we can estimate population density from the detection function. We must assume:

1. Animals directly on the transect line will never be missed (i.e. their detection probability = 1).

2. Animals are fixed at the initial sighting position; they do not move before being detected and none are counted twice.

3. Distances and angles are measured exactly with no measurement error and no rounding errors.

4. Sightings of individual animals are independent events.

There is a key assumption of uniformity that is critical to line transect sampling (Welsh 2002). We must assume that the items being sampled are distributed at random in the landscape so that no matter where we place the line transect we would get the same shaped detection function.

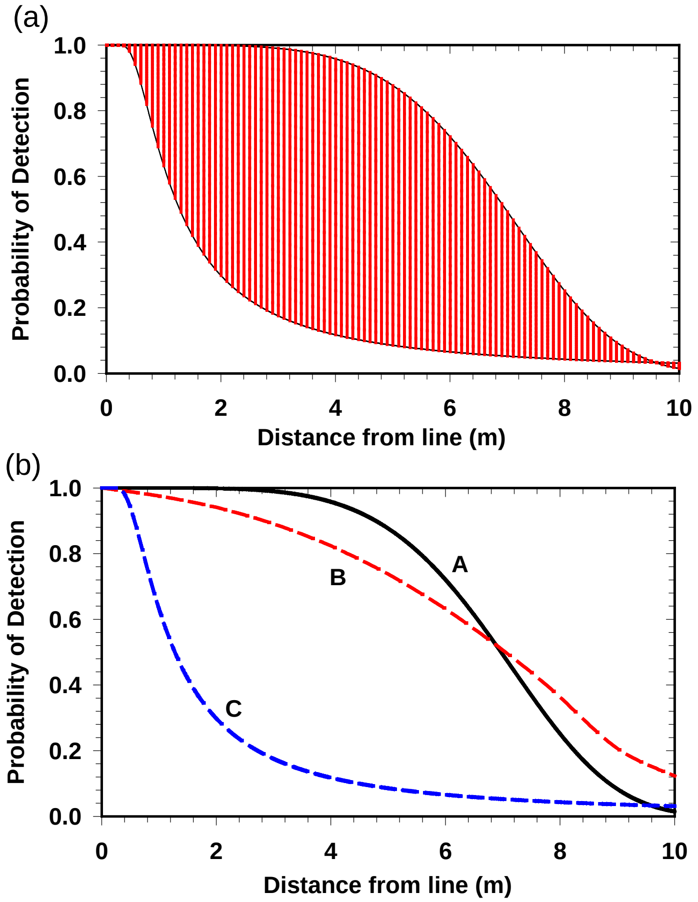

Figure 5.3 Some possible detection functions of line transect surveys. The basic idea of these models is that the probability of detection fall off the farther an animal is from the line transect baseline. (a) The shaded area encloses the general zone for detection functions for wildlife populations. (b) The detection function for any particular set of data may take a variety of shapes, and the statistical problem is to decide what mathematical function to use and what values of its parameters fit best. The generalized exponential (A), the half-normal (B), and the Hayes and Buckland (1983) function (C) are illustrated here. Note that for all these detection functions, the area under the function represents the items counted and the area above the function represents the items missed. (Modified from Burnham *et al*. 1980 and Routledge and Fyfe 1992.

If these assumptions are valid, we can estimate the density of the population by:

$$\hat{D} = \frac{n}{2La} \qquad (5.1)$$

where D = Density of animals per unit area

n = Number of animals seen on transect

L = Total length of transect

a = Half the effective strip width (a constant which must be estimated)

The constant a is simply the total area under the detection function (Fig. 5.3), and it estimates how wide the strip width would be if every organism was seen and none were missed. It is scaled in the same units of measurement as the lengths.

There are numerous ways of estimating a in the literature, and they have been reviewed comprehensively by Burnham *et al*. (1980; their Table 24) and by Buckland *et al.* (1993). We shall discuss three here.

5.1.1 HAYNE ESTIMATOR

This estimator was developed by Hayne (1949) to estimate densities of birds like grouse that flush as an observer comes within a certain radius. The basic assumption of this estimator is that there is a fixed flushing distance r such that if an observer comes closer than r units to the animal, it flushes and is observed. This is a restrictive assumption because it assumes the detection function of Figure 5.3 is rectangular. If this assumption is correct, then population density can be estimated by:

$$\hat{D}_H = \frac{n}{2L}\left(\frac{1}{n}\sum {}^{1}\!/_{r_i}\right) \tag{5.2}$$

where $\hat{D}_H$ = Hayne's estimator of density
n = number of animals seen
L = length of transect
r_i = sighting distance to each animal i (see Fig. 5.2)

The variance of this density estimate is:

$$\text{Var}\left(\hat{D}_H\right) = D_H^2\left[\frac{\text{var}(\text{n})}{\text{n}^2} + \frac{\sum\left({}^{1}\!/_{r_i} - R\right)^2}{R^2\, n(n-1)}\right] \tag{5.3}$$

where $\hat{D}_H$ = Hayne's estimator of density

n = number of animals seen

var(n) = variance of $n \cong n$

r_i = sighting distance for animal i (Fig. 5.2)

R = mean of the reciprocals of sighting distances i

The standard error of the mean density is estimated by the square root of this variance.

The one critical assumption of the Hayne estimator is that the sines of the angles θ of the observed sightings are a sample from a uniform random variable ranging from 0 to 1. This assumption implies[*] that the average sighting angle is 32.7°. This can be tested by the statistic:

$$z = \frac{\sqrt{n}\left(\bar{\theta} - 32.7\right)}{21.56} \tag{5.4}$$

where z = standard normal deviate

n = observed number of sightings

$\bar{\theta}$ = observed mean sighting angle (Fig. 5.2)

The decision rule is to reject the null hypothesis that the average angle is 32.7° if z is greater than 1.96 or less than -1.96 for $\alpha = .05$. If this null hypothesis is rejected, the Hayne estimator of density should not be used.

If the Hayne model is not applicable, because the angle of sightings does not average 32.7°, you may be able to use a modification of the Hayne model. Burnham and Anderson (1976) found that the average sighting angle θ was usually in the range 32° to 45°, and that in these cases a reasonable estimator is:

$$\hat{D}_{MH} = c\,\hat{D}_H \tag{5.5}$$

where $\hat{D}_{MH}$ = modified Hayne estimator

$\hat{D}_H$ = Hayne estimator (formula above, page 000)

c = correction factor = $1.9661 - 0.02954\,\bar{\theta}$

$\bar{\theta}$ = mean sighting angle for all n observations

The variance of this estimator is:

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[*] If the sine of θ ranges uniformly from 0 to 1, the mean value of θ is (D/2)-1 radians, or 32.7°. See Hayne (1949, p. 157).

$$\operatorname{Var}(\hat{D}_{MH}) \;=\; \hat{D}_{MH}^{2}\left\{\frac{\operatorname{var}(n)}{n^{2}}+\frac{0.000876}{c^{2}}\left[\frac{\sum\left(\theta_{i}-\bar{\theta}\right)^{2}}{n(n-1)}\right]+\frac{\sum(1-r_{i})-R^{2}}{R^{2}(n)(n-1)}\right\} \tag{5.6}$$

Box 5.1 illustrates these calculations.

Box 5.1 Line Transect Method of Density Estimation using the Hayne Estimator

The following data are part of the data from a line transect to estimate the abundance of white-eared kob in the Sudan. They are used only to illustrate the method, since in practice a larger sample size would be obtained.

Animal no.	Perpendicular distance, y_i (m)	Sighting distance, r_i (m)	Measured angle (θ)
1	92.35	150	38
2	163.80	200	55
3	22.27	160	8
4	58.47	200	17
5	157.30	250	39
6	86.99	130	42
7	26.05	150	10
8	50.80	130	23
9	163.80	200	55
10	71.93	100	46
11	72.11	140	31
12	84.52	200	25

Transect length was 10 km. For calculating convenience, express all the distances in kilometers (not in meters).

1. To calculate population density from equation (5.2) we have:

$$\hat{D}_{H} = \frac{n}{2L}\left(\frac{1}{n}\sum 1/r_{i}\right)$$

$$= \frac{12}{2(10)}\left[\frac{1}{12}\left(\frac{1}{0.150}+\frac{1}{0.200}+\frac{1}{0.160}+\frac{1}{0.200}+\cdots+\frac{1}{0.200}\right)\right]$$

$$= \frac{12}{20}(6.342) \quad = \quad 3.8055 \text{ animals/km}^{2}$$

The variance of this density estimate is (equation 5.3):

$$\operatorname{Var}\left(\hat{D}_H\right) = D_H^2 \left[\frac{\operatorname{var}(n)}{n^2} + \frac{\sum\left(1/r_i - R \right)^2}{R^2 \, n(n-1)} \right]$$

$$= (3.8055)^2 \left[\frac{12}{12^2} + \left(\frac{(1/0.150 - 6.34)^2 + (1/0.200 - 6.34)^2 + \cdots}{6.34^2 \, (12)(11)} \right) \right]$$

$$= \quad 1.2902$$

$$\text{S.E.}\left(\hat{D}_H\right) \quad = \quad \sqrt{1.2902} \quad = \quad 1.13589$$

2. Calculate the 95% confidence interval in the usual manner: with 11 d.f. the *t*-value is 2.20 and

$$\hat{D}_H \pm t_{.025} \left[\text{S.E.}\left(\hat{D}_H\right) \right]$$

3.8055 ± 2.20 (1.13589)
3.8055 ± 2.4990 kob / km^2

The wide confidence interval is due to the small sample size and thus the recommendation that n should be 40 or more.

3. To test the critical assumption of the Hayne method that the average angle of detection is 32.7^{o} for these data (equation 5.4):

$$z \; = \; \frac{\sqrt{n}\,\left(\bar{\theta} - 32.7\right)}{21.56} \; = \; \frac{\sqrt{12}\,(32.42 - 32.7)}{21.56} \; = \; -0.05$$

so the null hypothesis that the sighting angle is 32.7^{o} is tentatively accepted for these data.

Program HAYNE (Appendix 2, page 000) can do these calculations.

5.1.2 FOURIER SERIES ESTIMATOR

This is a robust estimator that is sufficiently general to fit almost any type of line transect data. It is a good general purpose estimator and is strongly recommended by Burnham *et al*. (1980) as the best model available. The estimate of density is the usual one:

$$\hat{D} \; = \; \frac{n}{2La} \tag{5.7}$$

where $\hat{D}$ = Estimated population density

n = Number of animals seen on the transect

L = Length of transect

a = Half the effective strip width (a constant)

The critical parameter *a* is estimated as:

$$\frac{1}{\hat{a}} = \frac{1}{w^*} + \sum_{r=1}^{m} a_k \tag{5.8}$$

where w* = transect width (largest perpendicular distance observed)

$$\hat{a}_k = \frac{2}{nw^*}\left[\sum_{i=1}^{n} \cos\left(\frac{K\pi x_i}{w^*}\right)\right] \tag{5.9}$$

where n = Number of animals seen

π = 3.14159

x_i = Perpendicular distance of animal i (Fig. 3.14)

k = Number of term in equation (1, 2, 3, 4...)

m = Maximum number of cosine terms in the summation (< 6)

Burnham *et al*. (1980) give a stopping rule for *m* as follows: choose *m* to be the smallest integer at which this inequality holds true:

$$\frac{1}{w^*}\left(\frac{2}{n+1}\right)^{1/2} \geq \left|a_{m+1}\right| \tag{5.10}$$

where w* = Transect width (largest perpendicular distance observed)

n = Number of animals counted

$\left|a_{m+1}\right|$ = Absolute value of a_{m+1} (defined above)

The variance of the Fourier series estimator is complex and should probably be done with the computer using Program TRANSECT described by Burnham *et al*. (1980). The procedure in capsule form is as follows:

(1) Estimate the variances of the a_k:

$$\text{var}\left(\hat{a}_k\right) = \frac{1}{n-1}\left[\frac{1}{w^*}\left(a_{2k} + \frac{2}{w^*}\right) - a_k^2\right] \qquad \text{for } k \geq 1 \tag{5.11}$$

(2) Estimate all the covariances of the a_k:

$$\text{cov}\left(\hat{a}_k, \hat{a}_j\right) = \frac{1}{n-1}\left[\frac{1}{w^*}\left(a_{k+j} + a_{k-j}\right) - a_k\, a_j\right] \qquad \text{for } k \geq j \geq 1 \tag{5.12}$$

(3) Having determined *m* above and given that cov(a_k,a_k) is the same as var(a_k), we obtain

$$\text{var}\left(\frac{1}{\hat{a}}\right) = \sum_{j=1}^{m}\sum_{k=1}^{m}\text{cov}\left(\hat{a}_j, \hat{a}_k\right) \tag{5.13}$$

(4) Estimate the variance of $\hat{D}$, the estimated population density, by:

$$\operatorname{var}\left(\hat{D}\right) = \hat{D}^2\left[\frac{\operatorname{var}(n)}{n^2} + \frac{\operatorname{var}\left(1/\hat{a}\right)}{\left(1/\hat{a}\right)^2}\right]$$

$$\text{S.E.}\left(\hat{D}\right) = \sqrt{\operatorname{var}\left(\hat{D}\right)} \tag{5.14}$$

$$\text{95\% confidence interval} = \hat{D} \pm (1.96)\left[\text{S.E.}\left(\hat{D}\right)\right]$$

One problem in these estimates for the variance of line-transect estimators is determining the variance of *n*, the number of animals counted. It is usually assumed that *n* is a Poisson variable, so the variance = the mean = *n*, but this assumption could be in error (Burnham *et al*. 1980). A better way to use the line transect statistically is to count a series of replicate lines, ensuring that each line is long enough to have an adequate sample size (*n* > 20 or 25). Then the variance of the density estimate *D* can be obtained directly. We define, for *R* replicate lines:

$$\hat{D}_i = \frac{n_i}{2 l_i \hat{a}_i} \tag{5.15}$$

where $\hat{D}_i$ = Density estimate for line *i*

n_i = Number of animals counted on line *i*

l_i = Length of transect line *i*

$\hat{a}_i$ = Estimated parameter for line *i*

i = 1, 2, 3... *R* lines (replicate number)

For each line we estimate *a* using one of the techniques just described.

The overall density estimate is the weighted average:

$$\hat{D} = \frac{\sum_{i=1}^{R} l_i D_i}{\sum_{i=1}^{R} l_i} \tag{5.16}$$

The empirical estimate of the variance of $\hat{D}$ is:

$$\operatorname{var}\left(\hat{D}\right) = \frac{\sum_{i=1}^{R}\left[l_i\left(\hat{D}_i - \hat{D}\right)^2\right]}{L(R-1)} \tag{5.17}$$

where $L = \sum l_i$

$\hat{D}$ = overall density estimate from equation (5.16)

R = number of replicate line transects

The standard error of the overall density estimate is:

$$\text{S.E.}\left(\hat{D}\right) = \sqrt{\text{var}\left(\hat{D}\right)} \tag{5.18}$$

and the 95% confidence interval is:

$$\hat{D} \pm t_{.025}\left[\text{S.E.}\left(\hat{D}\right)\right] \tag{5.19}$$

where $t_{.025}$ has (R - 1) degrees of freedom.

5.1.3 SHAPE-RESTRICTED ESTIMATOR

An efficient estimator of population density can be constructed for line transect data by placing two restrictions on the shape of the detection curve (Johnson and Routledge 1985). The first restriction is that the detection function must be a continuously decreasing function, as shown in Figure 5.3. The second restriction is more powerful and requires that the curve must have a concave shoulder followed by a convex tail with an inflection point between these two regions. Given these restrictions, Johnson and Routledge (1985) utilize a flexible least-squares procedure to specify the detection function. The procedure is too complex to summarize here, and is coded in a computer program TRANSAN described by Routledge and Fyfe (1992). This procedure permits one to specify the length of the horizontal shoulder (i.e the zone in which detectability is near 1), the inflection point, or the height of the right tail of the detection function. By altering assumptions about the shoulder width, the biologist can explore the impact on the resulting density estimates. For example, a biologist may from his or her experience be able to state that the horizontal shoulder extends 10 meters on either side of the transect line. Figure 5.4 illustrates data obtained on a line transect study of starfish (*Pisaster brevispinus*). The data suggest a rise in sightability over the first three meters from the transect line, but this is apparently only chance variation, and the first shape-restriction on these data would be that the shoulder width be at least 3 meters. A second restriction is the upper limit to the sighting distance. If starfish are not visible beyond 8 meters from the transect line, the upper limit can be constrained to be 8 m. Clearly the more you know about the natural history of the study animal, the more closely you can constrain the detection function. The detection function for these data is thus more like line A in Figure 5.3 than line B or C. Johnson and Routledge (1985) showed in simulations that the shape-restricted estimator of detection functions was more robust than any of the more commonly used methods like the Fourier-series estimator or the half-normal function.

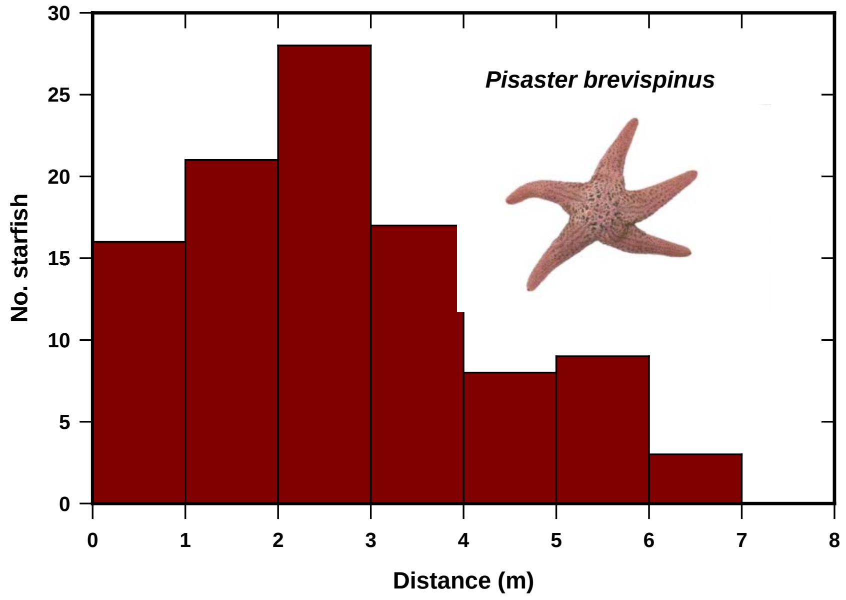

Figure 5.4 Observed perpendicular distances for a set of line transects of starfish (*Pisaster brevispinus*) near Vancouver, B.C. The shape of the smoothed detection function for these data will have a broad shoulder out to about 3 m, and will fall off to zero around 8-10 m. (Data from Routledge and Fyfe 1992).

Anderson *et al*. (1979) provide a useful set of guidelines for anyone using the line transect technique for population estimation. They recommend nine cautions in data collection:

1. The centerline of the transect must be straight and well marked.

2. Care must be taken that all animals on the centerline are seen with certainty.

3. Transect width should be effectively unbounded, and all animals seen should be recorded.

4. All measurements of distances and angles should be accurately done with a tape measure and compass.

5. All 3 measurements should be taken in the field: perpendicular distance, sighting angle, sighting distance (Fig. 5.2).

6. Measurements should be recorded separately for convenient lengths of transect; they can be combined later as needed.

7. Sample size (*n*) should be at least 40, and 60-80 would be better if this is possible.

8. Transects along roads or ridgetops should be avoided; a randomization procedure is essential for proper statistical inference.

9. Only competent, interested personnel should be used.

There is an extensive discussion of the practical and statistical problems of line transect sampling in Buckland *et al.* (2001), Burnham and Anderson (1984), Routledge and Fyfe (1992), Southwell (1994), Southwell et al. (2008) and Thomas et al. (2010). Southwell (1994) found that line transect population estimates for kangaroo populations of known size tended to underestimate the true density and this could be explained by a violation of assumption 2– animals on the centerline were often disturbed and moved slightly before they were sighted by the observers. Porteus et al. (2011) found the same problem with line transect trials with known populations of domestic sheep in England.

An important approach in line transect studies is to combine line transect estimation with mark-recapture studies so that detectability can be estimated directly and suitable corrections applied to the estimates. Borchers et al. (1998), Laake et al. (2008), and Thomas et al. (2010) discuss this approach. Southwell et al. (2008) illustrate the utility of this method for aerial census of penguin populations in Antarctica. Schmidt et al. (2012) gives another example of the use of line transect sampling in aerial census of Dall sheep in Alaska.

With species that can occur in groups rather than as single animals, the detection function may vary with group size, since groups are easier to see. Southwell et al. (2008) found this effect with penguins in Antarctica (Figure 5.5). Group size is only one of several factors that can affect detection probability and all of the factors that affect aerial survey accuracy (see Chapter 4 page 178) also apply to line transects whether done on the ground or in the air. .

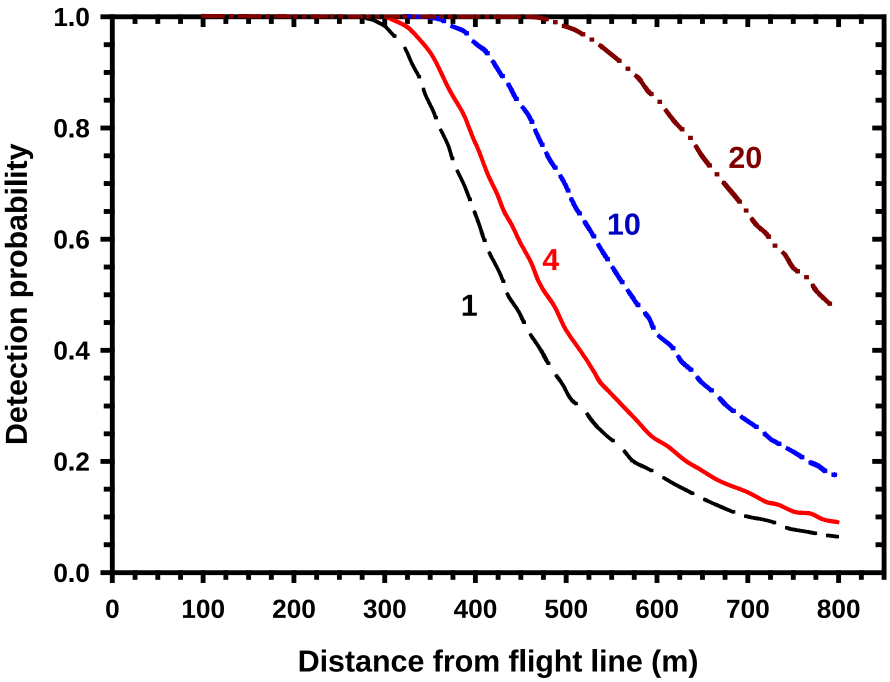

Figure 5.5 Observed detection functions for different group sizes of Adelie and emperor penguins from aerial surveys in Antarctica. Transect width ranged up to 800 m from the flight line. Virtually all penguins were sighted within about 300 m of the flight path, but at greater distances the detectability of single animals fell off rapidly. Groups of 20 penguins could be sighted at considerably greater distances from the flight line. (Data from Southwell et al. 2008).

Several computer programs are available to do line transect calculations. Program HAYNE (Appendix 2, page 000) computes the Hayne estimator and the modified Hayne estimator for line transect sampling. Program DISTANCE (http://www.ruwpa.st-and.ac.uk/distance/) of Buckland *et al*. (2001) is much larger and more comprehensive and will compute the Fourier-series estimator as well as a variety of other parametric functions like the half-normal. Program DISTANCE is the gold standard for line transect calculations. Program TRANSAN of Routledge and Fyfe (1992) computes the shape-restricted estimator for line transect data and is available in the programs set for Ecological Methodology (http://www.exetersoftware.com/cat/ecometh/ecomethodology.html).

5.2 DISTANCE METHODS

Plant ecologists have developed a variety of plotless sampling methods that work well on trees and shrubs. These are all called *distance methods* because they utilize distances measured by means of two general approaches:

- **1.** Select random organisms and measure the distance to its nearest neighbors
- **2.** Select random points and measure the distance from the point to the nearest organisms.

Plotless sampling is usually applied to a single species of plant or animal, and is popular in ecology because it is a two-edged sword. We can use plotless sampling to estimate the *density* of the population. On the other hand, if we know the density of a population, we can use plotless sampling to determine whether the *spatial pattern* is random, aggregated, or uniform. We are concerned here with the first approach, estimating density, and we will discuss the investigation of spatial pattern in the next chapter.

The general procedure in plotless sampling is illustrated in Figure 5.6. The *census zone* is the area of interest, but in practice a boundary strip must be added so that measurements made on individuals at the edge of the census zone are not biased. The data of interest are the measurements from a series of random points to the nearest organism, or from organisms to their nearest neighbor. In principle, one could extend this approach to measure, in addition, the distance to the second nearest neighbor, the distance to the third nearest neighbor, and so on. But, to begin, let us consider the simple case shown in Figure 5.6.

If the entire population can be mapped as is shown in Figure 5.6, we would know population density exactly and our estimation problem would be simple. But in most cases we must sample individuals scattered over a large area. For example, we may need to estimate the density of a tree species in a large region of 10 km^2 of forest. Statisticians call this 'sparse sampling' and state that the primary requirement of sparse sampling schemes is that the sample points should be well separated so that observations can be assumed to be independent. Usually this requires that we do not sample more than 5-10% of the total

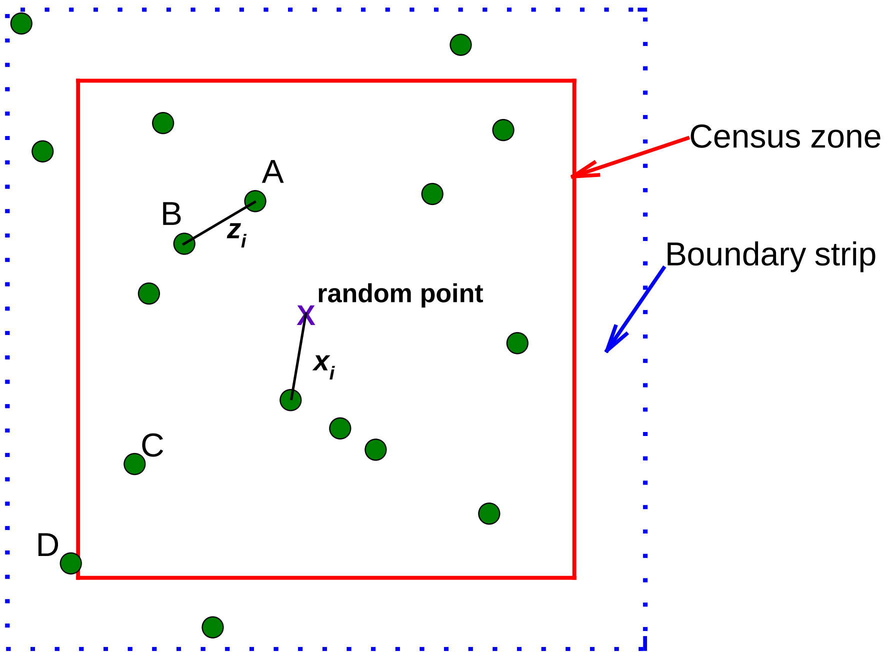

Figure 5.6 Schematic illustration of distance measures. The census zone is surrounded by a boundary strip, and in some cases the nearest organism is located in the boundary strip. Two types of measurements can be taken: (1) A random point *X* is located in the census zone and the distance x_i to the nearest organism is measured. (2) A random organism *A* is selected and the distance z_i to the nearest neighbor *B* is measured. The nearest neighbor might be in the boundary strip outside the census zone (e.g., C to D).

population, so that we assume sampling without replacement. Using the same general approach shown in Figure 5.6, we can make two kinds of measurements:

1. from random *points* to the nearest organism
2. from a random *organism* to its nearest neighbor.

There is in principle no problem with setting out random points in a large area, although it may be very time consuming and less easy to achieve in the field than statisticians tend to assume (Pollard 1971). But there is definitely a problem of selecting a random individual. In principle it is easy: mark each individual with a number and select *n* of these at random. But of course this is impossible in the field because we would have to enumerate the entire population! The next idea was to select a random *point* and use the individual closest to that random point as the equivalent of a random organism. But Pielou (1977 p. 154) showed that this procedure is biased in favor of isolated individuals and *thus should not be used to select a random individual.*

There appears to be no easy way out of this dilemma and the best compromises all involve some type of systematic sampling (see Chapter 8, page 000 for more discussion of systematic sampling). A variety of plotless sampling methods have been proposed, and while most of them perform adequately for organisms that are randomly spread in the landscape, there is considerable variation in how accurately they perform for clumped patterns (Engeman *et al.* 1994). There is a need for interaction between theory and field practice in developing the best methods for particular organisms. I will consider four distance techniques that appear to be relatively robust to deviations from random patterns. By applying them for equal time periods in the field one could determine which provides a more precise estimate of population density, but little work of this type has yet been done, and at present we must rely on computer simulation methods to evaluate the techniques (Engeman *et al*. 1994).

5.2.1 T-SQUARE SAMPLING PROCEDURE

A distance sampling scheme called T-square sampling was first described by Besag and Gleaves (1973). It is simple to implement in the field, and this simplicity if often preferred by field workers.

Figure 5.7 illustrates the principles of T-square sampling. Random points are located in the study region and at each random point two distances are measured:

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). If the closest neighbor is not within this angle, use the next closest organism until you find one that satisfies this angle.

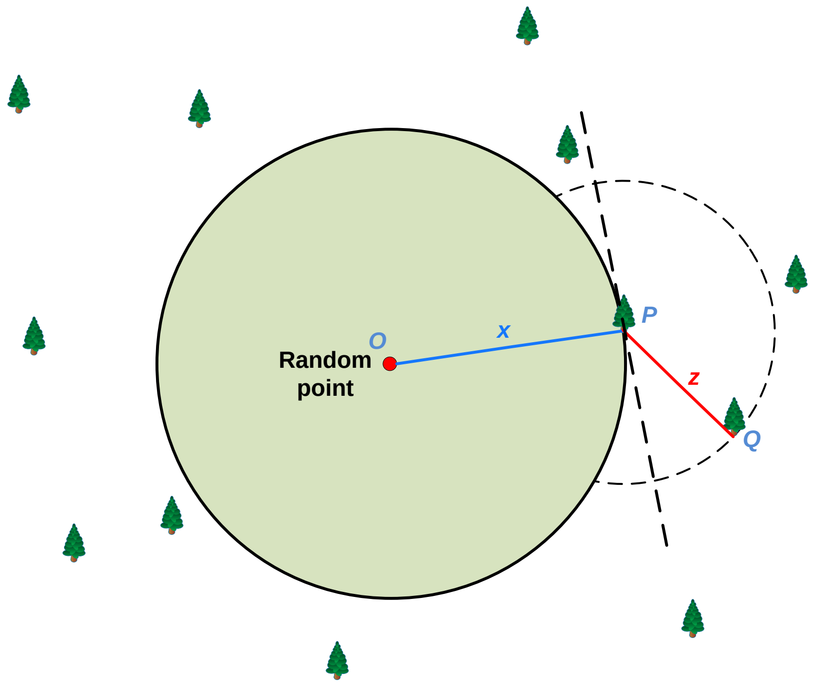

Figure 5.7 Schematic view of T-square sampling. A random point *O* is located within the study area, and the distance x is measured from this point to the nearest organism *P*. A second distance *z* is measured from organism *P* to its nearest neighbor constrained to be in the hemisphere to the right of the dashed line. The angle *OPQ* must be more than 90°. The study area is sampled with a series of *n* random points like this. Trees symbolize individual organisms.

The point-to-organism distances obtained in T-square sampling can be used to estimate population density as follows:

$$\hat{N}_1 = \frac{n}{\pi \sum (x_i^2)} \tag{5.20}$$

where $\hat{N}_1$ = Estimate of population density from point-to-organism data

n = Sample size

x_i = Distance from random point i to nearest organism

The T-square distances however are constrained by the 90° rule, and consequently the density estimator that utilizes T-square distances (z_i) has a different formula:

$$\hat{N}_2 = \frac{2n}{\pi \sum (z_i^2)} \tag{5.21}$$

where $\hat{N}_2$ = T-square estimate of population density (analogous to $\hat{N}_2$)
n = Number of samples
z_i = T-square distance associated with random point i

This estimator should not be used unless it is known that the organisms being sampled have a random pattern.

Byth (1982) showed that the most robust estimator of population density for use with T-square sampling was the following compound measure of $\hat{N}_1$ and $\hat{N}_2$:

$$\hat{N}_T = \frac{n^2}{2\sum(x_i)\left[\sqrt{2}\sum(z_i)\right]} \tag{5.22}$$

The standard error of $\hat{N}_T$ is calculated on the reciprocal of the density and is given by (Diggle 1983):

$$\text{Standard error}\left(\frac{1}{\hat{N}_T}\right) = \sqrt{\frac{8(\bar{z}^2 s_x^2 + 2\bar{x}\bar{z}s_{xz} + \bar{x}^2 s_z^2)}{n}} \tag{5.23}$$

where $\bar{x}$ = Mean value of point-to-organism distances

$\bar{z}$ = Mean value of T-square organism-to-neighbor distances

n = Sample size

s_x^2 .= Variance of point-to-organism distances

s_z^2 = variance of T-square organism-to-neighbor distances

s_{xz} = covariance of x and z distances

Box 5.2 gives an example of the use of these estimators. Program TREES (Appendix 2, page 000) does these calculations.

Box 5.2 Estimating Population Density from T-square Sampling

Using the T-square sampling procedure illustrated in Figure 5.7, an ecology class measured the following distances on white spruce trees in the southwestern Yukon (n = 16):

Sample point no.	Point-to-tree distance, x_i (m)	T-square distance from tree to neighbor, z_i (m)
1	12.6	8.7
2	9.3	16.4
3	7.5	9.3
4	16.2	12.6
5	8.8	3.5
6	10.1	11.2
7	6.2	13.6

8	1.5	9.1
9	14.3	2.7
10	9.6	8.6
11	11.3	7.9
12	8.9	12.1
13	6.3	15.6
14	13.9	9.9
15	10.8	13.7
16	7.6	8.4
Sum	154.9	163.3
Sum of items squared	1694.93	1885.05
Mean	9.681	10.206

From the usual statistical formulas we calculate:

$$\text{Variance of } (x) = \frac{\sum x^2 - (\sum x)^2 / n}{n - 1} = \frac{1694.93 - (154.9)^2 / 16}{15} = 13.020$$

$$\text{Variance of } (z) = \frac{\sum z^2 - (\sum z)^2 / n}{n - 1} = \frac{1885.05 - (163.3)^2 / 16}{15} = 14.558$$

$$\text{Covariance of } x \text{ and } z = \frac{\sum xz - (\sum x)(\sum z) / n}{n - 1} = \frac{1543.72 - (154.9)(163.3)/16}{15} = -2.4819$$

The density of trees is estimated from equation (5.22) as:

$$\hat{N}_T = \frac{n^2}{2 \sum (x_i) \left[\sqrt{2} \sum (z_i) \right]}$$

$$= \frac{16^2}{2(154.9)\left[\sqrt{2}(163.3)\right]} = 0.003578 \text{ trees per m}^2$$

Calculate the standard error of the reciprocal of this density estimate from equation (5.23):

$$\text{Standard error } (1/\hat{N}_T) = \sqrt{\frac{8(\bar{z}^2 s_x^2 + 2\bar{x}\bar{z} s_{xz} + \bar{x}^2 s_z^2)}{n}}$$

$$= \sqrt{\frac{8\left[(10.206)^2(13.02) + 2(9.681)(10.206)(-2.4819) + (9.681)^2(14.558)\right.}{16}}$$

$$= 33.3927$$

The 95% confidence interval for the reciprocal of this density estimate is thus

$$1/\hat{N}_T \pm t_\alpha\{\text{S.E.}(1/\hat{N}_T)\} \qquad (t_\alpha = 2.113 \text{ for 15 d.f.})$$

$$279.49 \pm (2.131)(33.3927) \quad \text{or} \quad 208.33 \text{ to } 350.65$$

Taking reciprocals, we obtain confidence limits of 2.9 X 10^{-3} to 4.8 X 10^{-3} trees/m^2, or 29 to 48 trees per hectare for this small sample.

Program TREES (Appendix 2, page 000) does these calculations.

5.2.2 ORDERED DISTANCE METHOD

The ordered distance method was first suggested by Morisita (1957) and further developed by Pollard (1971). The method involves measuring the distance from a random sampling point to the n^{th} closest individual. Pollard (1971) was the first to recognize that the variance of the density estimate falls as *n* increases, so that measurements to the second nearest individual have more precise density estimates that those to the nearest individual. In practice it is difficult in the field to locate individuals beyond the third-nearest, and this is the method we will discuss here. Simulation studies suggest that the third nearest individual gives satisfactory results for clumped patterns, although the method may also be used for the nearest or second nearest organism.

The general formula for estimating population density for the ordered distance method for the third nearest individual is as follows:

$$\hat{D} = \frac{3n - 1}{\pi \sum \left(R_i^2\right)} \tag{5.24}$$

where $\hat{D}$ = population density estimated by the ordered-distance method

n = number of random points sampled

π = 3.14159

R_i = distance from random point to third nearest organism

The variance of this density estimate is given by:

$$\text{Variance}\left(\hat{D}\right) = \frac{\left(\hat{D}\right)^2}{3n - 2} \tag{5.25}$$

and the standard error of the density estimate is the square root of this variance.

Confidence intervals for *D* can be obtained in the following way when 4*n* > 30. The 95% confidence limits are given by Seber (1982 p. 42) as:

$$\text{Lower confidence limit for } \sqrt{\hat{D}} \text{ is } \frac{\sqrt{12n-1} - 1.96}{\sqrt{4\pi\sum(R_i^2)}} \tag{5.26}$$

$$\text{Upper confidence limit for } \sqrt{\hat{D}} \text{ is } \frac{\sqrt{12n-1} + 1.96}{\sqrt{4\pi\sum(R_i^2)}} \tag{5.27}$$

and these limits are then squared to convert them to population densities.

To apply this sampling method, one proceeds as follows:

1. Locate a random point in the study zone.

2. Determine the nearest individual, the second nearest individual, and the third nearest individual to the random point. You will need to use exact measurements to determine these if spacing of individuals is close.

3. Measure the distance from the random point to the **third individual** (R_i).

4. Repeat the entire procedure for the next random point. Try to obtain n = 30 to 50.

Note that you do *not* need to measure the distances to the nearest and second nearest individuals. Only one distance is measured per random point. If you are measuring trees, measure to the center of the tree. If you measure in meters, your density estimate will be in numbers per square meter.

The procedure is illustrated schematically in Figure 5.8 and Box 5.3 gives some sample calculations for the ordered distance method of density estimation.:

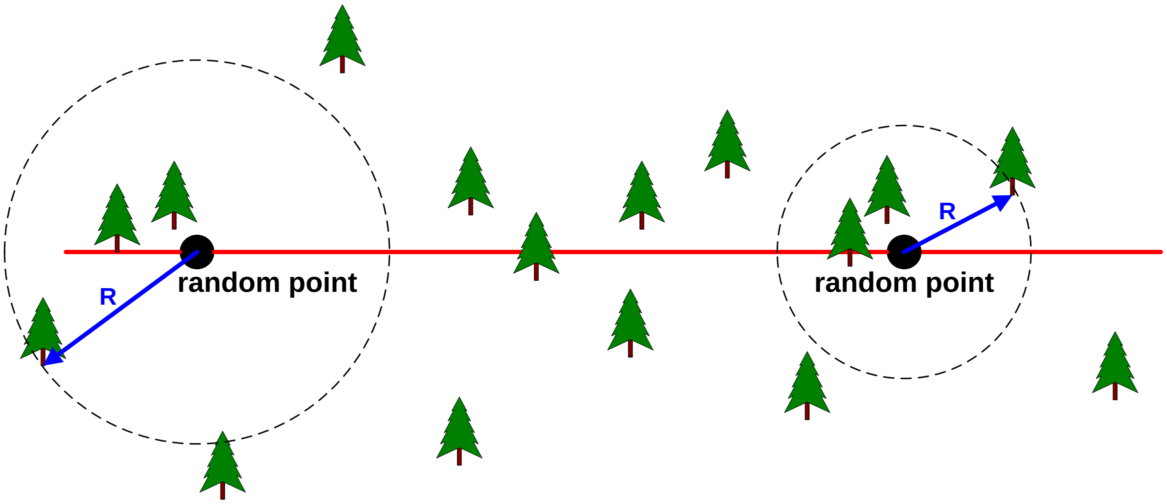

Figure 5.8 Schematic illustration of the ordered distance method procedure of Morisita (1957) utilizing the third-nearest organism. Only one distance (blue arrow) is recorded for each random point, the distance

to the third-nearest organism (R_i). Note that one does not need to measure the distances to the first and second nearest organisms (unless you need to do so to decide which is the third nearest organism

Box 5.3 Estimating Population Density from Ordered Distance Sampling

A forest ecologist used the ordered distance sampling procedure illustrated in Figure 5.8 to determine the regeneration success of loblolly pine trees in Georgia. She measured the following distances from 24 random points to the third nearest pine tree:

Sample point no.	Point-to-third nearest tree distance, x_i (m)
1	18.5
2	4.1
3	7.2
4	6.2
5	8.3
6	10.1
7	16.2
8	3.5
9	13.2
10	6.6
11	10.9
12	5.9
13	6.8
14	3.9
15	2.8
16	7.2
17	8.1
18	5.2
19	9.0
20	4.4
21	3.2
22	7.5
23	9.9
24	7.6
Sum	186.3
Sum of items squared	1802.75
Mean	7.7625

Estimate the density of trees from equation (5.30):

$$\hat{D} = \frac{3n - 1}{\pi \sum \left(R_i^2\right)} = \frac{(3)(24)-1}{3.14159(1802.75)} = 0.012536 \text{ trees per sq. m}$$

or expressed per hectare , 125 trees per ha.

The variance of this density estimate is from equation (5.31):

$$\text{Variance}\left(\hat{D}\right) = \frac{\left(\hat{D}\right)^2}{3n-2} = \frac{0.012536^2}{3(24)-2} = 2.2451\times10^{-7}$$

which gives the standard error of the density as:

$$\text{Standard error of } (\hat{D}) = \sqrt{\text{Variance of } (\hat{D})}$$

$$= \sqrt{2.24516\times10^{-7}} = 0.001498$$

The 90% confidence interval for this density estimate is obtained from equations (5.26) and (5.27), with a change of the *z*-value to $z_{.10} = 1.645$ from $z_{.05} = 1.96$:

$$\text{Lower confidence limit for } \sqrt{\hat{D}} = \frac{\sqrt{12n - 1} - 1.645}{\sqrt{4\pi\sum(R_i^2)}}$$

$$= \frac{\sqrt{12(24) - 1} - 1.645}{\sqrt{4(3.14159)(1802.75)}} = 0.10162$$

so the lower 90% confidence limit is 0.10161^2 or 0.01033 trees per sq. m, or 103 trees per hectare.

$$\text{Upper confidence limit for } \sqrt{\hat{D}} = \frac{\sqrt{12n - 1} + 1.645}{\sqrt{4\pi\sum(R_i^2)}}$$

$$= \frac{\sqrt{12(24) - 1} + 1.645}{\sqrt{4(3.14159)(1802.75)}} = 0.12348$$

so the upper 90% confidence limit is 0.12348^2 or 0.015249 trees per sq. m, or 152 trees per hectare.

In practice one would like a larger sample size to reduce the width of the confidence band.

Program TREES (Appendix 2, page 000) can do these calculations.

5.2.3 VARIABLE AREA TRANSECT METHOD

This method is a combination of distance and quadrat methods and was first suggested by Parker (1979). A fixed width strip is searched from a random point until the n^{th} individual is located in the strip. A field worker needs to search in only one direction from the random point, and once the n^{th} individual is found, the length of transect is measured from the random point to point at which the n^{th} individual occurred. This method can be used for any number of individuals, and we shall use n = 3 as a convenient number for field workers.

The formula for population density estimated by the variable area transect methods was derived by Parker (1979) as follows:

$$\hat{D}_v = \frac{3n - 1}{w\sum(l_i)} \tag{5.28}$$

where $\hat{D}_v$ = Estimate of population density for the variable area transect method
n = Number of random points
w = Width of transect searched (fixed)
l_i = Length of transect i searched until the third organism was found

The variance of this estimate of population density is given by Parker (1979) as:

$$\text{Variance}\left(\hat{D}_v\right) = \frac{\left(\hat{D}_v\right)^2}{3n - 2} \tag{5.29}$$

Note that this is the same variance formula used in the ordered distance estimator. Confidence limits for population density are given by Parker (1979, now corrected) as:

$$\begin{aligned} \text{Lower 95\% confidence limit} &= \frac{C_1}{2wn\bar{l}} \\ \text{Upper 95\% confidence limit} &= \frac{C_2}{2\,wn\bar{l}} \end{aligned} \tag{5.30}$$

where C_1 = Value from chi-square distribution at α = 0.025 for $6n$ degrees of freedom
C_2 = Value from chi-square distribution at α = 0.975 for $6n$ d.f.
w = Transect width
n = Sample size
$\bar{l}$ = Mean length of transect searched until third organism is located
$\hat{D}$ = Estimate of population density from equation (5.28)

The variable area transect method is illustrated in Figure 5.9.

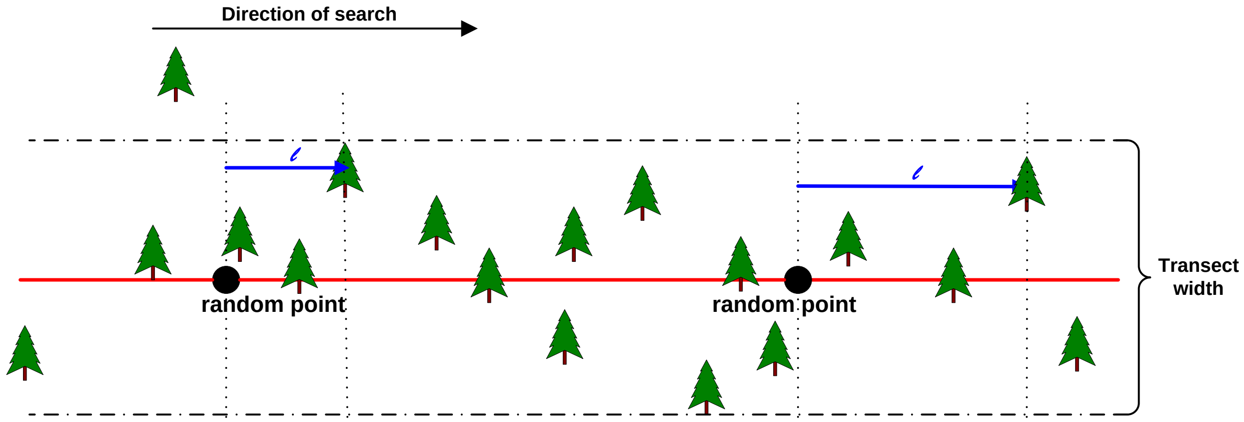

Figure 5.9 Schematic illustration of the variable area transect method of population estimation. This is a combination of quadrat and distance methods. One moves along a transect line from a random point, counting the organisms within a specified distance (dashed lines) from the line of travel, and marks the distance at which the third individual is located. These distances (l_i) are the data used in equation (5.28).

To apply the variable area transect method one proceeds as follows:

1. Locate a random point on a transect line in your study area.

2. Move along the transect from the random point until you have found three individuals of the species being studied. Project a perpendicular to the line of travel (marked by a tape measure usually).

3. Measure the distance *l* along the tape from the random point to the perpendicular line that projects to the third individual.

4. Repeat the procedure until you have a sample of at least 30-50 distances.

Density estimates from these plotless sampling methods can be obtained from Program TREES (Appendix 2, page 000), which includes the confidence limits for the density estimates.

5.2.5 POINT QUARTER METHOD

The classic distance method is the point quarter method which was developed by the first land surveyors in the U.S.A. in the nineteenth century. The four trees nearest to the corner of each section of land (1 sq. mile) were recorded in the first land surveys and they form a valuable data base on the composition of the forests in the eastern U.S. before much land had been converted to agriculture. The point quarter technique has been a commonly used distance method in forestry. It was first used in plant ecology by Cottam *et al.* (1953) and Cottam and Curtis (1956). Figure 5.10 illustrates the technique. A series of random points is selected often along a transect line with the constraint that points should not be so close that the same individual is measured at two successive points. The area around each random point is divided into four 90° quadrants and the distance to the nearest tree is measured in each of the four quadrants. Thus 4 point-to-organism distances are generated at each random point, and this method is similar to measuring the distances from a random point to the 1st, 2nd, 3rd and 4th nearest neighbors.

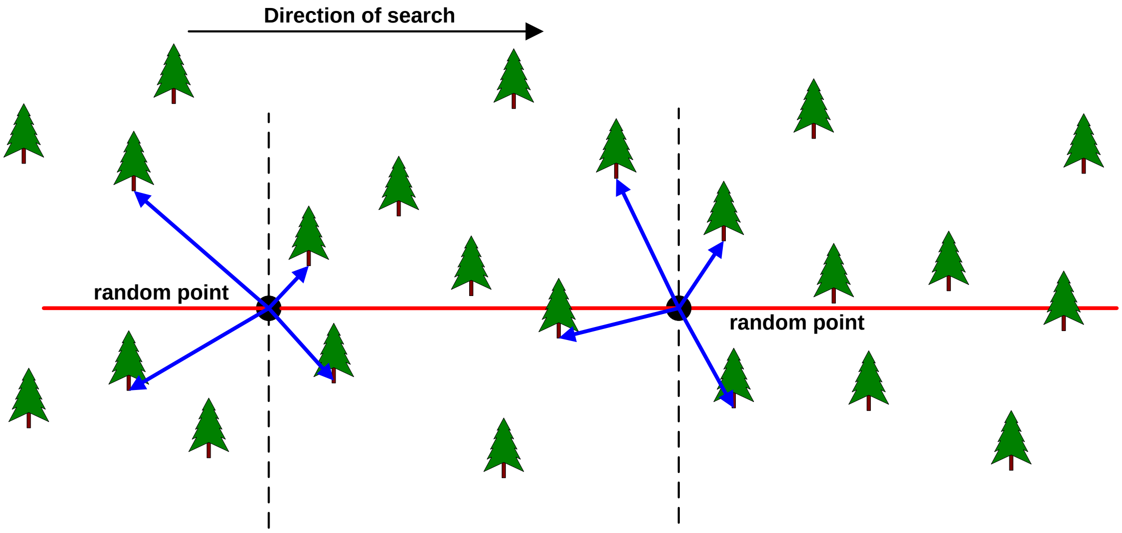

Figure 5.10 Point-quarter method of density estimation. The area around each random point is subdivided into four 90° quadrants and the nearest organism to the random point is located in each quadrant. Thus four point-to-organism distances (blue arrows) are obtained at each random point. This method is commonly used on forest trees. Trees illustrate individual organisms.

The appropriate unbiased estimate of population density for the point-quarter method is from Pollard (1971):

$$\hat{N}_p = \frac{4\,(4n-1)}{\pi \sum (r_{ij}^2)} \tag{5.31}$$

where $\hat{N}_p$ = Point-quarter estimate of population density
n = Number of random points
π = 3.14159
r_{ij} = Distance from random point i to the nearest organism in quadrant j (j = 1,2,3,4; i = 1, ...n)

The variance of this density estimate is given by Pollard (1971) as:

$$\text{Variance}\,(\hat{N}_p) = \frac{\hat{N}_p^2}{4n-2} \tag{5.32}$$

and the standard error is:

$$\text{Standard error of } \hat{N}_P = \sqrt{\frac{\text{Variance of } N_P}{4n}} \tag{5.33}$$

Confidence intervals for N_p can be obtained in the following way when $4n > 30$. The 95% confidence limits are given by Seber (1982 p. 42) as:

$$\text{Lower confidence limit for } \sqrt{\hat{N}_P} \text{ is } \frac{\sqrt{16n - 1} - 1.96}{\sqrt{\pi \sum (r_{ij}^2)}} \tag{5.34}$$

$$\text{Upper confidence limit for } \sqrt{\hat{N}_P} \text{ is } \frac{\sqrt{16n - 1} + 1.96}{\sqrt{\pi \sum (r_{ij}^2)}} \tag{5.35}$$

and these limits are then squared to convert them to population densities.

Program TREES in Appendix 2 (page 000) can do these calculations for point-quarter data.

The point-quarter method is very efficient when it is easy to divide the area around the random points into 4 quadrants accurately, and when random points take a long time to locate in the field. There have been two general criticisms of the point quarter method. First, since 4 trees are measured at each point, the number of points sampled is often too low to be representative of a large population spread over a large area. Second, the density estimates obtained from the point-quarter method are susceptible to bias if the spatial pattern is not random (Pollard 1971). But recent simulation studies by Engeman *et al*. (1994) suggest that In general the bias of the point quarter estimator for clumped patterns is as low as that of the ordered distance estimator and the variable area transect estimator that they recommend. Table 5.1 summarizes the size of the bias of these estimators in the simulations run by Engeman *et al*. (1994). It may be better to use the more statistically robust ordered-distance sampling procedure (Fig. 5.8) or variable-area-transect sampling (Fig. 5.9) in preference to point-quarter sampling, but more field data are needed to test these potential biases when organisms are clumped and not spread in a random pattern. If point-quarter sampling is used, it is important to measure the 90^o quadrant boundaries accurately. The difficulty of doing this in the field has been one of the arguments used against the application of this method in routine field surveys (Engeman *et al*. 1994).

Table 5.1 Relative bias of density estimates for four distance methods. Simulation studies of 5 spatial patterns ranging from uniform to random to 3 types of clumped distributions were run 5000 times for 4 different sample sizes to obtain these estimates. Relative bias is expressed as a proportion of the true density. Negative bias means that the estimates were too low relative to the true values, positive bias means that the estimates were too high. (Data from Engeman *et al*. 1994.)

Estimator	Random pattern	Uniform pattern	Clumped-50 pattern[a]	Clumped-15 pattern[a]	Double clumping[a]
T-square	0.28	0.26	0.21	0.52	0.50
Ordered distance	0.02	0.13	-0.09	-0.25	-0.48
Variable area transect	0.02	0.13	-0.06	-0.21	-0.41
Point-quarter	0.01	0.17	0.06	-0.22	-0.29

[a] The clumped-50 pattern is moderately clumped, the clumped-15 pattern more severely clumped, and the double clumping pattern is extremely clumped.

Other possible distance measures are reviewed in Diggle (1983) and Seber (1982). Batcheler (1971, 1975) has developed techniques for estimating population density from distance measurements that utilize empirically derived correction factors. Batcheler (1975) used this approach to estimate deer density from fecal pellet groups in New Zealand. Byth (1982) suggested that these kinds of empirically-derived estimates are not robust to many types of non-random spatial patterns in natural populations, and thus she recommends avoiding them in favor of more robust estimators like those discussed above.

5.3 SUMMARY

Plotless sampling methods provide another method for estimating the abundance of plants and animals. This chapter discusses two approaches to estimating density that do not involve setting out quadrats or marking individuals. The line transect method utilizes the distances organisms are sighted from transect lines to estimate density. Distance methods use distances from random points to the nearest organism and distances from random organisms to their nearest neighbor to estimate density. For all these plotless estimators, sample sizes of the order of 40-60 are needed to achieve good precision.

Line transects can be done on foot or in vehicles or airplanes and the critical assumption is that all the organisms directly on the transect line are seen. Detection falls with distance away from the transect line, and the rate at which it falls can be used to estimate the effective width of strip counted along the transect. The critical problem is specifying the form of the detection function, and many different mathematical functions can be used. If ecological constraints can be set on the shape of the detection function, more precise estimates of density can be obtained.

Distance measures have been used extensively in plant ecology. Five methods are described that utilize distances from random points to the nearest organism and distances from random individuals to their nearest neighbor to estimate density. While random points are easy to locate, the practical problems associated with sampling random individuals are considerable. When organisms are randomly spread in space, there are few problems. But when the spatial pattern is clumped most distance measures are negatively biased. Three sampling procedures are available that successfully overcome many of these problems. The ordered distance method, the variable area plot method, and the point-quarter sampling procedure are relatively easy to apply in the field and statistically robust. When patchiness occurs, distance methods typically underestimate the true density but for the better methods this bias is relatively small.

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QUESTIONS AND PROBLEMS

5.1. Mallard duck nests were searched for on foot by walking transect lines on the Monte Vista National Wildlife Refuge in Colorado. A total of 272 km (169 miles) was walked. The strip width was limited to 3.66 m (12 ft). In 1986 102 duck nests were found with the following distribution of perpendicular distances to the transect lines:

Perpendicular distance class (ft.)	Number of nests found
0-1	10
1-2	4
2-3	14
3-4	14
4-5	10
5-6	10
6-7	11
7-8	6
8-9	8
9-10	4
10-11	7
11-12	4

Discuss the shape of the detection function for these data and suggest possible improvements in how these surveys might be carried out.

5.2. Discuss the possibility of applying line transect methods of analysis to data collected by aerial survey. What factors might limit the use of line- transect methods from aircraft? What advantages would accrue if you could use line transects for aerial surveys. Read Burnham and Anderson (1984) and discuss the application of their recommendations.

5.3. The following data were gathered from a 160 meter line transect for pheasants in southern England. Strip width (*w*) was 65 m.

Observation no.	Sighting distance, x_i	Sighting angle, θ
1	27.6 m	46^o
2	25.2	27
3	16.2	8
4	24.7	31
5	44.4	42
6	48.0	28

7	13.1	2
8	6.9	18
9	23.5	48
10	5.3	29
11	14.9	36
12	23.7	31
13	36.7	56
14	10.9	68
15	24.1	0
16	61.8	46
17	27.6	22
18	8.3	18
19	16.2	27
20	25.2	34

Calculate the Hayne estimate of population density for these data and compare the resulting confidence limits with those obtained using the Modified Hayne estimator and the Fourier -series estimator.

5.4. Calculate an estimate of density from the variable area transect method for ground squirrel burrows counted along a transect of 7 m total width in which the following distances were measured from the start of the random quadrat to the perpendicular at which the third burrow was located: (*n* = 30)

6.7, 19.6, 32.2, 7.2, 12.4, 11.1, 27.8, 12.4, 16.4, 8.9, 19.0, 12.1, 19.5, 23.3, 17.9, 12.3, 18.0, 24.7, 21.8, 28.0, 12.2, 8.4, 19.2, 13.0, 26.2, 21.8, 13.9, 14.7, 37.7, and 24.5 m.

Estimate 90% confidence limits for the density of burrows.

5.5. Point-quarter sampling was done on Amabilis fir in the Coast Range of British Columbia by an ecology class with the following results: (*n* = 10 random points)

	Distance from point to tree (m)			
Point	Quadrant 1	Quadrant 2	Quadrant 3	Quadrant 4
1	3.05	4.68	9.15	7.88
2	2.61	12.44	19.21	3.87
3	9.83	5.41	7.55	11.16
4	7.41	9.66	1.07	3.93
5	1.42	7.75	3.48	1.88
6	8.86	11.81	6.95	7.32

7	12.35	9.00	8.41	3.16
8	10.18	3.16	7.14	2.73
9	3.49	5.70	9.12	8.37
10	5.88	4.15	13.95	7.10

Estimate population density for these trees and calculate a 95% confidence interval for your estimate. What assumptions must you make to do these estimates?

5.6 Plan a study to estimate the density of grizzly bears in a national park. Consider mark-recapture, quadrat-based, and plotless-type methods of estimating density, and list their potential advantages and disadvantages.

5.7 Lemmings living on the tundra construct overwinter nests of grass at the ground surface for insulation under the snow. In spring these nests are highly visible and can be used to index overwinter population abundance (Duchesne et al. 2011). One possible census method for winter nests is line transects. But the tundra has very uneven topography, and it is nearly impossible to walk a straight line in a line transect. What implication does the fact that the transect line cannot be straight have for estimating the density of winter nests by the line transect method?