CHAPTER 4

ESTIMATING DENSITY: QUADRAT COUNTS

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Counts of plants or animals on areas of known size are among the oldest techniques in ecology. Counts are simple to comprehend and can be used in a great variety of ways on organisms as diverse as trees, shrubs, barnacles, kangaroos, and sea-birds. The basic requirements of all these techniques are only two: (1) that the area (or volume) counted is known so that density is determined directly, and (2) that the organisms are relatively immobile during the counting period so none are missed. Quadrat counts have been used extensively on plants, which rarely run away while being counted, but they are also suitable for kangaroos or caribou if the person counting is swift of vision or has a camera. In this chapter we will illustrate the various ways in which counts on areas can be used to estimate the density of plants and animals.

4.1 QUADRAT SIZE AND SHAPE

If you are going to sample a forest community to estimate the abundance of sugar maple trees, you must first make two operational decisions: (1) what *size* of quadrat should I use? (2) What *shape* of quadrat is best? The answers to these simple questions are far from simple. Two approaches have been used. The simplest approach is to go to the literature and use the same quadrat size and shape that everyone else in your field uses. Thus if you are sampling mature forest trees you will find that most people use quadrats 10 m x 10 m; for herbs, 1 m^2. The problem with this approach is that the accumulated wisdom of ecologists is not yet sufficient to assure you of the correct answer. Table 4.1 shows the size and shapes of quadrats used by benthic marine ecologists since the 1950s. Pringle (1984) suggested that areas of 0.25 m^2 were best for marine benthic organisms, and that less than 25% of the studies carried out used the optimal-sized quadrat. Note that there is not one universal "best" quadrat size, so Pringle's (1984) recommendations are both area and species specific. So even if you were doing a benthic marine survey in South America, you should not assume these data will apply to your particular ecosystem. You need to employ his methods, not his specific conclusions.

TABLE 4.1   Survey of Sampling Units Employed by Biologists doing Benthic Marine Surveys

	Area (m^2)				
	< 0.25	0.25	1.0	> 1.0	Total
Square quadrats	3	4	6	1	14
Circles	3	1	0	0	4
Rectangles	3	0	0	0	3
Total	9	5	6	1	21

Source: Pringle (1984)

A better approach, then (if time and resources are available) is to determine for your particular study system the optimal quadrat size and shape. To do this, you first need to decide what you mean by "best" or "optimal" quadrat size and shape. *Best* may be defined in three ways: (1) *statistically*, as that quadrat size and shape giving the

highest statistical precision for a given total *area* sampled, or for a given total amount of *time* or *money,* (2) *ecologically*, as that quadrat size and shape that are most efficient to answer the question being asked, and (3) *logistically*, as that quadrat size and shape that are easiest to put out and use. You should be wary of the logistical criterion since in many ecological cases the easiest is rarely the best. If you are investigating questions of ecological scale, the processes you are studying will dictate quadrat size. But in most cases the statistical criterion and the ecological criterion are the same. In all these cases we define:

highest statistical precision = lowest standard error of the mean

= narrowest confidence interval for the mean

We attempt to determine the quadrat size and shape that will give us the highest statistical precision. How can we do this?

Consider first the *shape* question. The term "quadrat" strictly means a four-sided figure, but in practice this term is used to mean any sampling unit, whether circular, hexagonal, or even irregular in outline. There are two conflicting problems regarding shape. First, the edge effect is minimal in a circular quadrat, and maximal in a rectangular one. The ratio of length of edge to the area inside a quadrat changes as:

circle < square < rectangle

Edge effect is important because it leads to possible counting errors. A decision must be made every time an animal or plant is at the edge of a quadrat — *is this individual inside or outside the area to be counted?* This decision is often biased by keen ecologists who prefer to count an organism rather than ignore it. Edge effects thus often produce a positive bias. The general significance of possible errors of counting at the edge of a quadrat cannot be quantified because it is organism- and habitat-specific, and can be reduced by training. If edge effects are a significant source of error, you should prefer a quadrat shape with less edge/area. Figure 4.1 illustrates one way of recognizing an edge effect problem. Note that there is no reason to expect any bias in *mean abundance* estimated from a variety of quadrat sizes and shapes. If there is no edge effect bias, we expect in an ideal world to get the same mean value regardless of the size or shape of the quadrats used, if the mean is expressed in the same units of area.

This is important to remember — quadrat size and shape are *not* about biased abundance estimates but are about narrower confidence limits. If you find a relationship like Figure 4.1 in your data, you should immediately disqualify the smallest quadrat size from consideration to avoid bias from the edge effect.

The second problem regarding quadrat shape is that nearly everyone has found that long thin quadrats are better than circular or square ones of the same
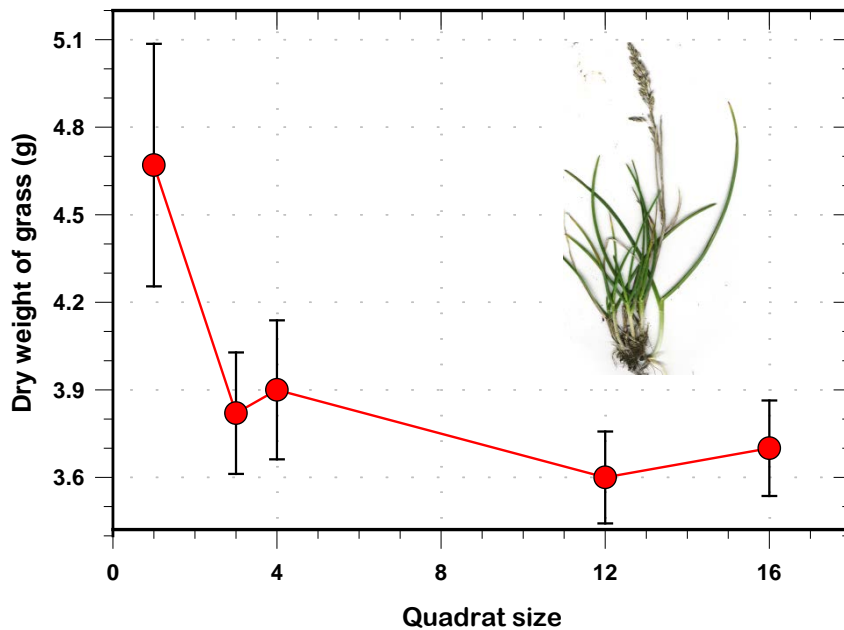

Figure 4.1   Edge effect bias in small quadrats. The estimated mean dry weight of grass (per 0.25 m^2) is much higher in quadrats of size 1 (0.016 m^2) than in all other quadrat sizes. This suggests an overestimation bias due to edge effects, and that quadrats of size 1 should not be used to estimate abundance of these grasses. Error bars are 95% confidence limits. Estimates of mean values (per unit area) should not be affected by quadrat size. (Data of Wiegert (1962).

area. The reason for this is habitat heterogeneity. Long quadrats cross more patches. Areas are never uniform and organisms are usually distributed somewhat patchily within the overall sampling zone. Clapham (1932) counted the number of *Prunella vulgaris* plants in 1 m^2 quadrats of 2 shapes: 1m x 1m and 4m x 0.25m. He counted 16 quadrats and got these results:

	Mean	Variance	S.E.	95% confidence interval
1 X 1 m	24	565.3	5.94	± 12.65

4 X 0.25 m   24   333.3   4.56 $\pm$ 9.71

Clearly in this situation the rectangular quadrats are more efficient than square ones. Given that only two shapes of quadrats were tried, we do not know if even longer, thinner quadrats might be still more efficient.

Not all sampling data show this preference for long thin quadrats and for this reason each situation should be analyzed on its own. Table 4.2 shows data from basal area measurements on trees in a forest stand studied by Bormann (1953). The observed standard deviation almost always falls as quadrat area increases, as shown in Table 4.2. But if an equal total *area* is being sampled, the highest precision (= lowest S.E.) will be obtained by taking 70 4 x 4 m quadrats rather than 2 4 x 140 m quadrats. If, on the other hand, an equal *number* of quadrats were to be taken for each plot size, one would prefer the long-thin quadrat shape.

Table 4.2   Effect of Plot Size on Standard Deviation for Measurements of Basal Area of Trees in an Oak-hickory Forest in North Carolina[a]

(1) Plot size (m)	(2) Observed standard deviation (per 4 m^2)	(3) Sample size needed to cover 1120 sq.m.[b]	(4) Standard error of mean for sample size in column (3)
4 $\times$ 4	50.7	70	6.06
4 $\times$ 10	47.3	28	8.94
4 $\times$ 20	44.6	14	11.92
4 $\times$ 70	41.3	4	20.65
4 $\times$ 140	34.8	2	24.61

[a] If equal total areas are sampled with each plot size, the best plot size is clearly 4 $\times$ 4 m

[b] Number of quadrats of a given size needed to sample 1120 m^2.

Source: Bormann (1953), Table IV.

Two methods are available for choosing the best quadrat size statistically. Wiegert (1962) proposed[*] a general method that can be used to determine optimal size or shape. Hendricks (1956) proposed a more restrictive method for estimating optimal size

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[*] Following the analysis by Cochran (1953, Chap. 9).

of quadrats. In both methods it is essential that data from all quadrats be standardized to a single unit area – for example, per square meter. This conversion is simple for means, standard deviations and standard errors: divide by the relative area. For example:

$$\text{Mean no. per sq. meter} = \frac{\text{Mean number per } 0.25 \text{ m}^2}{0.25}$$

$$\text{Standard deviation per sq. meter} = \frac{\text{Standard deviation per } 4 \text{ m}^2}{4}$$

For variances, the square of the conversion factor is used:

$$\text{Variance per sq. meter} = \frac{\text{Variance per } 9 \text{ m}^2}{9^2}$$

For both Wiegert's and Hendricks' methods you should standardize all data to a common base area before testing for optimal size or shape of quadrat. They both assume further that you have tested for and eliminated quadrat sizes that give an edge effect bias (c.f. Figure 4.1).

4.1.1 Wiegert's Method

Wiegert (1962) proposed that two factors were of primary importance in deciding on optimal quadrat size or shape — *relative variability* and *relative cost*. In any field study, *time* or *money* would seem to be the limiting resource and we must consider how to optimize with respect to sampling time. We will assume that time = money, and in the formulas which follow either units may be used. Costs of sampling have two components (in a simple world):

$$C = C_0 + C_x$$

where C = total cost for one sample

C_0 = fixed costs or overhead

C_x = cost for taking one sample quadrat of size x

Fixed costs involve the time spent walking or flying between sampling points and the time spent locating a random point for the quadrat; these costs may be trivial in an open grassland or enormous when sampling the ocean in a large ship. The cost for taking a single quadrat may or may not vary with the size of the quadrat. Consider a simple example from Wiegert (1962) of grass biomass in quadrats of different sizes:

	Quadrat size (area)				
	1	3	4	12	16
Fixed cost ($)	10	10	10	10	10
Cost per sample ($)	2	6	8	24	32
Total cost for one quadrat ($)	12	16	18	34	42
Relative cost for one quadrat	1	1.33	1.50	2.83	3.50

We need to balance these costs against the relative variability of samples taken with quadrats of different sizes:

	Quadrat size (area)				
	1	3	4	12	16
Observed variance per 0.25 m^2	0.97	0.24	0.32	0.14	0.15

The operational rule is: *pick the quadrat size that minimizes the product of* (relative cost) (relative variability).

In this example we begin by disqualifying quadrat size 1 because it showed a strong edge effect bias (Fig. 4.1). Figure 4.2 shows that the optimal quadrat size for grass in this particular study is 3, although there is relatively little difference between the products for quadrats of size 3, 4, 12, and 16. In this case again the size 3 quadrat gives the maximum precision for the least cost.
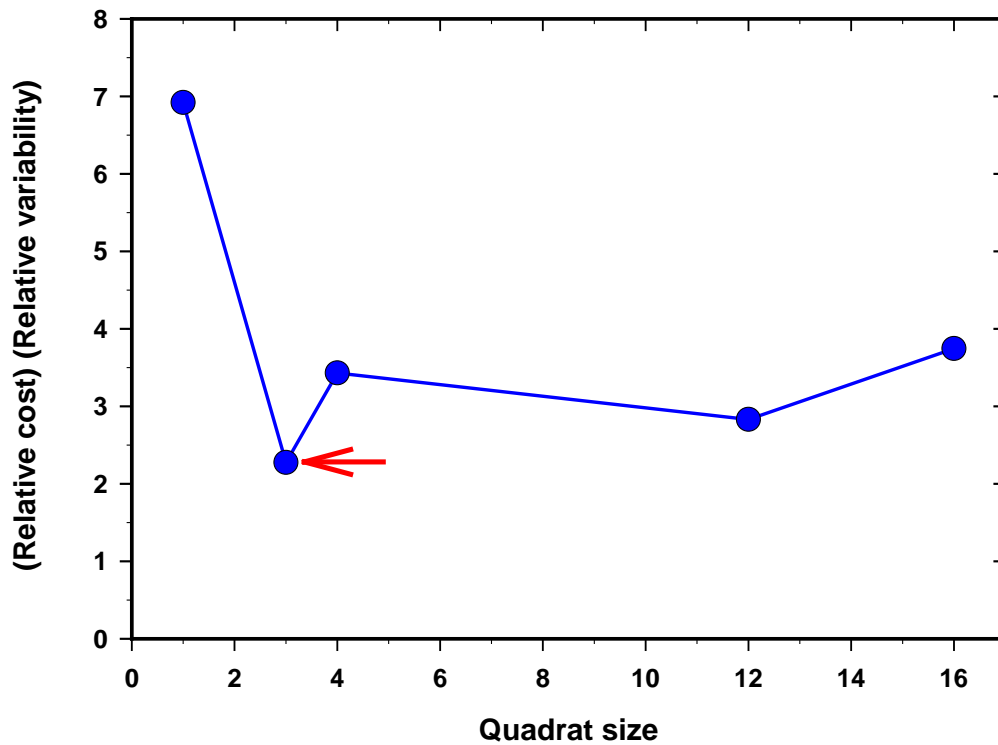
Figure 4.2 Determination of the optimal quadrat size for sampling. The best quadrat size is that which gives the minimal value of the product of relative cost and relative variability, which is quadrat size 3 (red arrow) in this example. Quadrat size 1 data are plotted here for illustration, even though this quadrat size is disqualified because of edge effects. Data here are dry weights of grasses in quadrats of variable size. (After Wiegert 1962).

Box 4.1 illustrates the application of Wiegert's procedures for deciding on the optimal size or the optimal shape of quadrat for counting animals or plants.

Box 4.1 Wiegert's Method to Determine Optimal Quadrat Size for Biomass Estimates of the Seaweed *Chondrus crispus* ("Irish moss"). (Data from Pringle 1984.)

Quadrat size (m)	Sample size[a]	Mean biomass[b] (g)	Standard deviation[b]	S.E. of mean[b]	Time to take one sample (min)
0.5 x 0.5	79	1524	1022	115	6.7
1 x 1	20	1314	963	215	12.0
1.25 x 1.25	13	1037	605	168	13.2

1.5 x 1.5	9	1116	588	196	11.4
1.73 x 1.73	6	2021	800	327	33.0
2 x 2	5	1099	820	367	23.0

[a] Sample sizes are approximately the number needed to make a total sampling area of 20 m^2.
[b] All expressed per square meter.

If we neglect any fixed costs and use the time to take one sample as the total cost, we can calculate the relative cost for each quadrat size as:

$$\text{Relative cost} = \frac{\text{Time to take one sample of a given size}}{\text{Minimum time to take one sample}}$$

In this case the minimum time = 6.7 minutes for the 0.5 x 0.5 m quadrat. We can also express the variance [= (standard deviation)^2] on a relative scale:

$$\text{Relative variance} = \frac{(\text{Standard deviation})^2}{(\text{Minimum standard deviation})^2}$$

In this case the minimum variance occurs for quadrats of 1.5 x 1.5 m. We obtain for these data:

Quadrat size (m)	(1) Relative variance	(2) Relative cost	Product of (1) x (2)
0.5 x 0.5	3.02	1.00	3.02
1 x 1	2.68	1.79	4.80
1.25 x 1.25	1.06	1.97	2.09
1.5 x 1.5	1.00	1.70	1.70
1.73 x 1.73	1.85	4.93	9.12
2 x 2	1.94	3.43	6.65

The operational rule is to pick the quadrat size with minimal product of (cost) x (variance), and this is clearly 1.5 x 1.5 m, which is the optimal quadrat size for this particular sampling area.

There is a slight suggestion of a positive bias in the mean biomass estimates for the smallest sized quadrats but this was not tested for by Pringle (1984) and does not appear to be statistically significant.

The optimal quadrat shape could be decided in exactly the same way.

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

Not all sampling will give the same answer and when several species are being counted or clipped in each quadrat, the optimal size and shape of quadrat may well

differ among species. Brummer et al. (1994) measured the efficiency of different quadrat sizes and shapes for estimating grass standing crop in tall grass prairie in Nebraska. They pointed out that it is important to distinguish in any analysis the time to move between quadrats in the measure of relative costs. If many small quadrats are used, the movement time over the entire sampling period may comprise a large fraction of the time in the field (Figure 4.3). In this particular case for sand bluestem grass they found that long thin, relatively large quadrats (1x40) were best for minimizing the amount of time needed to sample to achieve a designated confidence interval. For the four main species sampled the best quadrats tended to be larger quadrats that were rectangular and long and thin. Some grassland species required many more than others to achieve the same precision, highlighting the need to do this kind of analysis before starting a long term study.
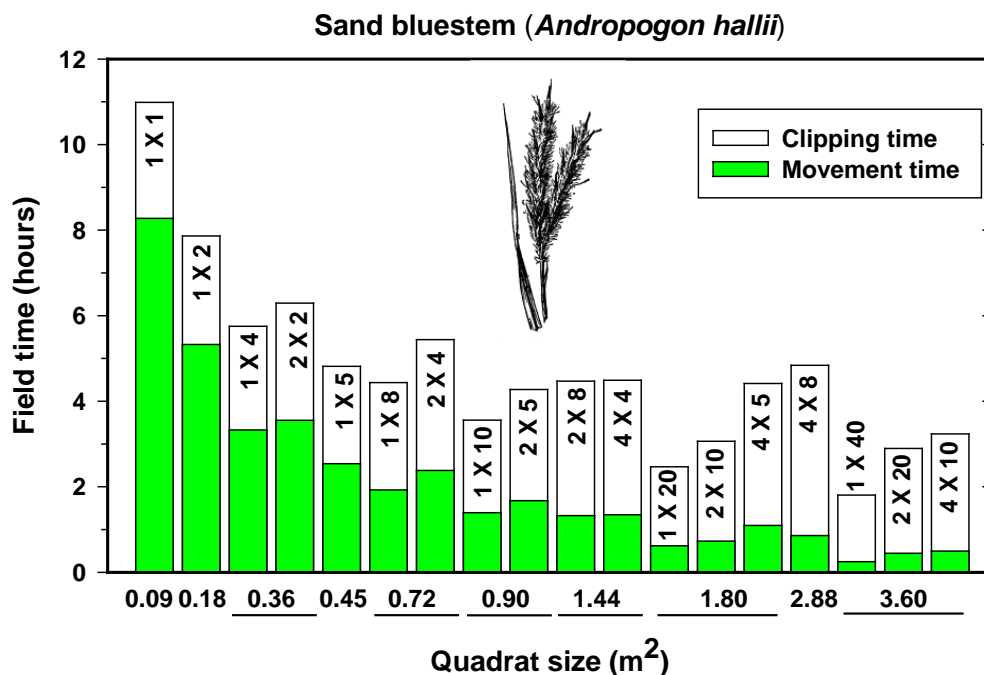

Figure 4.3 The total sampling time to estimate the standing crop of sand bluestem grass in Nebraska tall grass prairie. Each histogram bar gives the time required to move between quadrats and the clipping time, which together give the total field time for a set of 18 quadrats that varied in size and shape. The sample size (number of quadrats) was adjusted to provide a fixed precision within 10% of the mean with 95% confidence. To achieve this precision many more small quadrats had to be counted compared with larger quadrats. Quadrat sizes with the same area but different shapes are underlined. In every case the longer thinner quadrats were more efficient. (After Brummer et al. 1994.)

4.1.2 Hendricks' Method

Hendricks (1956) noted that the variance (per standard area) usually decreased with larger quadrat sizes. In a simple situation the log of the variance will fall linearly with the log of quadrat size, and one critical parameter is how fast the variance declines with quadrat size. Hendricks assumes that the slope of this line will be between 0 and -1. This is a very restrictive assumption, and if the slope is not within this range, Hendricks' method cannot be used.

In many cases the amount of time or money needed to count quadrats of different sizes is directly proportional to quadrat size. Thus a 2m^2 quadrat will require twice as much time to count as a 1m^2 quadrat. Hendricks makes a second assumption that this is true for all quadrat sizes. In this simple situation the critical cost is the fixed cost for each quadrat, the cost to select and move to and locate a single new random quadrat.

Given these simplifying assumptions, Hendricks (1956) shows that optimal quadrat size is determined as:

$$\hat{A} = \left(\frac{a}{1-a}\right)\left(\frac{C_0}{C_x}\right) \tag{4.1}$$

where $\hat{A}$ = Estimate of optimal quadrat size

a = Absolute value of the slope of the regression of log (variance) on log (quadrat size) (assumed to be between 0 and 1)

C_0 = Cost of locating one additional quadrat

C_x = Cost of measuring one unit area of sample

Because Hendricks' method makes so many simplifying assumptions, it cannot be applied as generally as Wiegert's method. And because it is concerned only with quadrat size, it cannot answer questions about quadrat shape. But Hendricks' method can be a simple yet rigorous way of deciding on what size of quadrat is best for a particular sampling program.

Program QUADRAT (Appendix 2, page 000) does the calculations for Wiegert's method and for Hendricks' method for estimating the optimal quadrat size or shape.

Considerations of quadrat size and shape are complicated by seasonal changes within a population, and by the fact that in many cases several different species are being counted in the same quadrat. There is no reason why quadrat size cannot change seasonally or change from species to species. One simple way to do this is to use nested quadrats:
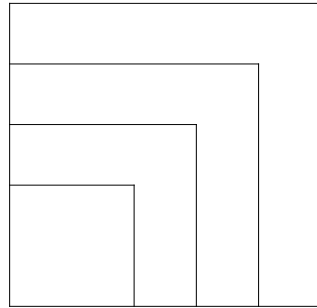
Plant ecologists use nested quadrats to define a species-area curve for a plant community and to investigate vegetation patterns (McGill 2003). The number of species typically rises with quadrat size but then should plateau at a quadrat size that determines the number of species in a community. But the description of species-area relationships has been highly controversial (Chiarucci, 2012) and the use of nested quadrats for vegetation sampling has shown that they are not always the most precise quadrat-based method (Goslee 2006).

Nested quadrats may be square, circular, or any shape. Table 4.3 can be useful in designing nested quadrats.

TABLE 4.3 Sample Plots of Different Sizes and Shapes

Area	Circular plots (radius)	Square plots (side)	Rectangular quadrats (ratio of sides)		
			1:2	1:5	1:10
1	0.56	1.00	0.71 x 1.41	0.44 x 2.20	0.32 x 3.16
2	0.80	1.41	1.00 x 2.00	0.63 x 3.16	0.45 x 4.47
3	0.98	1.73	1.22 x 2.44	0.78 x 3.86	0.55 x 5.48
4	1.13	2.00	1.41 x 2.82	0.89 x 4.45	0.63 x 6.32
5	1.26	2.24	1.58 x 3.16	1.00 x 5.00	0.71 x 7.07
10	1.78	3.16	2.24 x 4.47	1.41 x 7.07	1.00 x 10.00
20	2.52	4.47	3.16 x 6.32	2.00 x 10.00	1.41 x 14.14

30	3.09	5.48	3.94 x 7.88	2.45 x 12.25	1.73 x 17.32
40	3.57	6.32	4.47 x 8.94	2.83 x 14.15	2.00 x 20.00
50	3.99	7.07	5.00 x 10.00	3.16 x 15.81	2.24 x 22.36
100	5.64	10.00	7.07 x 14.14	4.47 x 22.36	3.16 x 31.62
200	7.98	14.14	10.00 x 20.00	6.32 x 31.62	4.47 x 44.72
300	9.77	17.32	12.25 x 24.50	7.74 x 38.70	5.48 x 54.77
400	11.28	20.00	14.14 x 28.28	8.94 x 44.70	6.32 x 63.24
500	12.62	22.36	15.81 x 31.62	10.00 x 50.00	7.07 x 70.71
1000	17.84	31.62	22.36 x 44.72	14.14 x 70.71	10.0 x 100.0

Source: Table courtesy of E.A. Johnson, University of Calgary.

The message is that no single quadrat size or shape can be universally recommended for estimating the abundance for all species or even for a single species in all habitats. In any long-term study it is desirable to do a pilot study to gather the means, variances, and costs for quadrats of different size and shape, and then to decide objectively on the size and shape of the sampling unit you will use. Such a pilot study can save you a great deal of time and money, and should be a required part of every experimental design.

4.1.3 When Should You Ignore these Recommendations ?

Sampling plant and animal populations with quadrats is done for many different reasons, and it is important to ask when you might be advised to ignore the recommendations for quadrat size and shape that arise from Wiegert's method or Hendricks' method. As with all ecological methods, the ecological questions of the study should be carefully specified before you decide on the methods to use.

There are two common situations when you may wish to ignore these recommendations. In some cases you will wish to compare your data with older data gathered with a specific quadrat size and shape. Even if the older quadrat size and shape are inefficient, you may be advised for comparative purposes to continue using the old quadrat size and shape. In principle this is not required, as long as no bias is introduced by a change in quadrat size. But in practice many ecologists will be more comfortable using the same quadrats as the earlier studies. This can become a more

serious problem in a long-term monitoring program in which a poor choice of quadrat size in the early stages could condemn the whole project to wasting time and resources in inefficient sampling procedures. In such cases you will have to decide between the Concorde strategy (continuing with the older, inefficient procedure) and the Revolutionary strategy (sweeping the decks clean with proper methods). Ecological wisdom is making the right choice in these matters. If the old method and the new method can be used together for several sampling periods, it should be possible to determine if their estimates are congruent.

If you are sampling several habitats, sampling for many different species, or sampling over several seasons, you may find that these procedures result in a recommendation for a different size and shape of quadrat for each situation. It may be impossible to do this for logistical reasons and thus you may have to compromise. For example, sampling plankton from a ship requires a standard size of net and while some variation can be utilized, cost will prevent many implementations of the most efficient quadrat sizes. In multispecies studies it may be possible to use nested quadrats, but again only a restricted array of sizes and shapes may be feasible logistically. The human element is important to recognize here, and very complex sampling designs may be self-defeating if they are difficult to implement in the field and tiring for the observers. It is important to keep in mind that an average sampling strategy that is adequate but not optimal for all species or habitats may still save you time and energy.

4.2 STATISTICAL DISTRIBUTIONS

Plants or animals in any geographical area are scattered about in one of three spatial patterns - *uniform*, *random*, or *aggregated*[*] (Figure 4.4). There are degrees of uniformity and aggregation that we can describe so it is possible to say that redwood trees are *more* or *less* aggregated in certain forest stands. But randomness is randomness and it is *not* correct to say that one pattern is more random than another.

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[*] The terminology for these patterns can be most confusing. Some synonyms are:
uniform = regular = even = negative contagion = under-dispersed;
aggregated = contagious = clustered = clumped = patchy = positive contagion = over-dispersed.
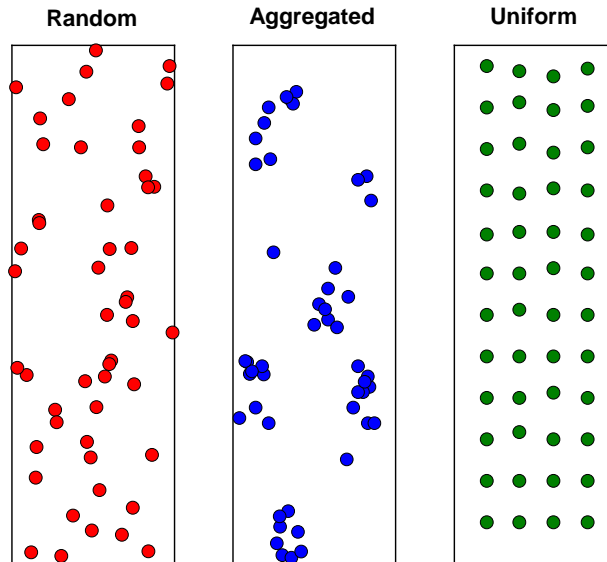
Figure 4.4   Three possible types of spatial patterning of individual animals or plants in a population

One approach to spatial patterning can be obtained by adopting an individual-orientation, and asking the question: *given the location of any one individual in a large area of known density, what is the probability that another individual is nearby*? There are 3 possibilities:

1. The organisms are *aggregated* so the probability is relatively high

2. The organisms are *uniformly spread* so the probability is relatively low

3. The organisms are spread at *random* so the probability is relatively unaffected.

Ecologists have an intuitive feeling for these spatial patterns (Fig. 4.4) but they have given the measurement problem to statisticians who have analysed the problem of spatial pattern in the following way.

Statisticians have employed many different statistical distributions to describe these three basic spatial patterns in populations. In doing so the jargon of ecology and statistics have become enmeshed and somewhat confused. Following Pielou (1977) I shall try to keep the terminology distinct for the following words:

• *Distribution -*

(a) in **statistics**, a mathematical frequency distribution that defines the frequency of counts in quadrats of a given size (see Figure 4.4). In this book *distribution* will always

mean a statistical frequency distribution.

(b) in **ecology**, the observed geographic dispersion or patterning of individuals (as in Figure 4.4).

In this book I will use *spatial pattern* or *pattern* to describe the distribution of individuals in geographic space.

- *Population*

(a) in **statistics**, the universe of items under study is called the population. I will distinguish this concept as the *statistical population*.

(b) in **ecology**, a population is a defined group of organisms of one species living in a particular area at a particular time. I will distinguish this concept as the *biological population*.

There is no end to the confusion that these two simple words have sown in ecological statistics, and you should try to use them only in a clear context.

Why should we be concerned about statistical distributions? For any particular kind of ecological data, the proper statistical distribution will determine how to calculate confidence limits correctly and how to set up a sampling program for a proper experimental design. Because quadrat sampling has an explicit spatial framework, we need to know about spatial patterns to estimate abundance properly.

We shall begin by considering the simplest case - random spatial patterns and one corresponding simple statistical distribution, the Poisson.

4.3.1 Poisson Distribution

The approach to the statistical analysis of spatial patterns in biological populations is simple and straightforward. First, a frequency distribution is tallied of the counts in randomly placed quadrats of a given size (Figure 4.5). Then a statistician asks what this frequency distribution would look like if it were generated by completely random processes. In biological terms this is equivalent to asking if the organisms are distributed randomly in space. By spatial randomness we mean organisms whose *x*- and *y*-coordinates in geographical space are taken from a random number table.

(a) Observed data
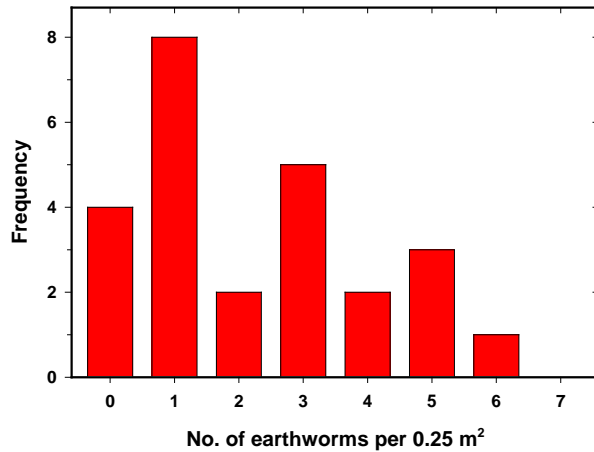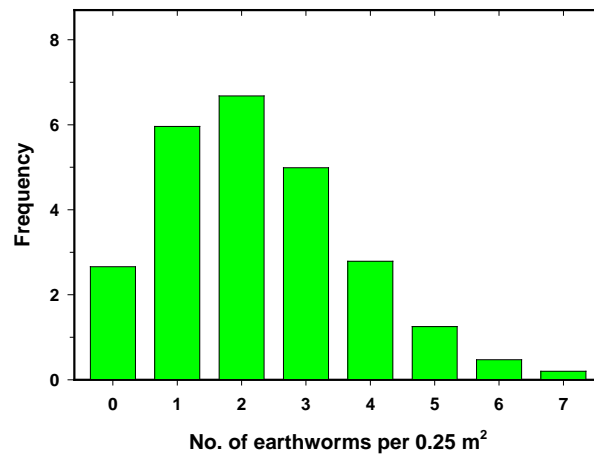

(b) Expected Poisson Distribution

Figure 4.5 (a) Observed frequency distribution of the number of earthworms (*Lumbricus terrestris*) counted on 25 quadrats of 0.25 m^2 in Cairnshee pasture, Scotland, July 1977. $\bar{x}$ = 2.24 worms per 0.25 m^2; s^2 = 3.28. (b) Expected frequency distribution based on the Poisson.

If randomness of spatial pattern prevails, the *Poisson distribution* is one statistical descriptor of the data. The Poisson distribution is a discrete frequency distribution which is mathematically very simple because it depends on only one parameter, the *mean* (Greek letter μ). The terms of the Poisson distribution are defined as follows: (relative frequency = proportion = probability)

Probability of observing zero individuals in a quadrat = $e^{-\mu}$

Probability of observing one individual in a quadrat = $e^{-\mu} \left(\dfrac{\mu}{1} \right)$

$$\text{Probability of observing two individuals in a quadrat} = e^{-\mu}\left(\frac{\mu^2}{2}\right)$$

$$\text{Probability of observing three individuals in a quadrat} = e^{-\mu}\left(\frac{\mu^3}{3!}\right)$$

It is simpler to write out one general term to describe the Poisson distribution:

$$P_x = e^{-\mu}\left(\frac{\mu^x}{x!}\right) \qquad\qquad\qquad (4.2)$$

where P_x = probability of observing x individuals in a quadrat

x = an integer counter; 0, 1, 2, 3.........

μ = true mean of the distribution

$x!$ (or x-factorial) = (x) $(x$-1) $(x$-2)..........(1) and $0! = 1$ by definition

In fitting the Poisson distribution to observed data, we need only to estimate the mean, which we do in the usual way by assuming that:

$$\bar{x} = \mu$$

The Poisson distribution assumes that the expected number of organisms is the same in all quadrats and is equal to μ. Thus it assumes a uniform world with no habitat patchiness, no "good" and "poor" quadrats.

Let us consider one example. Earthworms (*Lumbricus terrestris*) were counted on 25 quadrats in a Scottish pasture with these results: the numbers in each quadrat were -

3   4   1   1   3   0   0   1   2   3   4   5   0

1   3   5   5   2   6   3   1   1   1   0   1

For these data $n = 25$, $\bar{x} = 2.24$, $s = 1.809$. The observed data are plotted in Figure 4.5(a). The terms of the theoretical Poisson distribution for these data can be calculated as follows:

e = base of natural logarithms = 2.71828...

P_0 = proportion of quadrats expected to have no earthworms

$\quad = e^{-2.24} = 0.1065$

P_1 = proportion of quadrats expected to have 1 earthworm

$$= e^{-2.24} \left(\frac{2.24}{1} \right) = 0.2385$$

P_2 = proportion of quadrats expected to have 2 earthworms

$$= e^{-2.24} \left(\frac{2.24^2}{2} \right) = 0.2671$$

P_3 = proportion of quadrats expected to have 3 earthworms

$$= e^{-2.24} \left(\frac{2.24^3}{(3)(2)} \right) = 0.1994$$

similarly:

$$P_4 = e^{-2.24} \left(\frac{2.24^4}{(4)(3)(2)} \right) = 0.1117$$

$$P_5 = e^{-2.24} \left(\frac{2.24^5}{(5)(4)(3)(2)} \right) = 0.0500$$

$$P_6 = e^{-2.24} \left(\frac{2.24^6}{(6)(5)(4)(3)(2)} \right) = 0.0187$$

Note that we *could* continue these calculations forever but the proportions grow small very quickly. We know that

$$P_0 + P_1 + P_2 + P_3 + P_4 + P_5 + \cdots\cdots = 1.000$$

In this case

$$P_0 + P_1 + P_2 + P_3 + P_4 + P_5 + P_6 = 0.992$$

so that all the remaining terms $P_7 + P_8 + P_9$ .... must sum to 0.008. We can calculate that $P_7 = 0.006$, so we can for convenience put all the remainder in P_8 and say

$$P_8 \approx 0.002$$

to round off the calculations. These calculations can be done by Program QUADRAT (Appendix 2, page 000). We have calculated the *proportions* in the expected Poisson distribution, and the final step to tailor it to our earthworm data is to multiply each proportion by the number of quadrats sampled, 25 in this case.

Expected number of quadrats with no earthworms = (P_0) (total number of quadrats)

$$= (0.1065) (25) = 2.66$$

Expected number of quadrats with one earthworm = (P_1) (total number of quadrats)

$\qquad$ = (0.2385) (25) = 5.96

And similarly:

No. worms x	Expected number of quadrats
2	6.68
3	4.99
4	2.79
5	1.25
6	0.47
7	0.20

for a grand total of 25.00 expected. These expected numbers are plotted in Figure 4.5(b). The observed and expected frequency distributions in Figure 4.5 are fairly similar, and we need a statistical technique to test the null hypothesis that the Poisson distribution provides an adequate fit to the observed data. This statistical hypothesis is inferred to be testing the ecological hypothesis that the spatial pattern observed is a random one.

Tests for Goodness-of-Fit There are two methods for testing the goodness of fit of the Poisson distribution.

(1) *Index of Dispersion Test*: we define an index of dispersion I to be:

$$I = \frac{\text{Observed variance}}{\text{Observed mean}} = \frac{s^2}{\bar{x}} \qquad (4.3)$$

For the theoretical Poisson distribution, the variance equals the mean and so the expected value of I is always 1.0 in a Poisson world. The simplest test statistic for the index of dispersion is a chi-squared value:

$$\chi^2 = I(n-1) \qquad (4.4)$$

$\qquad$ where I = index of dispersion (as defined in eq. 4.3)

$\qquad$ n = number of quadrats counted

χ^2 = value of chi-squared with (n-1) degrees of freedom.

For the earthworm data with mean 2.24 and variance 3.27

$$I = \frac{s^2}{\overline{x}} = \frac{3.27}{2.24} = 1.46$$

and

$$\chi^2 = I(n-1) = 1.46(25-1) = 35.0$$

The index of dispersion test is a 2-tailed χ^2 test because there are two possible directions of deviations: if organisms are uniformly spaced (Fig. 4.4), the variance will be much less than the mean, and the index of dispersion will be close to zero. If organisms are aggregated, the observed variance will be greater than the mean, and the index of dispersion will be much larger than 1.0. Figure 4.6 gives the critical values of chi-squared for this two-tailed test. In more formal terms the decision rule is: provisionally fail to reject the null hypothesis of an index of dispersion of 1.0 if

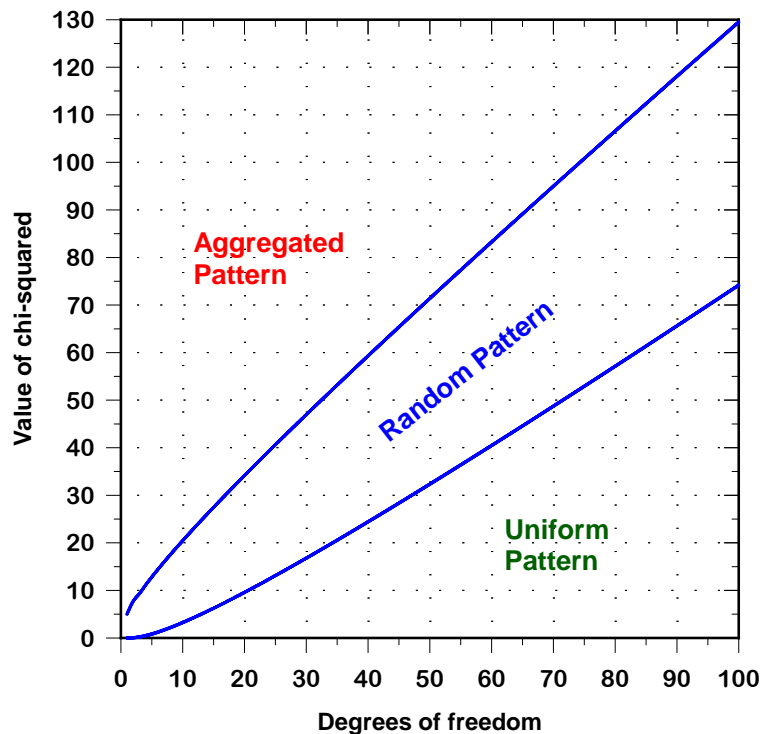$$\chi^2_{.975} \leq \text{Observed chi-square} \leq \chi^2_{.025}$$

> **Figure 4.6** Critical values of the chi-square test of the index of dispersion (*I*) for $\alpha = 0.05$ and for n < 101. Large values of χ^2 indicate an aggregated pattern, and small values indicate a uniform pattern.

For our example, with 24 degrees of freedom

$\chi^2_{.975} = 12.40$

$\chi^2_{.025} = 39.36$

so we tentatively fail to reject the null hypothesis that the index of dispersion is 1.0.

If sample size is large (n > 101) Figure 4.6 cannot be used to determine the critical values of chi-square. In this case calculate the normal approximation to the chi-squared value:

$$z = \sqrt{2\chi^2} - \sqrt{(2v - 1)} \tag{4.5}$$

where z = standard normal deviate ($\mu = 0$, $\sigma = 1$)

χ^2 = observed value of chi-square

v = number of degrees of freedom = (*n* - 1)

The decision rule is to fail to reject the null hypothesis that the index of dispersion is 1.0 if *z* is between 1.96 and -1.96 (for $\alpha = 0.05$).

(2) *Chi-squared Goodness of Fit Test*: To test whether the Poisson distribution provides an adequate fit to the observed data, we can use the old standard:

$$\chi^2 = \Sigma \left[\frac{(\text{Observed frequency - expected frequency})^2}{\text{Expected frequency}} \right] \tag{4.6}$$

where we sum over each possible class (0, 1, 2...) with due attention to the rule that all *expected* values should be 3 or more[*]. The tails of the distribution will have to be summed to satisfy this criterion.

For the earthworm data given above:

---

[*] This rule is somewhat subjective and some authors say that all expected values should be 5 or more, others say 1 or more. In my experience 3 is sufficient and often 1 is adequate. Zar (1996, p. 466) discusses the rules for the use of χ^2 with low expected values.

$$\chi^2 = \frac{(4-2.66)^2}{2.66} + \frac{(8-5.96)^2}{5.96} + \frac{(2-6.68)^2}{6.68} + \frac{(5-4.99)^2}{4.99} + \frac{(6-4.71)^2}{4.71}$$

$$= 5.00 \qquad (3 \text{ d.f.})$$

Observed and expected numbers are shown in Figure 4.5. Note that quadrat counts for 4, 5 and 6 were added together to form the last class.[‡]

The number of degrees of freedom for this test is two less than the number of terms in the summation (because two parameters, the mean and the sample size, were obtained from the data). From the chi-squared table:

$$\chi^2_{.05} = 7.815 \qquad \text{for 3 d.f.}$$

and the decision rule is: reject the null hypothesis if the observed chi-squared is *larger* than the tabular value for α = .05. Hence in this case we tentatively accept the null hypothesis, as we did above.

Note that the chi-squared goodness of fit test is a much better test than the index of dispersion test to detect strong departures from randomness. Hurlbert (1990) pointed out that the Poisson distribution is only one of many distributions that provide a variance/ mean ratio of 1.0. He provided 6 hypothetical data sets which all show a variance to mean ratio of 1.0 but which are clearly not random patterns. All of these hypothetical data sets were recognized as non-random by the chi-squared test just described. The problem of measuring spatial pattern is discussed in detail in Chapter 6 (page 000).

Many statisticians recommend the log-likelihood ratio for goodness of fit tests which have typically used chi-square in the past (Sokal and Rohlf 1995, p. 690). Twice the log-likelihood ratio is distributed approximately as chi-square so that the usual chi-square tables may be used for hypothesis testing. For the goodness of fit of a Poisson distribution we have:

[‡] If we had grouped only the counts for 5 and 6 we would have obtained χ^2 = 7.13 with 4 d.f. and made the same decision.

$$G = 2\sum \left\{ (\text{observed frequency}) \left[\log_e \left(\frac{\text{observed frequency}}{\text{expected frequency}} \right) \right] \right\} \qquad (4.7)$$

where G = test statistic for log-likelihood ratio

For the earthworm data $G = 7.71$ with 4 degrees of freedom, and so again we tentatively fail to reject the null hypothesis that the index of dispersion is 1.0 for the observed counts. The G-test has the same restrictions as chi-square for having all expected values above 1. When sample sizes are small (n < 200), it is useful to apply Williams' (1976) correction to the G-statistic:

$$G_{adj} = \frac{G}{q} \qquad (4.8)$$

where G_{adj} = G-statistic adjusted by Williams' (1976) correction for continuity

G = G-statistic calculated as in equation (4.7)

$$q = 1 + \frac{(a+1)}{6n}$$

where a = no. of frequency classes used to calculate G

n = total no. of individuals in the sample

The result of Williams' correction is to reduce slightly the value of the log-likelihood ratio.

These statistical tests are carried out in Program QUADRAT (Appendix 2, page 000).

Confidence Limits for the Mean of a Poisson Distribution

Confidence limits for the mean of counts that can be adequately described by a Poisson distribution are exceptionally easy to obtain. The reliability of a Poisson mean is completely determined by the number of items counted *in total*. Table 2.1 (page 27) gives the resulting 95% and 99% confidence limits, which can also be calculated in Program EXTRAS (page 000). For our earthworm example, having counted a total of 56 worms, Table 2.1 gives 95% confidence limits of 41.75 and 71.28. These limits are normally converted back to a per-quadrat basis by dividing by the number of quadrats counted. For the earthworm example:

$$\text{mean} = \frac{56}{25} = 2.24 \text{ worms per } 0.25 \text{ m}^2$$

$$\text{lower 95\% confidence limit} = \frac{41.75}{25} = 1.67 \text{ worms per } 0.25 \text{ m}^2$$

$$\text{upper 95\% confidence limit} = \frac{71.28}{25} = 2.85 \text{ worms per } 0.25 \text{ m}^2$$

As the mean of a theoretical Poisson distribution gets larger, the asymmetry of the distribution disappears. Figure 4.7 illustrates the changing shape of the Poisson distribution as the mean increases. Once the mean of the Poisson exceeds 10, or in ecological terms when the organism being counted is abundant, the Poisson takes on the shape of the *normal*, bell-shaped distribution. Indeed, the Poisson distribution approaches the normal distribution as a limit when the mean becomes very large (Pielou 1977).

If the Poisson distribution is an adequate representation of the counts you have made, you should be celebrating. The Poisson world is a very convenient world in which sampling is very easy and the statistics are simple (see Chapters 5 and 6). But often the result of these tests is to reject the Poisson model, and we now turn to consider what to do when the spatial pattern is not random but aggregated or clumped.

4.2.2 Negative Binomial Distribution

Not very many species show spatial random patterns in nature, and we need to consider how to describe and study populations that show clumped patterns. A variety of statistical distributions have been used to describe aggregated spatial patterns in biological populations (Patil *et al*. 1971). The most common one is the negative binomial distribution, but it is important to remember that once we leave the world of random patterns we open Pandora's box to find an infinite variety of possibilities of aggregated patterns (Fig. 4.8). There are many aggregated patterns that can not be adequately described by the negative binomial distribution and many other statistical distributions that can be used to mimic aggregated spatial patterns.

The negative binomial distribution is mathematically similar to the positive binomial, and is an expansion of the series:

$$(q - p)^{-k}$$

The negative binomial is another discrete probability distribution and is governed by two parameters, the exponent k (often called *negative-binomial k*) and p (= q - 1) which is related to the mean of the negative binomial as:

$$\text{Mean} = \mu = kp$$

From our point of view, it is simplest to consider the individual terms of the negative binomial distribution:

$$\left.\begin{array}{l}\text{Probability of observing zero} \\ \text{individuals in a quadrat}\end{array}\right\} = \left(1 + \frac{\overline{x}}{k}\right)^{-k}$$

$$\left.\begin{array}{l}\text{Probability of observing one} \\ \text{individual in a quadrat}\end{array}\right\} = \left(\frac{k}{1}\right)\left(\frac{\overline{x}}{\overline{x}+k}\right)\left(1 + \frac{\overline{x}}{k}\right)^{-k}$$

$$\left.\begin{array}{l}\text{Probability of observing two} \\ \text{individuals in a quadrat}\end{array}\right\} = \left(\frac{k}{1}\right)\left(\frac{k+1}{2}\right)\left(\frac{\overline{x}}{\overline{x}+k}\right)^{2}\left(1 + \frac{\overline{x}}{k}\right)^{-k}$$

$$\left.\begin{array}{l}\text{Probability of observing three} \\ \text{individuals in a quadrat}\end{array}\right\} = \left(\frac{k}{1}\right)\left(\frac{k+1}{2}\right)\left(\frac{k+2}{3}\right)\left(\frac{\overline{x}}{\overline{x}+k}\right)^{3}\left(1 + \frac{\overline{x}}{k}\right)^{-k}$$
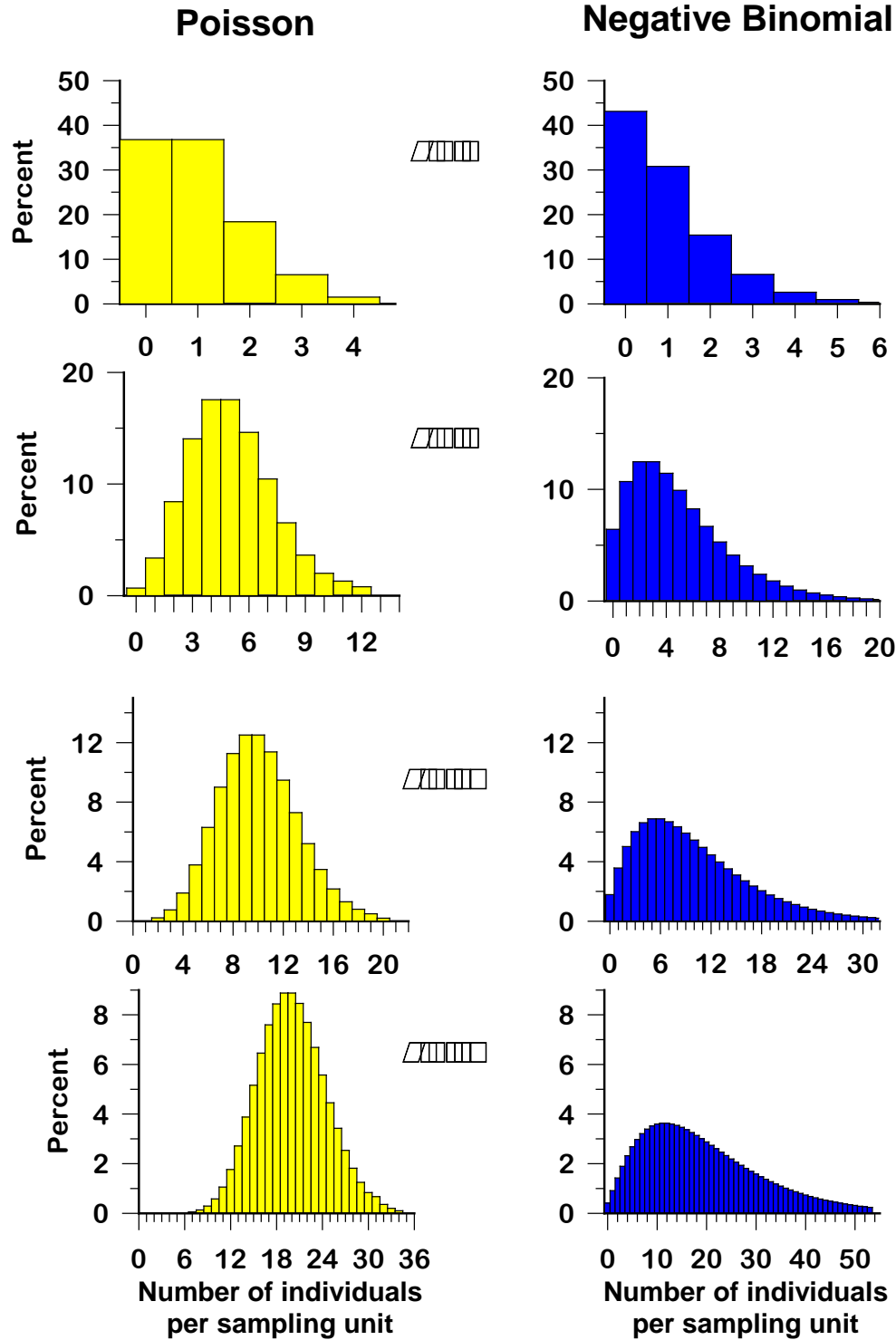
etc.

Figure 4.7 Comparison of the shape of the Poisson frequency distribution and the negative binomial distribution. A range of means from 1 to 20 is shown for each theoretical distribution. For all negative binomial distributions, $k = 2.5$

The general term for the negative binomial distribution is:

$$P_x = \left[\frac{\Gamma(k+x)}{x!\ \Gamma(k)}\right]\left(\frac{\mu}{\mu+k}\right)^x\left(\frac{k}{k+\mu}\right)^k \tag{4.9}$$

where P_x = probability of a quadrat containing x individuals

x = a counter (0, 1, 2, 3......)

μ = mean of distribution

k = negative-binomial exponent

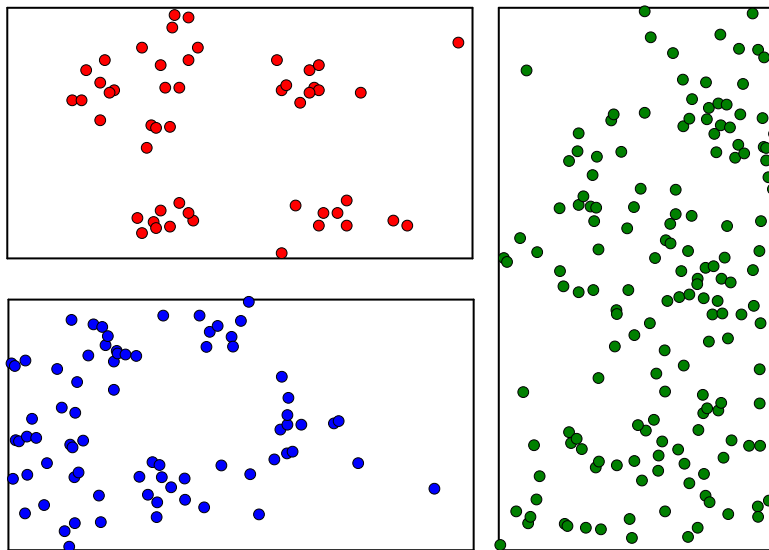Γ = Gamma function (see Appendix 1, page 000)

Figure 4.8 Clumped distributions can occur in an infinite variety of forms. Three different types of clumping are shown here. (a) Small clumps. (b) Large clumps with individuals randomly distributed within each clump. (c) Large clumps with individuals uniformly distributed within each clump. The ecological problem is to find the best way of obtaining confidence limits on abundance estimates from such clumped distributions and to find out the best way to sample clumped patterns.

The negative binomial is a unimodal frequency distribution like the Poisson. Figure 4.7 shows how the shape of the negative binomial changes as the mean increases and k is held constant. Note that as k becomes large and the mean is above 10, the negative binomial approaches the normal distribution in shape (Fig. 4.9). For this reason k can be thought of as an inverse index of aggregation; the larger the k, the less the aggregation; and conversely the smaller the k, the greater the clumping.

Negative Binomial
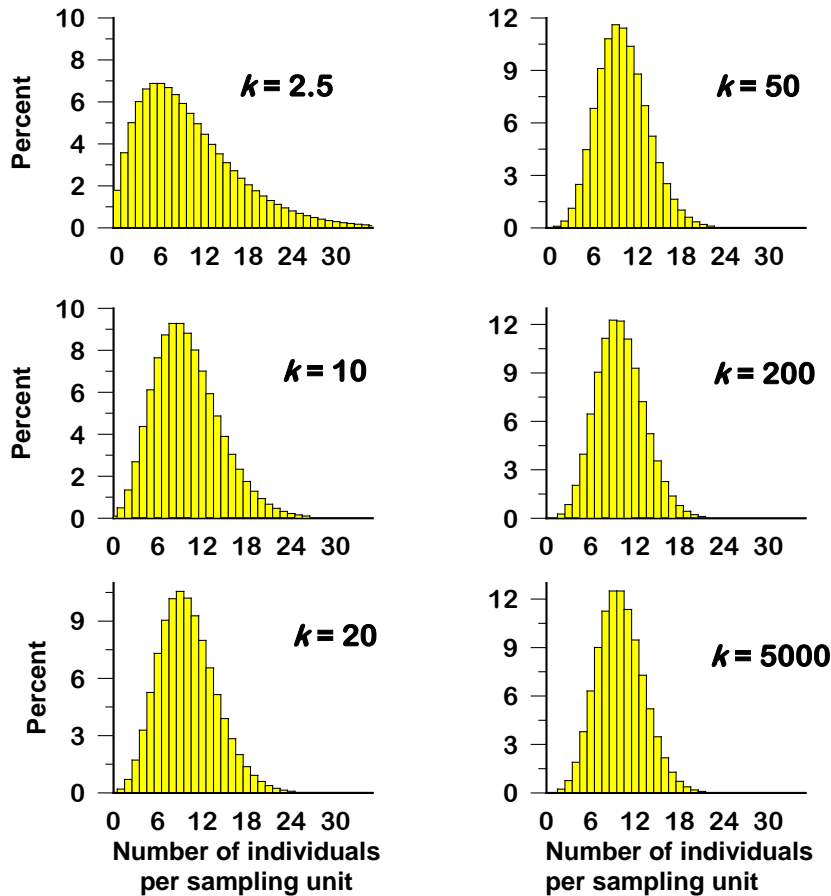
Figure 4.9 Effect of k on the shape of the negative binomial distribution. The mean of all six frequency distributions is 10, and various values of k are shown from 2.5 to infinity. As k approaches infinity, the negative binomial approaches the Poisson distribution. (After Elliott, 1977.

The theoretical variance of the negative binomial is given by:

$$\text{Variance of the negative bionomial distribution} = \mu + \frac{\mu^2}{k} \qquad (4.10)$$

Thus the variance of the negative binomial is *always greater than the mean*, and this is one simple hallmark suggesting aggregation in field data.

To fit a theoretical negative binomial distribution to some actual data, two parameters must be estimated. The *mean* is the easy one and we use the usual expectation:

$$\text{Estimated mean} = \mu = \overline{x}$$

The exponent k is more difficult to estimate because the best way to estimate it depends on the mean and k (Bliss and Fisher 1953). First, calculate an approximate estimate of k:

$$\text{Approximate } \hat{k} = \frac{\overline{x}^2}{s^2 - \overline{x}} \qquad (4.11)$$

which is just a rearrangement of the theoretical variance formula given above. I will call this approximate method (equation 4.11) *Method 1* for estimating k, following Anscombe (1950). After you have used Method 1, follow this key, which is summarized in Figure 4.10:
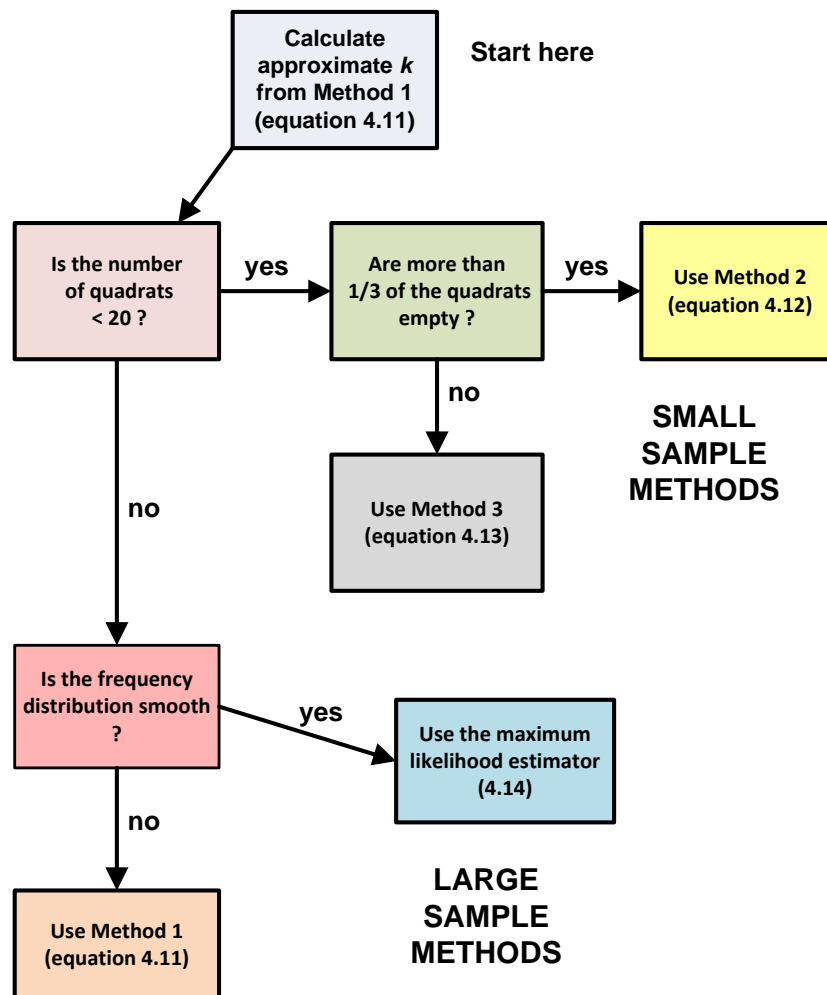

Figure 4.10 Decision tree for estimating the negative binomial exponent k.

(1) _Small sample size_: number of quadrats < 20 and counts are too few to arrange in a frequency distribution.

(a) *More than 1/3 of the quadrats are empty*: calculate an estimate of *k* by solving equation (4.12) iteratively (i.e. by trial and error):

$$\log_e\left(\frac{N}{n_0}\right) = \hat{k}\log_e\left(1+\frac{\overline{x}}{\hat{k}}\right) \tag{4.12}$$

where N = total number of quadrats counted

n_0 = number of quadrats containing zero individuals

$\overline{x}$ = observed mean

$\hat{k}$ = estimate of the negative binomial exponent

Begin with the approximate value of *k* calculated above and raise or lower it to make the two sides of this equation balance. Following Anscombe (1950) I will call this method of estimating *k* using equation (4.12) *Method 2*.

(b) *Less than 1/3 of the quadrats are empty*:

$$\hat{k} = \frac{\overline{x}^2 - \left(s^2/n\right)}{s^2 - \overline{x}} \tag{4.13}$$

I will call this *Method 3*. When the mean is above 4.0 and less than 1/3 of the quadrats are empty, Elliott (1977 pg. 56) gives another method for estimating *k* using transformations, but it is usually not worth the extra effort to calculate.

(2) *Large sample size*: number of quadrats > 20 and counts can be arranged in a frequency distribution.

(a) *frequency distribution smooth with no extremely large counts*: calculate a maximum likelihood estimate for *k* by solving this equation by trial and error:

$$(N)\log_e\left(1+\frac{\overline{x}}{\hat{k}}\right) = \sum_{i=0}^{\infty}\left(\frac{A_x}{\hat{k}+x}\right) \tag{4.14}$$

where N = total number of quadrats counted

$\overline{x}$ = observed mean

$\hat{k}$ = estimated negative-binomial exponent

$A_x = \sum_{j=x+1}^{\infty}\left(f_j\right) = f_{x+1} + f_{x+2} + f_{x+3} + f_{x+4} + \cdots$

i = a counter (0, 1, 2, 3......)

x = a counter (0, 1, 2, 3…..)

f_x = observed number of quadrats containing x individuals

j = a counter (1, 2, 3, 4......)

The best estimate of k is always obtained by this *maximum-likelihood method* using equation (4.14). Anscombe (1950) calculated the relative efficiencies of Methods 1 and 2 of estimating k, relative to the maximum-likelihood method. Figure 4.11 gives a contour map of these relative frequencies, and can be used to
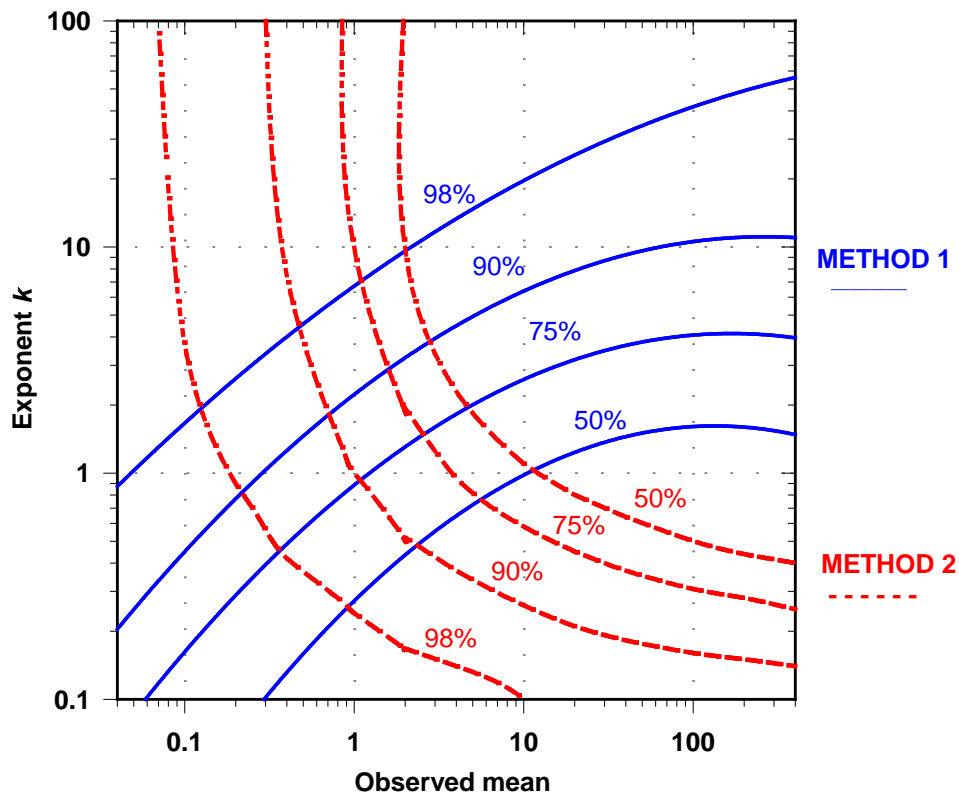
Figure 4.11 Relative efficiency of the two methods of estimating the negative binomial exponent k from field data. If you cannot use the maximum likelihood estimator (eq. 4.14), locate your sample on this graph using the observed mean and the approximate estimate of the exponent k from equation (4.11) and use the method with the highest relative efficiency. (After Anscombe 1950).

determine the best method to use (if the maximum likelihood estimator will not converge to a solution) as follows:

1. Estimate approximate k by Method 1 above (eq. 4.11).

2. Try to use the maximum-likelihood estimator (eq. 4.14) and if it will not work on your data continue on to (3).

3. Locate your sample on Figure 4.11, given the observed mean and this approximate estimate of k.

4. Estimate from the contour lines the relative efficiency for Methods 1 and 2.

5. Use the method with the higher efficiency to recalculate k to achieve a better estimate.

This figure may also be used to decide on the best statistical test for goodness-of-fit to the negative binomial (see below, page 168).

As an example, use the aphid data in Box 4.2 on page 000. With a mean of 3.46 and an approximate k of 3.07, from the graph (Fig. 4.11) read:

relative efficiency of Method 1 ~ 83%

relative efficiency of Method 2 ~ 50%

Thus, if we could not use the maximum-likelihood method for these data, we should prefer Method 1 for estimating k.

(b) frequency distribution irregular with some extreme counts: try to use the maximum likelihood method just described (equation 4.14). If it does not converge to a good estimate, use the approximate estimate for large samples (equation 4.11).

Elliott (1977, Chapter V) has an excellent discussion of these problems of estimating k and gives several examples of the calculations involved.

Box 4.2 illustrates the use of the maximum likelihood estimator for k. It is more tedious than difficult. Program QUADRAT (Appendix 2, page 000) does these calculations.

Tests for Goodness-of-Fit

There are three approaches to testing the null hypothesis that a observed counts do not depart from those predicted by a negative binomial distribution. Note that this is *not* equivalent to asking the more general question - is there evidence of clumping in the data? If the index of dispersion ($s^2/\overline{x}$) is > 1 (see page 155), there is a suggestion of

aggregation in your data. But remember there are many different types of aggregation (Fig. 4.8) and the negative binomial distribution will fit only *some* of these clumped patterns.

(1) *Chi-squared Goodness-of-Fit Test.* This is another application of the standard test:

$$\chi^2 = \sum \left[\frac{(\text{Observed frequency - expected frequency})^2}{\text{Expected frequency}} \right] \tag{4.15}$$

This test (or its replacement, the *G*-test) should be used whenever the observed data can be arranged in a frequency distribution (n > 20). It is not a particularly sensitive test and is prone to Type II errors when there are too few classes or when the number of quadrats counted is below 50.

The expected frequencies for a theoretical negative binomial can be calculated from the individual terms given previously. To illustrate, we will use the aphid data in Box 4.2 (page 000):

$$n = 50 \qquad\qquad \bar{x} = 3.46 \qquad\qquad \hat{k} = 2.65$$

$$\left\{ \begin{matrix} \text{Proportion of stems expected} \\ \text{to have zero aphids} \end{matrix} \right\} = \left(1 + \frac{\bar{x}}{\hat{k}} \right)^{-k}$$

$$= \left(1 + \frac{3.46}{2.65} \right)^{-2.65} = 0.1093$$

$$\left\{ \begin{matrix} \text{Proportion of stems expected} \\ \text{to have one aphid} \end{matrix} \right\} = \left(\frac{\hat{k}}{1} \right) \left(\frac{\bar{x}}{\bar{x} + \hat{k}} \right) \left(1 + \frac{\bar{x}}{\hat{k}} \right)^{-k}$$

$$= \left(\frac{2.65}{1} \right) \left(\frac{3.46}{3.46 + 2.65} \right) \left(1 + \frac{3.46}{2.65} \right)^{-2.65}$$

$$= 0.1640$$

$$\left\{ \begin{matrix} \text{Proportion of stems expected} \\ \text{to have two aphids} \end{matrix} \right\} = \left(\frac{\hat{k}}{1} \right) \left(\frac{k+1}{2} \right) \left(\frac{\bar{x}}{\bar{x} + \hat{k}} \right)^2 \left(1 + \frac{\bar{x}}{\hat{k}} \right)^{-k}$$

$$= \left(\frac{2.65}{1} \right) \left(\frac{2.65 + 1}{2} \right) \left(\frac{3.46}{3.46 + 2.65} \right)^2 \left(1 + \frac{3.46}{2.65} \right)^{-2.65}$$

$$= 0.1695$$

and similarly:

> proportion of stems expected with 3 aphids = 0.1488
>
> proportion of stems expected with 4 aphids = 0.1190
>
> proportion of stems expected with 5 aphids = 0.0896
>
> "   "   "   "   "6 aphids = 0.0647
>
> "   "   "   "   "7 aphids = 0.0453
>
> "   "   "   "   "8 aphids = 0.0309
>
> "   "   "   "   "9 aphids = 0.0207
>
> "   "   "   "   "10 or more aphids = 0.0382

We convert these proportions to frequencies by multiplying each by the sample size (n = 50 in this example). We obtain:

No. of aphids x	Observed no. of stems, f_x	Expected no. of stems from negative binomial
0	6	5.47
1	8	8.20
2	9	8.47
3	6	7.44
4	6	5.95
5	2	4.48
6	5	3.23
7	3	2.26
8	1	1.54
9	4	1.04
≥10	0	1.91

$$\chi^2 = \frac{(6-5.47)^2}{5.47} + \frac{(8-8.20)^2}{8.20} + \cdots + \frac{(0-1.91)^2}{1.91} = 13.51$$

Classes 7 and 8 and classes 9 and 10 could be lumped to keep the expected frequency from being too low, but I have not done so here. The number of degrees of freedom for this test are (number of frequency classes used - 3), since three statistics - n, $\bar{x}$, and $\hat{k}$ - have been used to fit the negative binomial to these data. Each frequency class used

should have an expected frequency above 1. For these data, d.f. = 8 and the critical value of chi-squared is:

$$\chi^2_{0.05} = 15.51$$

and since the observed χ^2 is less than this critical value, we accept the null hypothesis that the negative binomial distribution is an adequate description of the clumped pattern in these data.

Box 4.2   Maximum Likelihood Estimation of Negative Binomial k for Counts of the Black bean Aphid (*Aphis fabae*) on Bean Stems

Number of aphids on one stem, X	Number of stems (= quadrats), f_x	Proportion of stems, P_x
0	6	.12
1	8	.16
2	9	.18
3	6	.12
4	6	.12
5	2	.04
6	5	.10
7	3	.06
8	1	.02
9	4	.08
	n = 50	1.00

Calculate the usual statistical sums, means, and variances:

$$\sum X f_x = 173 \qquad \overline{x} = \frac{173}{50} = 3.4600$$

$$\sum X^2 f_x = 959 \qquad s^2 = 7.35551$$

$$\sum X^3 f_x = 6413$$

1. Calculate the approximate k estimate (equation 4.11):

$$\text{Approximate } \hat{k} = \frac{\overline{x}^2}{s^2 - \overline{x}} = \frac{3.46^2}{7.356 - 3.46} = 3.07$$

Since we have a large sample and the frequency distribution is smooth, we use the maximum likelihood estimator (equation 4.14) to obtain a more precise estimate of k

as follows.

2. Determine the A_x sums:

$$A_0 = f_1 + f_2 + f_3 + f_4 + f_5 + f_6 + f_7 + f_8 + f_9$$
$$= 8 + 9 + 6 + 6 + 2 + 5 + 3 + 1 + 4 = 44$$

$$A_1 = f_2 + f_3 + f_4 + \cdots + f_9 = 9 + 6 + 6 + 2 + 5 + 3 + 1 + 4 = 36$$

$$A_2 = f_3 + f_4 + \cdots + f_9 = 6 + 6 + 2 + 5 + 3 + 1 + 4 = 27$$

Similarly, $A_3 = 21$, $A_4 = 15$, $A_5 = 13$, $A_6 = 8$, $A_7 = 5$, $A_8 = 4$, and $A_9 = 0$

3. Calculate the two sides of the equality (equation 3.15):

$$(N)\log_e\left(1 + \frac{\overline{x}}{\hat{k}}\right) = \sum_{i=0}^{\infty}\left(\frac{A_x}{\hat{k} + x}\right)$$

$$(N)\log_e\left(1 + \frac{\overline{x}}{\hat{k}}\right) = (50)\left[\log_e\left(1 + \frac{3.46}{3.07}\right)\right] = 36.7091$$

$$\sum_{i=0}^{\infty}\left(\frac{A_x}{\hat{k} + x}\right) = \frac{A_0}{k+0} + \frac{A_1}{k+1} + \frac{A_2}{k+2} + \cdots + \frac{A_8}{k+8}$$

$$= \frac{44}{3.07} + \frac{36}{4.07} + \frac{27}{5.07} + \cdots + \frac{4}{11.07} = 37.406$$

Since $36.7091 \neq 37.406$ and the summation term is smaller, we reduce our provisional estimate of k to, say, 3.04 and start again at step (3).

$$(N)\log_e\left(1 + \frac{\overline{x}}{\hat{k}}\right) = (50)\left[\log_e\left(1 + \frac{3.46}{3.04}\right)\right] = 37.997$$

$$\sum_{i=0}^{\infty}\left(\frac{A_x}{\hat{k} + x}\right) = \frac{44}{3.04} + \frac{36}{4.04} + \frac{27}{5.04} + \cdots + \frac{4}{11.04} = 37.711$$

Since $37.997 \neq 37.711$ and the summation term is still smaller, we reduce our provisional estimate of k once again to, say, 3.02 and start again at step (3).

3b. We continue this trial-and-error procedure as follows:

$$\hat{k} = 3.02 \qquad 38.173 \neq 37.898$$
$$\hat{k} = 2.90 \qquad 39.266 \neq 39.063$$
$$\hat{k} = 2.80 \qquad 40.228 \neq 40.096$$
$$\hat{k} = 2.60 \qquad 42.310 \neq 42.354$$

We have now gone too far so we increase provisional $\hat{k}$ to $\hat{k} = 2.65$ and now obtain for the two sides of the equation:

$$41.768 = 41.764$$

which is accurate enough for $n = 50$ quadrats, and we accept 2.65 as the best estimate of the negative binomial exponent k for these data.

These calculations can be carried out in Program QUADRAT (Appendix 2, page 000).

U-Statistic Goodness-of-Fit Test:

This test compares the observed and expected variances of the negative binomial distribution (Evans 1953) and has more statistical power than the chi-squared goodness-of-fit test just described.

$$U = \text{observed variance - expected variance}$$

$$= s^2 - \left(\overline{x} + \frac{\overline{x}^2}{k} \right) \tag{4.16}$$

The expected value of U is zero. To test if the observed value of U is different from zero, calculate the standard error of U as follows:

$$a = \overline{x} \Big/ \hat{k}$$

$$b = 1 + a$$

$$c = \frac{ba^4}{\left[b(\log_e b) - a \right]^2} \left[b^{(1 + \overline{x}/a)} - \left(\overline{x} + b \right) \right]$$

then:

$$\text{S.E.}(\hat{U}) = \sqrt{ \frac{1}{n} \left\{ 2\overline{x}(\overline{x} + a)(b) \left[\frac{(b^2)(\log_e b) - a(1 + 2a)}{(b)(\log_e b) - a} \right] + c \right\} } \tag{4.17}$$

If the observed value of U exceeds 2 standard errors of U then the null hypothesis is rejected that the negative binomial is an adequate fit to the observed data (at $\alpha = 0.05$). Note that this is true only for large samples and only approximately correct for small samples.

For the bean aphid data in Box 4.2 (page 000) we obtain:

$$U = s^2 - \left(\bar{x} + \frac{\bar{x}^2}{k} \right)$$

$$= 7.356 - \left(3.46 + \frac{3.46^2}{2.65} \right) = -0.622$$

The standard error of U is estimated as:

$$a = \bar{x}\big/\hat{k} = \frac{3.46}{2.65} = 1.306$$

$$b = 1 + a = 2.306$$

$$c = \frac{ba^4}{\left[b(\log_e b) - a \right]^2} \left[b^{(1+\bar{x}/a)} - (\bar{x}+b) \right] = \frac{2.306(1.306^4)}{\left[2.306(\log_e 2.306) - 1.306 \right]} \left[(2.306^{3.65}) - 5.765 \right]$$

$$= 266.8957$$

$$\text{S.E.}(\hat{U}) = \sqrt{\frac{1}{50} \left\{ 2(3.46)(4.76)(2.306) \left[\frac{(2.306^2)(\log_e 2.306) - 1.306(3.611)}{(2.306)(\log_e 2.306) - 1.306} \right] + 266.8957 \right\}}$$

$$= 2.16$$

Since the observed value of U (-0.62) is much less then twice its standard error (4.32), we accept the null hypothesis that the negative binomial fits these data.

T-Statistic Goodness-of-Fit Test:

This test compares the observed and expected third moments of the negative binomial distribution. The third moment is a measure of skewness of a distribution.

$$T = \text{observed measure of skewness - expected measure of skewness}$$

$$T = \left(\frac{\sum f x^3 - 3\bar{x} \sum f x^2 + 2\bar{x}^2 \sum f x}{n} \right) - \hat{s}^2 \left(\frac{2\,\hat{s}^2}{\bar{x}} - 1 \right) \tag{4.18}$$

The expected value of T is zero. To determine whether the observed data deviate significantly from the amount of skewness expected, calculate the standard error of T as follows. As above,

$$a = \frac{\bar{x}}{k}$$

then:

$$\text{S.E.}(\hat{T}) = \sqrt{\frac{2\bar{x}(\bar{x}+a)(1+a)^2\left[2a(3+5a)+3\bar{x}(1+a)\right]}{n}} \tag{4.19}$$

If the observed value of T exceeds 2 standard errors of T, then the null hypothesis is rejected at the 5% level. Note that a large positive value of T indicates that the observed data are more skewed than predicted by the negative binomial distribution. A large negative value of T indicates less skewness than predicted by the negative binomial. The estimate for the standard error of T is the large-sample estimate, and you should treat it as only approximate for small samples.

For the bean aphid data in Box 4.2 (page 166) we obtain:

$$T = \left(\frac{\sum f x^3 - 3\bar{x}\sum f x^2 + 2\bar{x}^2\sum f x}{n}\right) - \hat{s}^2\left(\frac{2\,\hat{s}^2}{\bar{x}} - 1\right)$$

$$= \left(\frac{6413 - (3)(3.46)(959) + (2)(3.46^2)(173)}{50}\right) - 7.356\left(\frac{14.712}{3.46} - 1\right)$$

$$= -11.91$$

$$\text{S.E.}(\hat{T}) = \sqrt{\frac{2\bar{x}(\bar{x}+a)(1+a)^2\left[2a(3+5a)+3\bar{x}(1+a)\right]}{n}}$$

$$a = \frac{\bar{x}}{k} = \frac{3.46}{2.65} = 1.306$$

$$\text{S.E.}(\hat{T}) = \sqrt{\frac{2(3.46)(3.46+1.306)(2.306)^2\left[2(1.306)(3+6.528)+3(3.46)(2.306)\right]}{50}}$$

$$= 13.09$$

Since the observed value of T is less than twice its standard error, we accept the null hypothesis that the negative binomial fits the data.

Anscombe (1950) has shown that the U-test and the T-test are most efficient when used with different combinations of $\bar{x}$ and k. He recommends proceeding as follows:

1. Refer to Figure 4.11 (page 162) and determine for your sample whether Method 1 or Method 2 is more efficient for estimating k.

2. If Method 1 is more efficient, use the *T*-test as the best way of assessing goodness-of-fit of the negative binomial.

3. If Method 2 is more efficient, use the *U*-test.

Both the *T*- and the *U*-test are more precise than the chi-square test in detecting departures from the theoretical negative binomial distribution, especially with small samples ($n < 50$).

The calculations for the *T*- and *U*-tests can be carried out by Program QUADRAT (Appendix 2, page 000) for data which have already been fitted to a negative binomial distribution.

Confidence Limits for the Mean – Negative Binomial Distribution

Given that you have data which are adequately described by the negative binomial, how can you get confidence limits for the observed mean? This is one of the key problems that we began with — estimating confidence limits for abundance when the underlying spatial pattern is clumped. Confidence limits for means from a negative binomial distribution are not easy to obtain. The original data counts must be transformed in one of the following ways (Elliott 1977):

(a**) If *n* > 30** (large sample size) use the normal approximation with the square root of the variance (eq. 4.10) and the standard *t*-table value.

(a**) If *n* < 30** (small sample size) use one of the following two methods:

(1) *if k is less than 5*: Use the logarithmic transform by replacing each observed count *x* by

$$\log\left(x + \frac{k}{2}\right) \tag{4.20}$$

 (2) *if k is greater than 5*: Use the inverse hyperbolic sine transform by replacing each observed count *x* by

$$\sinh^{-1}\sqrt{\frac{x + 0.375}{k - 0.75}} \tag{4.21}$$

where $\sinh^{-1}$ = the inverse of the hyperbolic sine approximated by

$$\sinh^{-1}(x) = \log_e\left(x + \sqrt{(x^2+1)}\right)$$

x = observed count
k = negative binomial exponent

The inverse of the hyperbolic sine can be calculated easily with most pocket calculators. It is also tabulated in many books of statistical tables. Once you have replaced each observed value by its transformed value indicated above, calculate the mean of the transformed counts, and proceed to calculate confidence intervals in the following way:

Let y = the mean of transformed values as determined from equations (4.20) or (4.21).

(1) if you used the *logarithmic transform* from equation (4.20): confidence limits are:

$$y \pm t_\alpha \sqrt{\frac{0.1886\ \text{trigamma}(k)}{n}} \tag{4.22}$$

where t_α = Student's t value for (n-1) degrees of freedom for the appropriate α

value

Trigamma(k) = a mathematical derivative of the gamma function

$$\approx \frac{1}{k} + \frac{1}{2k^2} + \frac{1}{6k^3} - \frac{1}{30k^5} + \frac{1}{42k^7} - \frac{1}{30k^9}$$

n = sample size = number of quadrats counted

(2) if you used the *inverse hyperbolic sine transform* from equation (4.21): confidence limits are

$$y \pm t_\alpha \sqrt{\frac{0.25\ \text{trigamma}(k)}{n}} \tag{4.23}$$

where all symbols are described above.

These confidence limits must be transformed back to the original scale of counts by reversing the original transformation (log-antilog, inverse hyperbolic sine-hyperbolic sine). Elliott (1977) gives an example of these calculations, which are also provided in Program QUADRAT (Appendix 2, page 000).

An alternative strategy for estimating confidence limits for a negative binomial distribution is to use a generalized transformation like the Box-Cox transform (Chapter 15, page 000) to normalize the data and then to use conventional confidence limits

based on the *t*-distribution. Unfortunately this strategy will not always work well with small samples and with highly skewed data with many zero counts.

There are many other statistical frequency distributions that have been used to describe quadrat counts of plants and animals (Moore and Chapman 1986, Dale 1999, Legendre et al. 2002). You should refer to the more specialized literature if you need to consider other frequency distributions because you have clumped patterns that do not fit the negative binomial, or consult a professional statistician. Johnson and Kotz (1969) give a good general summary of many discrete frequency distributions. For much ecological data the Poisson and the negative binomial distributions are adequate descriptors.

Much of the early literature on the statistical analysis of quadrat counts was infused with the belief that general laws might be derived from count data, and that one might infer biological mechanisms of pattern formation by fitting different statistical frequency distributions. But it was quickly realized that this could not be done, and that these statistical distributions are only approximate descriptions and tell us little about the biological processes generating the observed spatial patterns. But if we cannot infer ecology from statistics, the adequate description of the statistical distribution of quadrat counts is still most important to an ecologist because it dictates sampling strategies, as we shall see in Chapters 7 and 8, and allows for valid tests of hypotheses about abundance data gathered from quadrat counts.

4.3 LINE INTERCEPT METHOD

Plant ecologists have for many years been interested in measuring the cover of plants in a community using line transects. This is a general procedure that can be applied to estimating the cover of tree or shrub canopies, the area covered by lakes within a geographical region, or the area covered by squirrel burrows. To estimate cover is relatively simple. Figure 4.12 illustrates the line intercept method and the measurements that need to be taken

Estimates of abundance or density of plants can also be derived from line intercept data (Eberhardt 1978). To set out line intercept transects, you need to establish a baseline of length *W* along which you randomly locate individual transects. For each

plant or sample unit intercepted, measure the longest perpendicular width w. This width determines the probability that any individual plant will be bisected by the sampling line, as you can see from Figure 4.12. Eberhardt (1978) shows that the appropriate estimate of population size is:

$$\hat{N} = \left[\frac{W}{n}\right] \sum_{i=1}^{k}\left(\frac{1}{w_i}\right) \tag{4.24}$$

where $\hat{N}$ = Estimate of population size

W = Width of the base line from which the transects begin

w_i = Perpendicular width of plants intersected

n = Number of transect lines sampled

k = Total number of plants intercepted on all lines (i = 1, 2, 3, …k)
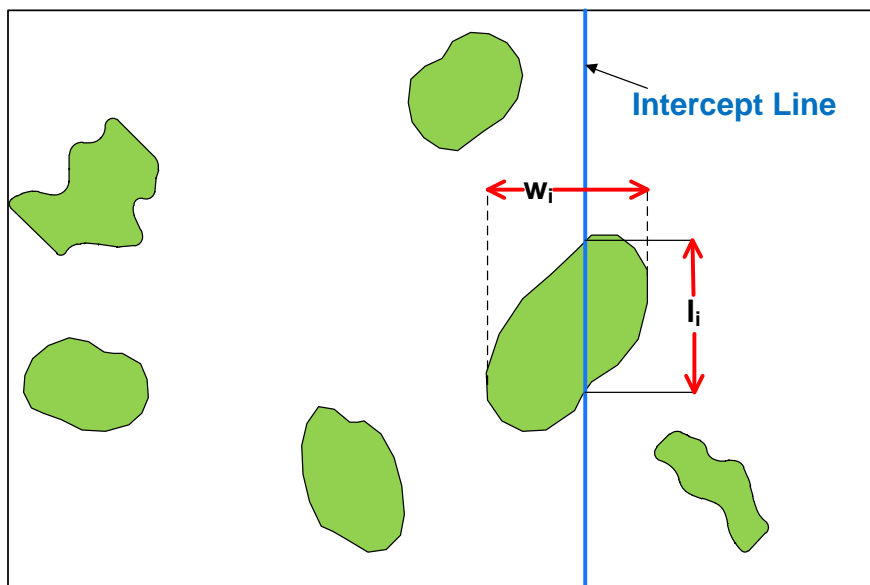
Figure 4.12 Schematic illustration of the line intercept method as used for density estimation of shrubs and trees. The shaded areas represent the canopy coverage of a shrub. The measurements l_i are for cover estimates (fraction of the line covered by the canopy of this particular species), and the intercept distances w_i are the maximum perpendicular distance coverage and are used to estimate numbers and density of the plants.

To estimate the density of organisms, for any shape of area, simply divide this estimate of numbers by the area being studied. If the area being studied has not been measured, density can be estimated from randomly oriented transects by the equation:

$$\hat{D} = \left[\frac{1}{L}\right] \sum_{i=1}^{k} \left(\frac{1}{w_i}\right) \tag{4.25}$$

where $\hat{D}$ = Estimate of population density

   L = Length of all lines combined

   w_i = Perpendicular width of plants intersected

k = Total number of plants intercepted on all lines (i = 1, 2, 3, …k)

If a series of line intercepts are measured, each one can be used to generate an estimate of population size and thus an estimate of variability in order to obtain confidence limits in the usual way. But if the line intercept lengths vary, it is necessary to obtain the standard error of the mean density estimate from Eberhardt (1978) as follows:

$$s_{\hat{D}} = \hat{D} \sqrt{\frac{\left(\frac{s_{\hat{y}}}{\bar{y}}\right)^2 + \left(\frac{s_L}{\bar{L}}\right)^2 - 2\left(C_{yL}\right)}{(n-1)}} \tag{4.26}$$

where $s_{\hat{D}}$ = Standard error of the mean density estimate

   $s_{\hat{y}}$ = Standard deviation of the observed $y_i = \sum \frac{1}{w_i}$ for each line

   $\bar{y}$ = Observed mean value of $y_i = \sum \frac{1}{w_i}$ for each line

   s_L = Standard deviation of the observed lengths of each line

   $\bar{L}$ = Observed mean value of the lengths of each line

$$C_{yL} = \frac{\sum(y_i - \bar{y})(L_j - \bar{L})}{(n-1)\bar{y}\bar{L}} \tag{4.27}$$

   n = Number of lines in sample

Box 4.3 illustrates the use of the line intercept method to estimate the density of willow shrubs.

Box 4.3   Line Intercept Method of Density Estimation for Willow Shrubs.

Three lines were laid out at random along a 125 m baseline to estimate the willow density on an irregular area bordering a stream. The study area was 6.3 ha. The following data were recorded for the intercept distances (w_i):

Line 1 (438 m): 1.3, 3.1, 0.8, 2.2, 0.4, 1.7, 0.2, 1.5, 1.9, 0.4, 0.1m (n = 11)

Line 2 (682 m): 1.1, 0.1, 1.8, 2.7, 2.4, 0.7, 0.4, 0.3, 1.4, 0.1, 2.1, 2.3m (n = 12)

Line 3 (511 m): 0.3, 1.7, 2.1, 0.2, 0.2, 0.4, 1.1, 0.3m (n = 8)

Line 4 (387 m): 3.3, 3.0, 1.4, 0.2, 1.7, 1.1, 0.2, 1.9, 0.9m (n = 9)

Begin by calculating the sum of the reciprocals: for Line 1-

$$y_i = \sum \frac{1}{w_i} = \frac{1}{1.3} + \frac{1}{3.1} + \frac{1}{0.8} + \cdots + \frac{1}{0.1} = 24.577$$

An estimate of population size can be obtained for each line from equation (4.23). For line 1:

$$\hat{N} = \left[\frac{W}{n}\right] \sum_{i=1}^{k} \left(\frac{1}{w_i}\right) = \left[\frac{125}{1}\right] (24.577) = 3072 \text{ shrubs}$$

Repeating these calculations for each of the four lines gives these results:

	Line 1	Line 2	Line 3	Line 4	Totals
$y_i = \sum \dfrac{1}{w_i}$	24.577	31.139	21.140	14.485	91.342
$\hat{N}$	3072	3892	2642	1811	2854
$\hat{D}$	488	618	419	287	453

Since we know the area is 6.3 ha, the density estimates ($\hat{D}$) for each line are obtained by dividing the population size by this area, and the results are given in the above table as number of willows per hectare.

Combined population size and density estimates for all the four lines can be obtained from these equations applied to all the data or simply by averaging the results of each of the individual lines.

To calculate confidence limits for the overall density of willows on the study area we use equation (4.26) to calculate the standard error of the density estimate:

$$s_{\hat{D}} = \hat{D} \sqrt{\frac{\left(s_{\hat{y}}/\overline{y}\right)^2 + \left(s_L/L\right)^2 - 2\left(C_{yL}\right)}{(n-1)}}$$

From the usual statistical formulas and the data in the table above we can calculate:

$$\overline{y} = \text{Observed mean value of } y_i = \sum \frac{1}{w_i} = 22.8355$$

$s_{\hat{y}} = $ standard deviation of the y_i values

$$= \sqrt{\frac{\sum(y_i - \bar{y})^2}{n-1}} = \sqrt{\frac{(24.577 - 22.835)^2 + \cdots}{4-1}} = 6.942$$

$\bar{L}$ = Observed mean value of the lengths of each line = 504.5

$s_L = $ standard deviation of the lengths of the lines

$$= \sqrt{\frac{\sum(L_i - \bar{L})^2}{n-1}} = \sqrt{\frac{(438 - 504.5)^2 + \cdots}{4-1}} = 128.82$$

We need to determine the sum of cross-products C_{yL} from equation (4.27):

$$C_{yL} = \frac{\sum(y_i - \bar{y})(L_j - \bar{L})}{(n-1)\bar{y}\bar{L}} = \frac{\left[(24.577 - 22.835)(438 - 504.5)\right] + \cdots}{(4-1)(22.835)(504.5)}$$

$$= \frac{2328.113}{34560.77} = 0.06736$$

Substituting these values in equation (4.26) we obtain:

$$s_{\hat{D}} = \hat{D}\sqrt{\frac{\left(\frac{s_{\hat{y}}}{\bar{y}}\right)^2 + \left(\frac{s_L}{\bar{L}}\right)^2 - 2(C_{yL})}{(n-1)}}$$

$$= 453.085\sqrt{\frac{\left(\frac{6.942}{22.835}\right)^2 + \left(\frac{128.81}{504.5}\right)^2 - 2(0.067)}{(4-1)}}$$

$$= 39.59$$

Calculate the 95% confidence limits in the usual way: from the *t*-table with 3 degrees of freedom, $t_\alpha = 3.182$ and we obtain

$$\hat{D} \pm t_\alpha s_{\hat{D}}$$

$$453 \pm 3.182(39.59)$$

or 327 to 579 willows per hectare for this area. Because of the small sample size in this example, the confidence limits are quite wide
.

4.4 AERIAL SURVEYS OF WILDLIFE POPULATIONS

Many wildlife surveys are carried out by aerial census, a specialized form of quadrat

sampling. Aerial surveying is discussed in detail in Caughley (1977), Fleming and

Tracey (2008), and Hone (2008). It has been used very extensively in the management

of large mammals and birds (e.g. Steinhorst and Samuel 1989; Udevitz et al. 2006, Rice

et al. 2009). I will discuss here the statistical problems that this form of quadrat sampling entails all associated with the problem of sightability or detectability (Williams et al. 2008). This discussion will be equally applicable to ground surveys or vehicle surveys, and will lead us into a discussion of line transect sampling in the next chapter.

Most research programs being done on large animals require three types of information:

- 1. Total numbers
- 2. Size and structure of populations (age ratios, sex ratios)
- 3 Distribution and movements.

The first important point to remember in designing a census is *decide in advance exactly what the objectives of the census are*. Many research workers come to grief trying to get all possible data in one census. It may be necessary to do 2 or even 3 censuses to achieve all your objectives.

Many factors will influence the way in which a census is done:

- *resources*: aircraft, vehicles, manpower, quality of crew
- *size of area*: small or very large
- *nature of the vegetation*: open plains, thick brush
- *nature of the country*: flat, mountainous, no roads
- species concerned

Norton-Griffiths (1978) discusses these factors in detail.

An aerial census can be done either as a *total count* or as a *sample count*. Total counts are expensive and rely on the assumption that no animals are counted twice and that no animals are missed. These assumptions are difficult to evaluate in any real situation and so total counts are often of dubious reliability.

Because of money alone most wildlife surveys are done as sample counts. Efforts have been directed along three lines in aerial sampling:

1. Raise the *precision* of the estimates by good survey design, high sampling intensity, and use of stratified sampling techniques (see Chapter 8).

2. Correct the estimates for *bias*; try to remove sources of inaccuracy in the sampling program.

3. Use aerial census as a measure of *relative density*, recognizing that it is biased and that the bias cannot be removed or estimated, but only held constant.

In any census in which an observer counts animals there are two sources of error. First, an observer may undercount on some occasions and overcount on others. Any one observation may be inaccurate but on the average the errors will cancel out. This is called *counting error*. Counting error increases with counting rate - this is very important. *Counting becomes less precise the faster you have to count.* Second, most biologists tend to undercount, and this is called *counting bias*. The direction of this error is consistent, but unfortunately this undercounting is not a constant bias because it usually gets worse the more animals there are to count and the faster they have to be counted. This can be complicated by the difficulties of spotting animals in thick brush. In addition this bias may vary among observers.

Counting bias can be measured only on populations of known size that are censused by aerial survey (Hone 2008). This has been done several times. LeResche and Rausch (1974) tried total counts on moose (*Alces alces*) populations enclosed in 1 sq. mile fenced areas located in a 25 year-old burn in Alaska. They knew from ground counts exactly how many moose were present in each enclosure. They used 49 observers, and allowed each to fly 15 minutes over each square mile enclosure. The pilot was always the same and he did not sight animals for the counting. Two variables were categorized - snow conditions (poor, good, excellent) and the experience level of the observer. They got the results given in Table 4.4.

TABLE 4.4   Counting Bias in Aerial Surveys of Moose[a]

Observer's experience	Observer's history	Snow conditions	Proportion of total moose seen
Inexperienced	None	Excellent	0.43
Inexperienced	None	Good	0.44
Inexperienced	None	Poor	0.19
Experienced	Not current		0.46
Experienced	Current	Excellent	0.68

Experienced	Current	Good	0.61
Experienced	Current	Poor	0.40
Experienced with pilot counting	Current	Excellent	0.70

[a] Total counts were made of moose (*Alces alces*) in 2.6 sq. km fenced areas in Alaska. The number of moose in each enclosure was known. Even the best observers saw only about 70% of the animals.

[b] *Current* means having been involved in an active counting program within the previous few weeks.

Source: LeResche and Rausch (1974).

Three experienced individuals were tested several times and on replicate counts the 95% confidence limits were from ± 10% to ± 18% of their means (and the means are only 71% of the true population value). LeResche and Rausch (1974) concluded that aerial counts were not valid estimates of absolute moose numbers because of the large counting bias. Caughley (1974) listed 17 analyses of the accuracy of aerial censusing for large mammals, and the percent counted of the known population ranged from 23% to 89%. Rice et al. (2009) found that 77-79% of mountain goat groups were located in aerial surveys. Undercounting is thus the rule in aerial census and the assumption that aerial counts (even by helicopter) count the entire population must be abandoned. .

Undercounting bias results from two different factors (Marsh and Sinclair 1989). *Availability* bias results from animals being concealed when the counting is being done. For example, a moose may be under a tree and not be visible, or a whale may be diving and not near the surface. *Perception* bias results from observers missing animals that are in view.

Several studies have used aerial census to estimate populations of large mammals that are of known size (e.g. Hone 1988 – feral pig carcasses, White et al. 1989 – mule deer, Tracey et al. 2008 – feral goats), and others have used ground- and air-based methods for comparisons of population estimates (e.g. Choquenot et al. (2008) – Himalayan thar). In general the estimates of population size derived are negatively biased (too low) but in some cases a positive bias (too high) does occur (Tracey et al. 2008). Careful work is needed to increase the accuracy of aerial counts.

Let us consider how we might correct for counting bias in an aerial survey of a closed population.

4.4.1 Correcting for Bias in Aerial Surveys

Four approaches have been used. The simplest approach is to photograph groups of animals as they are counted visually and get the bias directly:

$$\text{Counting bias} = \frac{\text{Number visually counted}}{\text{Number actually present on photographs}} \qquad (4.28)$$

In actual field work two complications may intervene. First we may decide not to photograph groups smaller than, say, 10 because the counting bias is negligible in that range. Second, we may miss taking some photographs and this complicates the bias correction.

We can define:

$\sum X_1$ = no. animals in small groups (<10) not photographed

$\sum X_2$ = no. of animals in large groups which missed getting photographed

$\sum X_3$ = no. of animals counted *visually* (field count) and photographed

$\sum X_4$ = no. of animals in the X_3 groups that are counted *photographically* (photograph count)

Y = total no. of animals on the transect, corrected for counting bias

If all animals are photographed in the larger groups, then:

$$Y = \sum X_1 + \sum X_4 \qquad (4.29)$$

If some animals cannot be photographed, we correct these counts by the observed bias in the other counts, and hence

$$Y = \sum X_1 + \frac{\sum X_2}{B} + \sum X_4 \qquad (4.30)$$

where B = counting bias = $\sum X_3 \Big/ \sum X_4$

This analysis presumes that the photographs provide a count without error. This is an important assumption and needs to be checked. Harris and Lloyd (1977) showed that photographic counts of seabird colonies could also vary greatly among observers (Table 4.5) and undercounting was the rule. Even experienced counters varied ±10% in their repeated counts of birds in photographs. This problem could be alleviated by automatic,

computer-based counting programs (Descamps et al. 2011). But photo quality is an important factor in producing good count data.

TABLE 4.5 Counts of Nests of Gannets (*Sula bassana*) from an Aerial Photograph of Grasshold, Dyfed, Wales

Observer	Number of counts	Mean count	Range	Standard error
A[b]	10	3222	3077-3323	28
B[b]	8	3051	2852-3192	38
C	3	2949	2823-3014	63
D[b]	3	3359	3358-3362	13
E[b]	3	3301	3274-3315	14
F	2	3173	3138-3209	
G[b]	1	3092		
H	1	3324		
I	1	3228		
J[b]	1	3000		

[a] The mean count of all observers was 3170 nests.
[b] Observers with previous experience in counting seabirds from photographs.

Source: Harris and Lloyd, 1977.

A variant of this approach is to use complete ground counts as a form of double sampling for at least part of the study zone (Jolly 1969). The ground count is assumed to be precise, and this is probably correct only for highly visible species in open habitats. For most species ground counts cannot be complete and one must rely on other methods for bias correction.

A second approach to bias correction in aerial survey is to use double counts by ground and air observers (Pollock and Kendall 1987). If individual animals can be recognized, the ground count does not need to be complete. One can use a variant of the Petersen method (page 22) in which M individuals are seen on the ground survey, and C individuals are seen in the second (aerial) survey, of which R individuals are recaptures in the sense of being seen from both ground and air observers. Clearly this approach demands individual recognition which may not be possible for many species. It has been used successfully for bald eagle nests by Grier (1982), and for emus in

Australia by Caughley and Grice (1982). Double counting can also be used by having two separate observers on either side of the airplane or helicopter (Tracey et al. 2008).

A third approach to bias correction is to mark and release a subset of animals in the study area. The proportion of the tagged animals seen from the air is then used to correct the aerial counts. One variant of this approach is to use radio-collared animals as marked animals. Bear *et al.* (1989) used colored tags to evaluate this method for an elk population. Packard *et al.* (1985) used radio-marked manatees to estimate the visibility bias for aerial censuses of this aquatic mammal, and found that there was high variability in the estimated bias. One must assume that the visibility bias is the same for the radio-tagged animals as it is for the population at large to use this approach.

A fourth approach to avoid bias in aerial counts is to use the line transect method described in the next chapter (page 000). This approach assumes that all the individuals along the flight line are counted without error. With the use of helicopters for counting this assumption would be more likely to be correct. White *et al.* (1989) evaluated line transect methodology for mule deer populations using a helicopter survey and found that population estimates were negatively biased, possibly because of a failure to see all deer along the flight lines. The details of the line transect approach are given in Chapter 5.

A critical factor in all aerial census is whether or not animals are seen. *Sightability* is the probability that an animal within the field of search will be seen by an observer. Sightability is related to many variables, but Caughley (1974) suggested that three are most important:

- *Transect width*: as strip width is increased, the mean distance between an animal and its observer is increased and the time available to locate an animal decreases. The human eye has to move more to cover the strip, and more animals may be hidden by the vegetation.

- *Altitude*: as altitude is increased, the mean distance between the observer and the animal increases, and this might be expected to increase the counting bias; but on the positive side, the required eye movements decrease and the amount of obscuring vegetation decreases because vision is more vertical.

- *Speed*: as speed is increased, the time available to locate and count an animal decreases, and the rate of eye movement must increase.

Transect width is probably the most complex factor influencing the chances of counting an animal. As transect width changes, sightability changes but not in a simple way. There is a growing list of factors that affect sightability. Caughley *et al.* (1976) examined the effects of 7 factors on aerial counts of kangaroos and sheep in Australia:

Speed
Altitude above ground
Transect width   } Significant effects
Observer

Time of day
Fatigue of observers } Unimportant effects
Length of survey

This list is clearly not exhaustive. Bayliss and Giles (1985) showed that ambient temperature affected kangaroo counts very strongly, and Broome (1985) showed that different bird species did not react the same to aerial counts. Gasaway *et al.* (1986) showed that moose in Alaska were more visible in May than in June. All these results show clearly that there will be no one universal method for correcting biases in visibility from aerial counts. In some cases the biases may remain of unknown magnitude and aerial counts should then *not* be used as absolute population estimates but only as an index of population size.

The general principles of determining optimal quadrat size and shape can also be applied to aerial censusing. In practice the best procedure is to try to check for counting bias using one of the four methods just described (Seber 1992) to see if bias is significant in your particular sampling problem. Then it is important to standardize speed, altitude, transect width, time of day, and any other variables that affect your counts.

4.4.2 Sampling in Aerial Surveys

We define a *census zone* as the whole area in which the number of animals is to be estimated. The sample zone is that part of the census zone which is searched and counted. Many of the problems that have to be overcome in sampling wildlife populations stem from the simple fact that animals are not distributed evenly within the

census zone. In most cases a clumped distribution occurs and unless we take account of this fact we cannot census very accurately.

We can sample the census zone in one of two basic ways - simple random sampling or stratified random sampling. We will discuss *sampling methods* in detail in Chapter 8 and I give here only a capsular summary of the methods as applied in aerial surveys. The census zone is divided into a number of discrete units known as *sample units* (equal or unequal size), and a number of these are chosen to sample. Figure 4.13 illustrates several ways the sample units may be arranged geographically.

There are 3 basic types of aerial surveys.

Aerial transect sampling This is the most common type of sampling. The aircraft flies in a straight line from one side of the census zone to the other at a fixed height above the ground. Streamers are attached to the wing struts of the plane so that the observer sees a strip demarcated on the ground. The width of the strip is decided in advance, and the observer counts all the animals within the streamers.

Sample units are located by drawing a base line on a map of the census zone (see Figure 4.13). The base line is divided like a ruler into pieces the width of the transect strip. The numbers of transects to be sampled are located by a random number table (once *n* has been set), and transects are run at right angles to the base line.

The transects can all be of different lengths if necessary and may be split if the census zone has a very irregular shape.
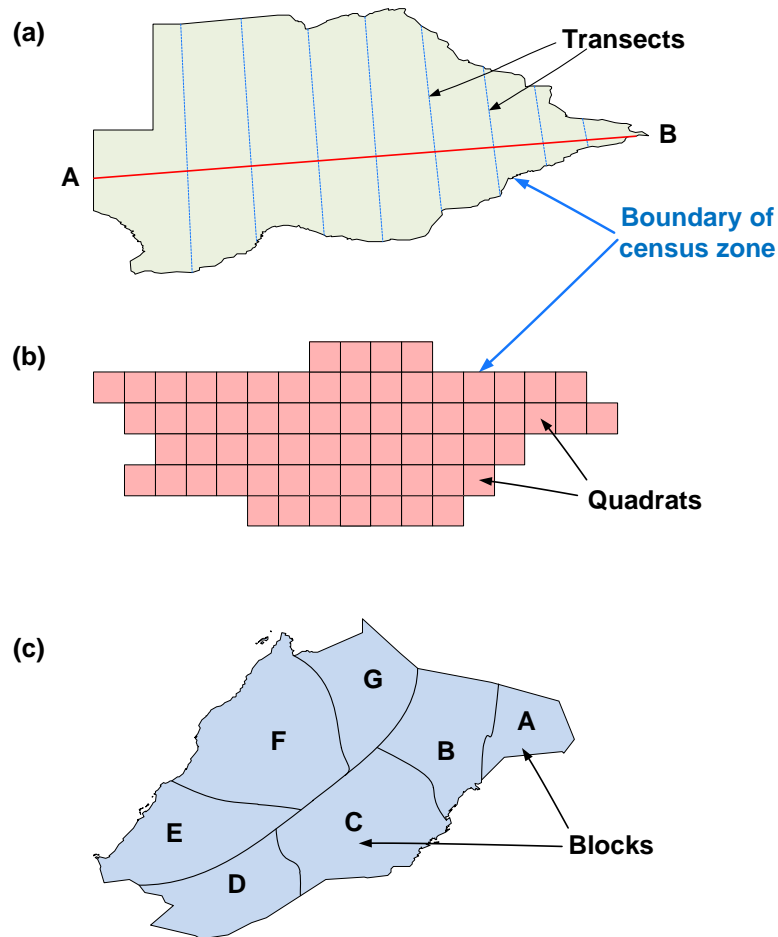
Figure 4.13 Three possible types of sampling frames in aerial census. (a) Unequal length *transects* across a census zone, laid at right angles to the baseline A-B. (b) Equal size *quadrats* covering the whole census zone. (c) Unequal size *blocks* delimited by topographic features like rivers.

Aerial quadrat sampling The sample units are square or rectangular quadrats located at random within the census zone. The whole census zone can be set up as a checkerboard, and the quadrats to be searched can be determined by random numbers. The aircraft can spend as long as necessary searching each quadrat.

Aerial block sampling Block sampling is similar to quadrat sampling except that the sample units are blocks of land demarcated by physical features, such as rivers. A sample of blocks to count can be chosen by locating random points in space and then counting the blocks in which a random point falls.

These three methods of sampling differ greatly in their practical application. Norton-Griffiths (1978) summarizes these problems as follows:

Costs: transects have the advantage because aircraft operate most efficiently flying in a straight line, and the proportion of "dead time" is minimal.

Navigation: easier with transects because the aircraft just needs to fly in a straight line.

Boundary effects: all methods suffer from boundary effects in having to decide whether or not a particular animal is inside or outside the sample unit. In transect sampling the observers count between the streamers and the pilot must maintain strict height control and strict bank control. Boundary effects are difficult to judge in quadrat sampling because there is no physical mark to judge the edge of the sample quadrat. Block counting is best from this point of view because the boundaries are natural.

Counting: in transect counting the observer usually has only one chance to see and count the animals in the transect. In block or quadrat counting the aircraft can make as many passes as is required to count all the animals. The transect method is impossible to use when the ground is very broken and there are many gullies and outcrops. It is also useless in thick vegetation, and useless in mountainous country. This severely limits its use in certain parts of the world.

Sample error: Long-thin transects usually reduce the variance of counts whenever a clumped distribution is being sampled, as discussed previously, and quadrat-shape arguments thus favor transect sampling.

Fatigue: Flying in a straight line is much less tiring than criss-crossing and making steep turns.

The net result of this analysis is that, of the three possible methods, transect sampling is usually best when it can be applied.

The principles of sampling which we discussed with reference to the Poisson and negative binomial distributions are applicable to aerial census problems. Three rules of thumb may be used:

- **1.** A sample of transects will usually have a lower variance than a sample of quadrats or blocks, when sample size is held constant.

- **2.** Transects should be oriented across the shorter dimension of a census zone, and should run at right angles to the major drainage systems.

- **3.** When block counting choose small blocks over large blocks, as long as the edge effect is negligible. Avoid very large blocks.

   Three general methods of estimation can be used for aerial surveys for closed populations, as described by Jolly (1969). They are divided in the first instance by whether the sampling units are of equal size or not.

Method 1 - Equal Size Sample Units:

A sample of n quadrats is drawn at random from the N quadrats comprising the total sample area. The quadrats are then counted and the number of animals in each is recorded. By the usual formulae:

$$\text{Mean no. of animals per quadrat} = \overline{x} = \frac{\sum x}{n}$$

$$\text{Variance of } x = \hat{s}^2 = \frac{\sum x^2 - \left(\sum x\right)^2 \big/ n}{n - 1}$$

$$\text{Standard error of } \overline{x} = \text{S.E.}(\overline{x}) = \sqrt{\frac{s^2}{n}}$$

These estimates are then converted to total population size for the whole census zone:

$$\text{Total numbers} = \hat{X} = N\overline{x} \tag{4.31}$$

where N is the total number of possible quadrats in the sample area.

   The variance of this estimate of total numbers depends on the type of sampling used:

   Sampling with replacement: Each quadrat has the possibility of being selected more than once. Of course the aerial count would be done only once, but the sample could be included 2, 3 or more times in the statistical calculations. For sampling *with replacement* -

$$\text{Variance of total numbers} = \left(Ns_{\overline{x}}\right)^2 = \frac{N^2}{n}s^2$$

$$\text{Standard error of total numbers} = \sqrt{\text{variance of total numbers}} \tag{4.32}$$

$$\text{95\% confidence limits for total numbers} = \hat{X} \pm t_{.025}\left(\begin{array}{c}\text{standard error}\\\text{of total numbers}\end{array}\right)$$

where $t_{.025}$ is Student's t-value for $(n - 1)$ degrees of freedom.

Norton-Griffiths (1978) works out an example of these calculations in detail.

   Sampling without replacement: Each quadrat is struck off a list as it is selected in the random sample, so it can appear only once in the statistical calculations. In this case the variance formula above overestimates the true variance and must be corrected as follows: for sampling *without replacement* -

$$\text{Variance of total numbers} = \left(Ns_{\bar{x}}\right)^2 = \frac{N^2}{n}s^2\left(1 - \frac{n}{N}\right) \tag{4.33}$$

where $\left(1 - \dfrac{n}{N}\right)$ = Finite population correction (see Chapter 8)

The standard error and the confidence limits are calculated as above.

   This method was first used on aerial surveys by Siniff and Skoog (1964) on caribou (*Rangifer tarandus*).

Method 2 -- Unequal Sized Units (The Ratio Method)

In a census with aerial transects of differing lengths, the approach is to calculate *density* for each transect and extrapolate this to the total census zone (Jolly 1969).

   This first step is to calculate average density for the whole area:

$$\text{Average density} = \hat{R} = \frac{\text{Total animals counted}}{\text{Total area searched}} = \frac{\sum x_i}{\sum z_i} \tag{4.34}$$

where x_i = total animals counted in transect i

   z_i = area of transect i

   i = sample number (1, 2, 3...n)

   n = total number of transects counted

The estimate of the total population is therefore:

$$\hat{X} = \hat{R}Z$$

where Z = area of total census zone

   $\hat{R}$ = average density per unit area

The variance of this estimate is more difficult to determine because both the density and the area of the transects vary. Jolly (1969) gives these formulae for the variance:

Sampling with replacement:

$$\text{Variance of total numbers} = \frac{N^2}{n(n-1)}\left[\sum x^2 + R^2 \sum z^2 - 2R\sum(xz)\right] \qquad (4.35)$$

where N = Total number of possible transects
and all the other terms are defined above.

Sampling without replacement:

$$\text{Variance of total numbers} = \frac{N(N-n)}{n(n-1)}\left[\sum x^2 + R^2 \sum z^2 - 2R\sum(xz)\right] \qquad (4.36)$$

Note that these are large sample estimates of the variance and they are only approximate when sample size is small ($n < 30$). Confidence intervals are obtained in the same way as in Method 1 above.

Box 4.4 gives an example of these calculations.

Box 4.4   Population Estimates from Aerial Census using Jolly's (1969) Methods 2 and 3

Method 2: The Ratio Method

Topi were counted by Norton-Griffiths (1978) on 12 transects of unequal length in a census area like that in Figure 4.13a. The area of the census zone was 2829 km^2. There were 126 possible transects of which 12 were selected at random without replacement.

Transect no., i	Area of transect, z_i (km^2)	No. of topi counted, x_i
1	8.2	2
2	13.7	26
3	25.8	110
4	25.2	82
5	21.9	89
6	20.8	75
7	23.0	42
8	19.2	50
9	21.4	47

10	17.5	23
11	19.2	30
12	20.8	54

$$\sum z = 8.2 + 13.7 + \cdots = 236.7$$

$$\sum z^2 = 8.2^2 + 13.7^2 + \cdots = 4930.99$$

$$\sum x = 2 + 26 + 110 + \cdots = 630$$

$$\sum x^2 = 2^2 + 26^2 + 110^2 + \cdots = 43{,}868$$

$$\sum xz = (8.2)(2) + (13.7)(36) + \cdots = 13{,}819.6$$

$$n = 12$$

$$N = 126$$

$$Z = 2829 \text{ km}^2$$

1. *Average density* (equation 4.34):

$$\hat{R} = \frac{\text{Total animals counted}}{\text{Total area searched}} = \frac{\sum x_i}{\sum z_i} = \frac{630}{236.7} = 2.661597 \text{ topi/km}^2$$

2. *Total population of topi:*

$$\hat{X} = \hat{R}Z = (2.66)(2829) = 7530 \text{ topi}$$

3. *Variance of total population* (sampling without replacement, equation 4.36):

$$\text{Variance of total numbers} = \frac{N(N-n)}{n(n-1)} \left[\sum x^2 + R^2 \sum z^2 - 2r \sum (xz) \right]$$

$$= \frac{126(114)}{12(11)} \left[43{,}868 + (2.66)^2(4931) - (2)(2.66)(13{,}819.6) \right]$$

$$= 569{,}686.1$$

4. *Standard error of total population:*

$$\text{S.E.}\left(\hat{X}\right) = \sqrt{\text{Variance}\left(\hat{X}\right)} = \sqrt{569{,}686.1} = 754.775$$

5. *95% confidence limits on total population size* ($t_{.025}$ for 11 d.f. is 2.201):

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

$$7530 \pm (2.201)(754.775) \;=\; 7530 \pm 1661 \text{ topi}$$

Method 3: Probability-Proportional-to-Size Sampling

Moose were counted on irregular blocks in the southern Yukon (see Figure 4.13c). The total census zone was 5165 km² subdivided by topography into 23 blocks. Random points were placed on the map ($n = 12$) and two blocks (C and G) received two random points while all the others got only one. Thus blocks C and G are counted twice in all the statistical calculations that follow.

Block	Area of Block, z (km²)	No. of moose counted, x	Density of moose, $d = x/z$
A	225	63	0.2800
B	340	52	0.1529
C	590	110	0.1864
D	110	15	0.1364
E	63	26	0.4127
F	290	30	0.1034
G	170	42	0.2471
H	410	79	0.1927
I	97	60	0.6186
J	198	51	0.2576

Only 10 blocks were counted but sample size is 12 because 2 blocks are used twice (equation 4.38).

1. *Mean density* $= \hat{\bar{d}} = \dfrac{\sum d}{n}$

$$= \frac{0.2800 + 0.1529 + 0.1864 + 0.1864 + 0.1364 + \cdots}{12}$$

$$= \frac{3.0213}{12} = 0.25177 \text{ moose / km}^2$$

2. *Variance of density* (equation 4.41):

$$\hat{s}_d^2 = \frac{\sum d^2 - \left(\sum d\right)^2 \big/ n}{n-1}$$

$$= \frac{0.97916 - (3.021276)^2 \big/ 12}{11} = 0.0198622$$

3. *Total population of moose* (equation 4.39):

$$\hat{X} = \bar{d}\,Z = (0.25177)(5165) = 1300 \text{ moose}$$

4. *Variance of total population* (equation 4.40):

$$\text{Var}\left(\hat{Y}\right) = \frac{Z^2}{n}\hat{s}_d^2 = \frac{(5165)^2}{12}(0.0198622) = 44{,}155.7$$

5. *Standard error of total population size:*

$$\text{S.E.}\left(\hat{X}\right) = \sqrt{\text{Var}\left(\hat{X}\right)} = \sqrt{44{,}155.7} = 210.13$$

6. *95% confidence limits on total population size:*

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

$$1300 \pm (2.201)(210.13) = 1300 \pm 462 \text{ moose}$$

These calculations can be done in the aerial census subprogram of Program QUADRAT (Appendix 2, page 000)

Method 3 -- Sampling with Probability Proportional to Size.

This method can be used on equal sized sampling units or unequal size units. Each stratum is divided into sampling units of any size or shape - transects, quadrats, or blocks.

Instead of selecting the units in a stratum from a single set of random numbers, the traditional way, we use a pair of random numbers to define the coordinates of a point on a map of the study area. We thus locate n_i random points on the map within the area, and our sample thus becomes the sample of units containing one or more of these points. If a sample unit happens to contain 2 or 3 points, it is counted 2 or 3 times in the subsequent calculations. We need to make the aerial count of it only once of course.

This is another example of *sampling with replacement*, and method 3 does not utilize sampling without replacement (Caughley 1977).

The chance of a sample unit being included in a calculation is thus *proportional to its size*, and there is no problem with sample units of irregular shape. This type of sampling is referred to as PPS sampling (probability proportional to size) and is discussed in Caughley (1977).

The calculations are as follows:

(1) Calculate for each sampling unit the density:

$$\hat{d} = \frac{x}{z} \tag{4.37}$$

where d = density in a sample unit

   x = number of animals counted in this sample unit

   z = area of sample unit

(2) Determine the average density for the sample units, noting that each d may be included several times in the totals if it was selected more than once:

$$\text{Average density} = \bar{d} = \frac{\sum \hat{d}}{n} \tag{4.38}$$

where n = number of units sampled (random points)

(3) Determine the total population size from:

$$\text{Total population} = \hat{X} = \bar{d}\,Z \tag{4.39}$$

where $\bar{d}$ = Average density per unit area

   Z = Total area of census zone

(4) Calculate the variance of total population size:

$$\text{Variance of total numbers} = \frac{Z^2}{n}\hat{s}_d^2 \tag{4.40}$$

where $\hat{s}_d^2 = \dfrac{\sum d^2 - \left(\sum d\right)^2 \Big/ n}{n-1} \tag{4.41}$

where d = density in each sample unit selected

          n = number of random points

This method is preferred by Jolly (1969) for all aerial census situations except those in which a nearly complete count is required.

Note that each of these methods provides only an estimate of numbers, and since detectability varies, some corrections must be made for bias, whether it be negative or positive (Hone 2008).

Box 4.4 illustrates calculations from aerial census. Program QUADRAT (Appendix 2, page 000) calculates total population estimates for these three methods of aerial census from Jolly (1969).

4.5 SUMMARY

One way to estimate density is to count the number of individuals in a series of quadrats. Quadrats may be small or large, circular or rectangular, and the first question you need to decide is the optimal shape and size of quadrat to use. The best quadrat is that which gives the highest precision for the lowest cost.

To calculate confidence limits on estimates of abundance from quadrat data you need to know the spatial pattern of the individuals. If organisms are spread randomly in space, counts from quadrats will fit a *Poisson* frequency distribution in which the variance and the mean are equal. More often, animals and plants are aggregated or clumped in space, and the variance of quadrat counts exceeds the mean count. Some types of clumped spatial patterns can be described by the *negative binomial* distribution. Techniques of fitting these distributions to observed quadrat counts are described, and ways of testing goodness-of-fit are available. Confidence intervals for means can be computed once the best underlying statistical distribution is determined.

Line intercept sampling is used in plant ecology to estimate plant cover but it can also provide an estimate of population abundance and population density. Measurements of plant size must be made perpendicular to the intercept lines to estimate density and parallel to the intercept line to estimate cover.

Aerial counts are a particularly graphic type of quadrat sampling in which the quadrats are often long, very thin strips. Not all animals are seen in aerial counts, and a serious undercounting bias is almost always present. Four methods are available for estimating the counting bias so that aerial counts can estimate true density. The sampling problems associated with aerial counts are easily seen and bring into focus problems that will be discussed in detail in Chapter 8.

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QUESTIONS AND PROBLEMS

4.1. Review the arguments in Box 4.1 (page 140) and read the conclusions in Pringle (1984: *Canadian Journal of Fisheries and Aquatic Science* 41: 1485-1489). Pringle (1984) recommends the use of 0.5 x 0.5 m quadrats from these same data. Why do the recommendations about optimal quadrat size not agree? How would the recommendation differ if (1) relative costs were equal for all sizes of quadrats; (2) relative costs were directly proportional to quadrat area?

4.2. A field plot was divided into 16 one-square meter quadrats and the numbers of the herb *Clintonia borealis* counted in each quadrat with these results:

3	0	5	1
5	7	2	0
3	2	0	7
3	3	3	4

Calculate the precision of sampling this universe with two possible shapes of 4 m^2 quadrats: 2 x 2 m and 4 x 1 m.

4.3. McNeil (1967) recorded the digging associated with spawning in female pink salmon in a 3 x 66 m section of stream in Alaska. He obtained these results:

No. of times digging occurred in a given quadrat	Observed occurrences
0	116
1	59
2	29
3	10
4	0
5	2
>5	0

Fit a Poisson distribution to these data and test the goodness of fit in the two ways given in the text. Discuss the general biological interpretation of your results. State the statistical null hypotheses and their ecological interpretation for these data.

4.4. Rice (1967: *Ecology* **48**: 1047-1049) recommends that quadrat size be selected so that the resulting measures of plant density have a reasonably normal distribution for the various species being measured. Why might this recommendation be impossible to implement?

4.5. Beall (1940) counted the number of European corn borer (*Pyrausta nubilalis*) larvae on four study areas, using 120 quadrats on each area. He obtained these data:

Number of individuals per plot	Study areas			
	1a	2a	3a	4a
0	19	24	43	47
1	12	16	35	23
2	18	16	17	27
3	18	18	11	9
4	11	15	5	7
5	12	9	4	3

6	7	6	1	1
7	8	5	2	1
8	4	3	2	0
9	4	4		0
10	1	3		1
11	0	0		1
12	1	1		
13	1			
14	0			
15	1			
16	0			
17	1			
18	0			
19	1			
26	1			
n	120	120	120	120

Determine if these data show a random or a clumped pattern. Fit the appropriate distribution and test the goodness-of-fit in the best manner.

4.6. Sinclair (1972) counted wildebeest in the Serengeti by aerial transect sampling of a census zone of 3245 km². He selected by sampling with replacement 15 transects as his sample, and he weighted the probability of selecting a given transect by the area of the transect. One transect (7) was selected twice, all others once. There were 96 possible transects in the total census zone, of unequal length. He got these results:

Transect number	Length (km)	Width (km)	No. of wildebeest counted
1	32	0.55	134
2	35	0.55	157
3	46	0.55	174
4	47	0.55	198
5	38	0.55	46
6	31	0.55	98
7	25	0.55	73
8	37	0.55	128
9	32	0.55	156
10	15	0.55	83
11	23	0.55	67
12	28	0.55	130
13	19	0.55	86
14	30	0.55	170

Estimate the total population of wildebeest in the census zone and calculate the 90% confidence interval for this estimate. What statistical and biological assumptions must you make to do these calculations?

4.7. The following data were gathered by students on three line intercepts randomly placed along a 760 m baseline. The data are the perpendicular width of oak trees intercepted by each line in southern Missouri.

Observation no.	Line A (350 m)	Line B (295 m)	Line C (375 m)
1	7.6 m	4.6°	0.8
2	5.2	2.7	4.9
3	1.2	1.8	3.6
4	4.7	3.1	3.2
5	4.4	4.2	1.7
6	3.0	2.8	5.4
7	3.1	2.3	7.6
8	6.9	1.8	3.1
9	3.5	4.8	2.0
10	5.3	2.9	4.6
11	1.9	3.6	3.7
12	2.7	3.1	4.9
13	6.7	5.6	
14	0.9	6.8	
15	4.1	0.5	
16	1.8	4.6	
17	4.6		
18	2.3		
19	6.2		
20	5.2		

Estimate population density of oak trees in this stand and compute the 90% confidence limits for this estimate.

4.8. Calculate 95% confidence limits for the mean density of black bean aphids from the data in Box 4.2 (page 165). Imagine that you were under the mistaken belief that counts of the black bean aphid were well described by the Poisson distribution. Compute confidence limits for these data under this mistaken assumption, and compare them with the correct limits. Is there a general relationship between confidence limits based on these two distributions such that one is always wider or narrower than the other for the same data?

4.9. Why are the data in Table 4.2 (page 137) not adequate for deciding that the best plot size is 4x4m for these trees?

4.10. High resolution satellite imagery has a strong potential for counting animals in remote locations. LaRue et al. (2011) use satellite imagery to count Weddell seals on the ice at Erebus Bay, Antarctica. Satellite counts averaged 72% of ground counts done at the same time (range 30% to 88%). Discuss reasons why high-resolution satellite imagery might underestimate populations of seals on ice, and read the discussion in LaRue et al. (2011, *Polar Biology* 34:1727-37).