Chapter 7

Spatial Pattern

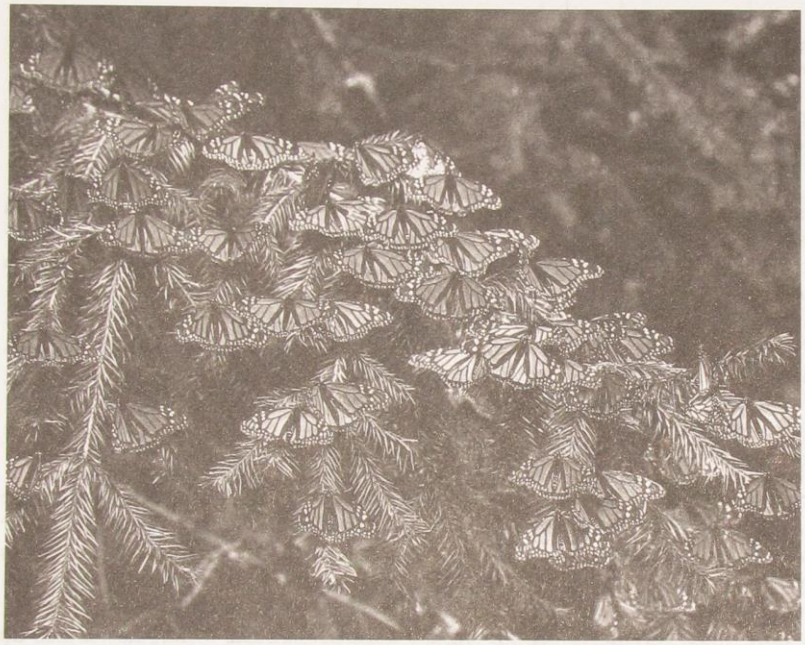
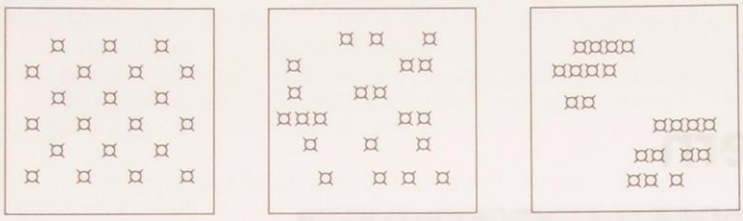


Figure 7.1 Monarch butterflies congregate during their fall migration.

INTRODUCTION

Members of a population constantly interact with physical features of their environment, one another, and other species in the community. Distinctive **spatial patterns**, describing the distribution of individuals within their habitat, result from these interactions. Movements, family groupings, and differential survival create spatial patterns that vary from one population to another. A population can also change the way it is scattered through space as seasons or conditions change. As an example, monarch butterflies spread out to feed and reproduce during the summer, but congregate in dense assemblies during fall migration and winter dormancy (Figure 7.1). The physical arrangement of organisms is of interest to ecologists because it provides evidence of interactions that have occurred in the past, and because it can significantly affect the population's fate in the future. Analyzing spatial distributions can reveal a lot more about the organism's natural history than we could ever know from estimates of population size alone.

Since it is often impossible to map the location of every individual, ecologists measure features of spatial pattern that are of particular biological interest. One such feature is the dispersion of the population. **Dispersion** refers to the evenness of the population's distribution through space. (Dispersion should not be confused with **dispersal**, which describes movement rather than pattern.) A completely uniform distribution has maximal dispersion, a randomly scattered population has intermediate dispersion, and an aggregated population with clumps of individuals surrounded by empty space has minimal dispersion (Figure 7.2).



Uniform distribution
High dispersion

Random distribution
Intermediate dispersion

Aggregated distribution
Low dispersion

Figure 7.2 Three types of spatial distribution. Individuals spread evenly through the environment are highly dispersed, individuals clumped together exhibit low dispersion.

How can we measure dispersion in populations? A typical approach involves **quadrat** sampling. Quadrats are small plots, of uniform shape and size, placed in randomly selected sites for sampling purposes. By counting the number of individuals within each sampling plot, we can see how the density of individuals changes from one part of the habitat to another. The word "quadrat" implies a rectangular shape, like a "quad" bounded by four campus buildings. Any shape will work, however, as long as quadrats are all alike and sized appropriately for the species under investigation. For creatures as small as barnacles, an ecologist may construct a sampling frame a few centimeters across, and simply drop it repeatedly along the rocky shore, counting numbers of individuals within the quadrat frame each time. For larger organisms such as trees, global positioning equipment and survey stakes may be needed to create quadrats of appropriate scale.

The number of individuals counted within each quadrat is recorded and averaged. The mean of all those quadrat counts (symbolized as $\bar{x}$) yields the **population density**, expressed in numbers of individuals per quadrat area (barnacles per square meter, for example, or pine trees per hectare). An alternative approach is to measure **ecological density**, expressed in numbers of individuals per resource unit (numbers of deer ticks per host, for example, or numbers of apple maggots per fruit). To get a measure of dispersion in our population, we need to know how much variation exists among the samples. In other words, how much do the numbers of individuals per sampling unit vary from one sample to the next? The **sample variance** (symbolized as s^2) gives us a good measure of the evenness of our distribution. (For an introduction to the variance, see Appendix 1—Variance.) Consider our three hypothetical populations, now sampled with randomly placed quadrats (Figure 7.3).

Notice that the more aggregated the distribution, the greater the variance among quadrat counts. To standardize our measurements for different populations, we can divide the variance by the mean number of individuals per quadrat. This gives us a reliable way to measure aggregation. Statisticians have demonstrated that the **variance/mean ratio,** symbolized as $s^2/\bar{x}$ yields a value close to 1 in a randomly dispersed population, because in samples from a random distribution the variance is equal to the mean. Any ratio significantly greater than 1 indicates aggregation, and a ratio less than 1 indicates a trend toward uniformity. We could therefore call the variance/mean ratio an index of aggregation, because it is positively related to the "clumping" of individuals in the population. The variance/mean ratio is also called an **index of dispersion**, even though dispersion is inversely related to $s^2/\bar{x}$. It is good to remember: a high value of $s^2/\bar{x}$ means high aggregation, but low dispersion.

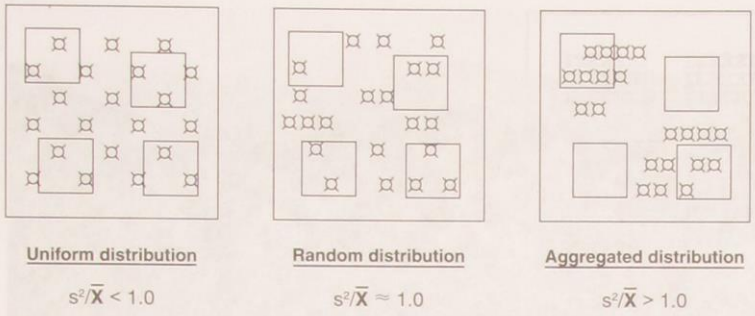


Figure 7.3 Quadrat sampling allows measurement of dispersion by counting numbers of individuals within each sampling frame, and then comparing the variance to the mean. Note that the mean number per frame is the same for all three patterns, but variance increases with aggregation.

Bear in mind that the size of the sampling frame can significantly influence the results of this kind of analysis. A population may be clumped at one scale of measurement, but uniform at another. For example, ant colonies represent dense aggregations of insects, but the colonies themselves can be uniformly distributed in space. Whether we consider the distribution of ants to be patchy or uniform depends on the scale of our investigation. Figure 7.4 illustrates a population that would be considered uniformly distributed if sampled with large quadrats, but aggregated if sampled with smaller quadrats. For organisms distributed in clusters, the $s^2/\bar{x}$ ratio will be maximized when the size of the sampling frame is equal to the size of the clusters.

Check your progress:

If densities are equal, which would yield a higher variance in numbers of individuals per quadrat: a highly aggregated population or a highly dispersed population?

Answer: High variance in relation to the mean results from highly aggregated spatial pattern.

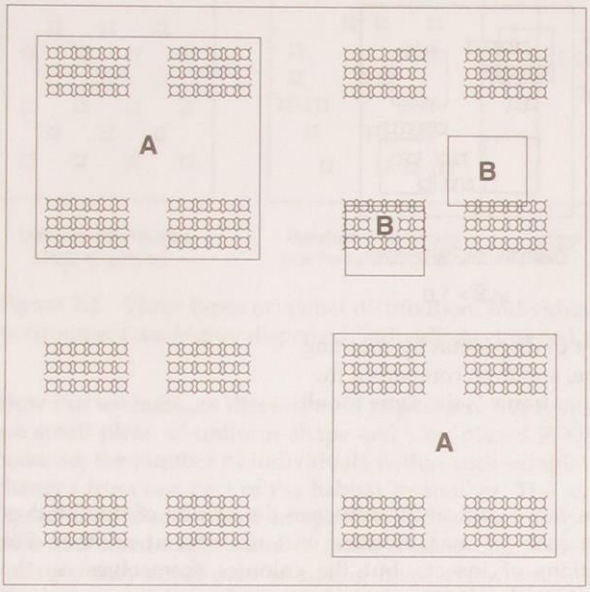


Figure 7.4 The calculated index of dispersion depends on the size of the quadrats used to sample the population. This hypothetical spatial pattern would exhibit a uniform dispersion index if sampled with large quadrats (A), but a clumped dispersion index if sampled with small quadrats (B).

The significance of aggregation or dispersion of populations has been demonstrated in many kinds of animal and plant populations. **Intraspecific competition**, for example, tends to separate individuals and create higher dispersion. Territorial animals, such as male robins on campus lawns in the spring, provide an excellent example. As each male defends a plot of lawn large enough to secure food for his nestlings, spaces between competitors increase, and the population becomes less aggregated. Competition can also create uniform plant distributions. In arid habitats, trees and shrubs become uniformly distributed if competition for soil moisture eliminates plants growing too close together (Figure 7.5).

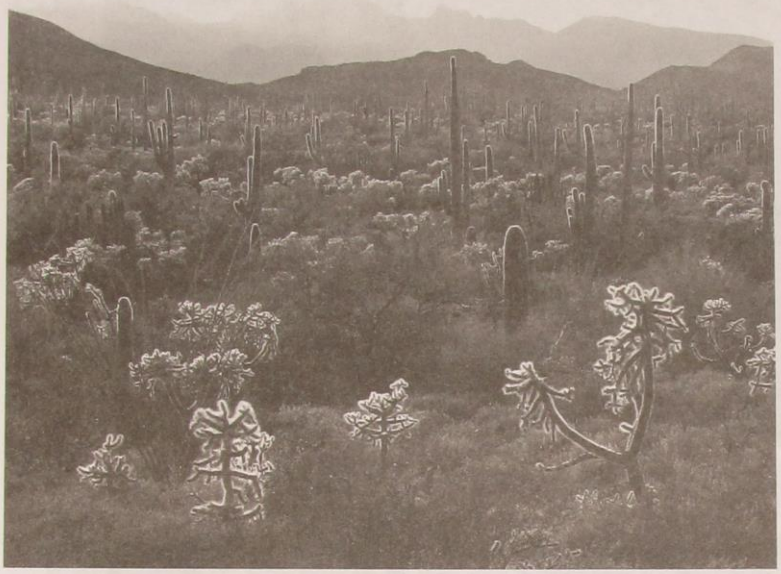


Figure 7.5 Saguaro and cholla cactus exhibit highly dispersed spatial patterns because of intense competition for water in a desert ecosystem.

If organisms are attracted to one another, their population shows increased aggregation. Schooling fish may limit the chance that any individual within the group is attacked by a predator. Bats in temperate climates conserve energy by roosting in tightly packed groups (Figure 7.6). Cloning plants and animals with large litter sizes create aggregation as they reproduce clusters of offspring. For example, the Eastern wildflower called mayapple generates large clusters of shoots topped by characteristic umbrella-like leaves as it spreads vegetatively across the forest floor (Figure 7.7). By setting up quadrats, and calculating the variance/mean ratio of the quadrat counts, you can gain significant insights about the biology of your organism.

Check your progress:

Give an animal example of high dispersion; of low dispersion.
Give a plant example of high aggregation; of low aggregation.

Hint: Dispersion is the opposite of aggregation.

Figure 7.6 Lesser horseshoe bats roost in clusters to conserve body heat.

Figure 7.7 Mayapple (*Podophyllum peltatum*) forms highly aggregated stands through asexual reproduction.

METHOD A: DISPERSION OF PLANTS IN A LAWN COMMUNITY

[Outdoors, spring, summer, or fall]

Research Question

What can we infer about the natural history of lawn species from their spatial distribution?

Preparation

Before laboratory, carefully examine lawns on campus. Regardless of maintenance efforts, few lawns are actually monocultures. Almost all lawn communities include some broad-leaved plants such as dandelions, plantain, or clover growing among the turf grasses (Figure 7.8).

Check with your facilities management department to ensure that pesticides have not been applied to campus lawns within a few days prior to this laboratory.

Figure 7.8 Three common broad-leaved lawn weeds: (A) dandelion (*Taraxicum*), (B) Plantain (*Plantago*), and (C) clover (*Trifolium*).

Materials (per laboratory team)

1 large nail (#16 galvanized or aluminum gutter nail)

1 meter stick

1 piece of nylon string, about 1-1/2 m long

Procedure

1. Make quadrat sampler by tying one end of the string around the nail, tightly enough to stay on, but loosely enough to swivel around the head (Figure 7.9). Then using the meter stick, mark a point on the string 56 cm from the nail by tying an overhand knot at that position. Repeat the procedure to make a second knot 80 cm from the nail, then a third knot 98 cm from the nail, and a fourth knot 113 cm from the nail. The distance from the nail to each knot will become the radius of a circle in your sampling plots. Distance to the first knot represents the radius of a circle of area 1 m^2. (Try verifying this calculation, using the formula Area = πr^2 for a radius of 0.56 m.) The knots farther along the string will be used to sample circles of areas 2 m^2, 3 m^2, and 4 m^2, respectively. Take your sampler with you to a lawn area.

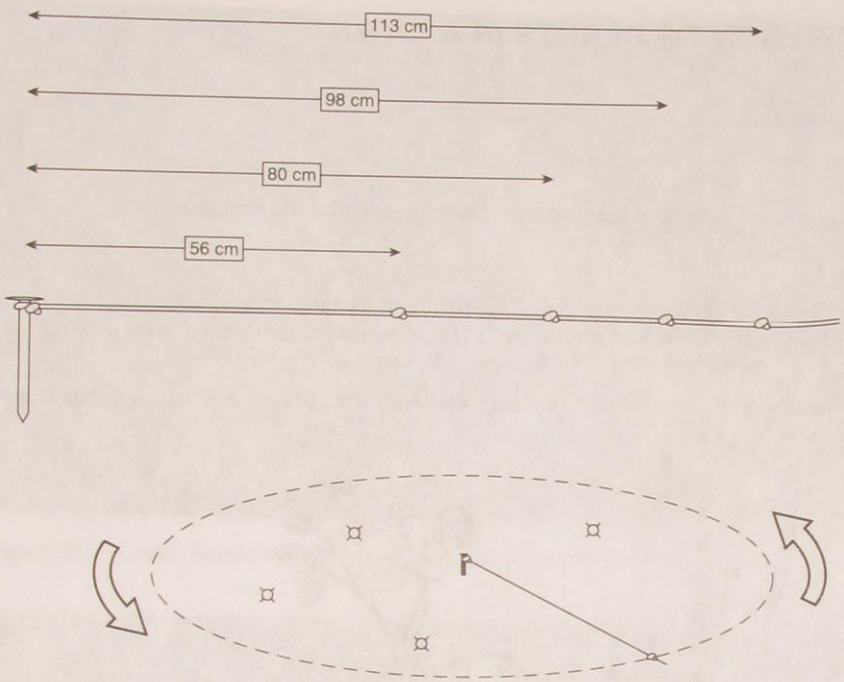


Figure 7.9 A string tied to a large nail, with knots tied at specified distances, can be used to sample a fixed area of lawn. Put the nail in the ground and pull the string taut. Moving the knot around the nail, count how many of your organisms fall within the circle.

2. Choose one lawn species exhibiting an interesting spatial pattern and common enough to find some specimens growing less than a meter apart. Decide what vegetative unit of this plant you will designate as an individual for the purpose of counting plots. For non-cloning plants such as dandelions, one rosette of leaves constitutes one individual. For cloning plants such as violets, choose a unit of plant growth, such as a shoot, as an arbitrary unit of population size.
3. Choose an area of lawn for sampling in which this species is relatively common. Before taking any samples, observe physical features of the habitat such as shade, soils, or small dips or mounds affecting water runoff that might help you interpret the pattern you see. Develop hypotheses relating the reproductive history of your species and habitat features with the distribution you are measuring.
4. Next, you must select sites for quadrat samples within your study area. You can obtain a fairly unbiased sample by tossing the nail within the sample area without aiming for any particular spot, and then pushing it into the soil wherever it lands. Hold the string at the first knot and stretch it out taut from the nail.
5. Now move the string in a circle (Figure 7.9). The length marked by your closest knot becomes a radius of a circular quadrat with area 1 m^2. If this circle is too small to include several individuals, move out to the second knot for a 2-m^2 quadrat, the third knot for a 3-m^2 quadrat, or the fourth knot for a 4-m^2 quadrat, as needed. After you decide on the appropriate scale, use the same size quadrat for all your samples.

6. As you move the string in a circle, count how many individuals fall within this quadrat. When the circle is complete, record this number in the Data Table for Methods A, B, and C. On the third column of the table, make notes of any landscape features that may affect your plant. Pull out the nail, make another toss to relocate your circular plot, and repeat for a total of 20 samples. Your sampling is complete when you have recorded 20 quadrat counts.
7. Analyze results on the Calculations for Methods A, B, and C page following the data table. By comparing the variance of your 20 quadrat counts with the mean, you will determine whether the plants you sampled are aggregated, random, or uniformly dispersed.

METHOD B: DISPERSION OF HERBIVORES ON PLANT RESOURCE UNITS

[Indoors/outdoors, employs biological collections, year-round]

In this exercise, we make use of plant parts serving as resource units for herbivorous animals. Leaves are resource units for plant-eating insects. Seeds and fruits, such as acorns or crab apples, serve as resource units for seed predators and fruit-eaters. An even-aged stand of campus trees can be considered a series of resource units for foraging birds or nesting squirrels.

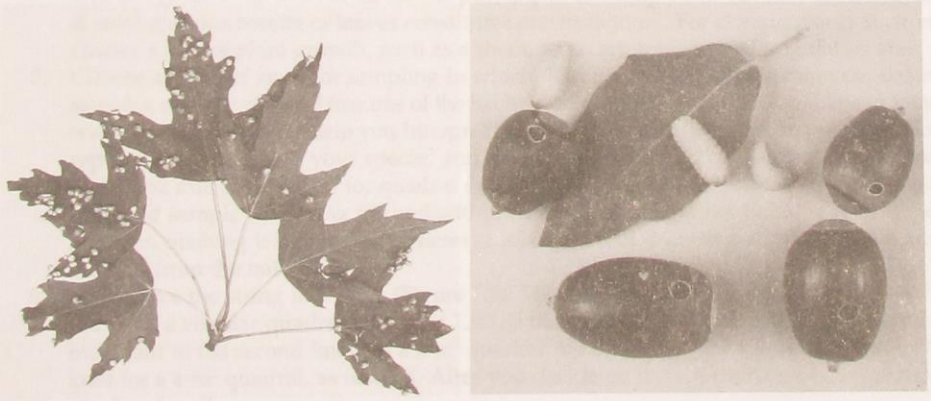
Rather than constructing quadrats to count individuals per unit of space (absolute density), we will count the number of animals per resource unit (ecological density). By counting animals or animal signs in each plant part in a collected sample, we can calculate a variance as well as a mean, and get a determination of the aggregation or dispersion of animals among their resource units. As seen with quadrat counts in the Introduction, analysis of pattern among resource units can yield interesting insights into the population biology of the species.

Research Question

When animals choose resources, or insects choose egg-laying sites, do they randomly disperse themselves (or their offspring) among resource units?

Preparation

Campus landscapes provide many options for collecting plant parts bearing evidence of associated animal species (Figure 7.10). Leaves of almost all temperate deciduous trees are riddled with leaf miner tunnels and insect galls in late summer. Close examination of nuts or acorns almost always reveals small, round emergence holes made by seed-eating weevils or bruchid beetles, which have matured inside the seed and escaped through the seed coat. Seeds are easy to preserve, so the instructor can make a large collection (on or off campus) to use repeatedly for this exercise. Leaf samples can be preserved in a plant press, and maintained as a permanent collection, provided the brittle specimens are handled carefully. (It is best not to use leaves from existing herbarium pages, since these tend to be biased toward perfect specimens without visible insect damage.)



a b

Figure 7.10 Ecological density is measured as numbers of individuals per resource unit. Insects on plant parts provide good study organisms: (A) Galls on maple leaves, (B) Acorn weevil larvae.

Alternatively, students may venture out onto the campus to collect their own specimens as part of this laboratory. Fall is best for collecting leaves, but seeds can be found throughout the year. In temperate locations, winter is the best time to find squirrel nests, which look like balls of leaves, in the bare branches of large deciduous trees. Empty bird nests are also apparent in winter and early spring, and provide a good index of ecological density if enough of them can be found. In spring, the class may find aphids or scale insects, which can be counted under a dissecting microscope. Once the collection is brought back to the laboratory, this exercise requires little time for data collection.

Materials (per laboratory team)

Collection of 20 resource units, or data from 20 resource units collected outside

Dissecting microscope or hand lens for small organisms

Procedure

1. If making your own collection, observe or collect 20 plant parts of equivalent size. Decide on a sampling plan in advance, so that the specimens are chosen with minimal bias. If using a laboratory collection such as a box of acorns, select 20 plant parts in a random sampling plan.
2. Count animals, or evidence of animal activity, on each plant part. Observe any life history observations you can, to help interpret intraspecific interactions that result in a pattern of dispersion among resource units.
3. Record numbers of animals for each of the 20 resource units as a data column in the Data Table for Methods A, B, and C at the end of this chapter. Bear in mind that one plant resource unit is a sampling unit in your study. Complete the Calculations section following the table, and answer the questions to discuss your results.

METHOD C: DISPERSION OF ISOPODS IN AN ARTIFICIAL HABITAT

[Laboratory, year-round]

Research Question

Do terrestrial isopods seek out conspecifics when selecting a habitat, or do they disperse to partition resources more evenly by avoiding habitat spaces occupied by others?

Preparation

Terrestrial isopods (Figure 7.11) include "pill bugs" (genus *Armadillium*), which roll into a ball when threatened, and the flatter and less flexible "sow bugs" (genus *Oniscus*). These arthropods are widely distributed, and are easily collected from leaf litter, under rocks and logs, or in lumber piles around buildings in most of North America. They can also be obtained from laboratory supply companies. Isopods feed on decaying organic material and are not difficult to handle or maintain in the laboratory. Use a covered container with some air exchange, such as a terrarium, plastic food container with perforated lid, or plastic shoe box. You might find a spoon and a small paintbrush handy to "sweep" them up and transport them from one place to another. It is very important to keep damp leaf mold or moistened paper toweling in their habitat at all times, because isopods use gills for respiration, and require high humidity.

Figure 7.11 Terrestrial isopods, also called "pill bugs" (genus *Armadillium*), roll into a ball when threatened.

If you are turning over logs, rocks, or lumber piles in search of isopods, remember that more aggressive animals, such as scorpions and venomous snakes, frequently hide in the same places. It is always wise to lift the side of a rock farthest from you first, and to be careful where you place your hands. When you are finished searching in a natural setting, replace rocks and logs where you found them.

Materials (per laboratory team)

Plastic sweater box or other box-shaped container with a flat bottom, about 30 × 50 cm

5 medium potatoes

3–4 inch paring knife

60 map pins (with round heads, about 5 mm diameter)

20–30 live terrestrial isopods

Cutting board or cutting surface on lab bench

Procedure

1. Prepare "resource islands" from potatoes. First, cross-section a potato with parallel cuts evenly spaced 1 cm apart. You should get four or five round sections from each potato. Discard the ends, and cut more potatoes until you have 20 sections of approximately equal size and thickness. Then insert three map pins in a triangle formation on the bottom of each potato slice, so that the potato slice will stand on the map pins like a three-legged stool (Figure 7.12). The pins should leave about ½ cm of space for the isopods to crawl underneath.

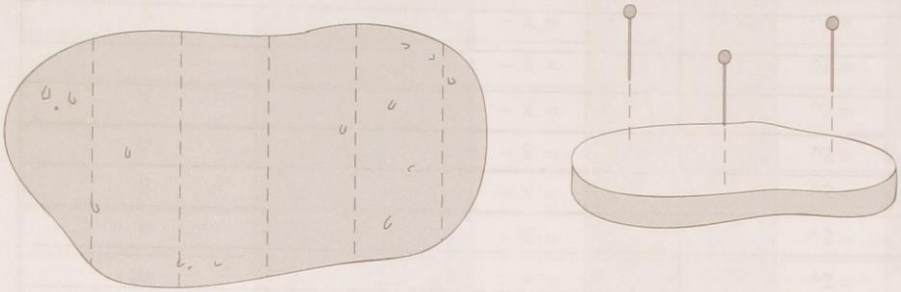


Figure 7.12 Slice potatoes and insert pins to make isopod shelters.

2. Arrange the 20 potato slices, pinheads down, in the bottom of the sweater box. Distribute the potato slices uniformly, with space separating each one. You now have an artificial habitat with 20 resource islands suitable for isopod colonization.
3. Release 20–30 isopods into the box. Take a few minutes to observe their behavior. How do they react to the box edges? to the potato "islands"? to one another?
4. Leave the isopods overnight. The underside of the potato slice islands provide a dark, humid microclimate that is preferred by isopods. They also feed on the potatoes. If lights are left on in the room, all isopods should select one of the potato slices to hide under.
5. After the isopods have had time to adjust to their habitat (12–48 hrs), count the number of isopods underneath each potato slice. You will need to pick up each "habitat island," because the isopods often invert themselves and cling to the potato. Record 0 if there are none in that sample. The 20 numbers you record should sum to the number of isopods you released into the box.
6. Complete the Data Table and calculation page at the end of this chapter. The mean number of isopods per potato slice ($\bar{x}$) is the ecological density, and the variance/mean ratio provides an index of aggregation for the captive isopod population.
7. Interpret your results by answering Questions for Methods A, B, and C.

Data Table for Methods A, B, and C

Sampling Unit	No. of individuals in the sample	Note any habitat features associated with this sample.
1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
15		
16		
17		
18		
19		
20		

CALCULATIONS FOR METHODS A, B, AND C

1. Enter your 20 counts of organisms per sampling unit ($\mathbf{x}_i$) in the second column of the table below.
2. Calculate a mean ($\bar{x}$) by summing all the counts and dividing by the sample size ($\mathbf{n} = 20$).
3. Subtract the mean from each data value to obtain the deviation from the average ($\mathbf{d}_i$).
4. Square each deviation $(\mathbf{d}^2)_i$. (Note that this step takes care of the negative signs.)
5. Add up all the squared deviations ($\sum \mathbf{d}^2$).
6. Divide the sum of $\mathbf{d}^2$ values by (sample size – 1) to calculate the sample variance ($\mathbf{s}^2$).
7. Finally, divide the variance by the mean ($\bar{x}$) to compute the variance/mean ratio ($\mathbf{s}^2/\bar{x}$).
8. Refer to the Introduction, and to the methods section you used, to interpret this ratio.

Sample number (i)	No. of organisms in sample i (x_i)		Deviations (d_i)		Squared deviations $(d^2)_i$
1		$- \bar{x} =$		^2 =	
2		$- \bar{x} =$		^2 =	
3		$- \bar{x} =$		^2 =	
4		$- \bar{x} =$		^2 =	
5		$- \bar{x} =$		^2 =	
6		$- \bar{x} =$		^2 =	
7		$- \bar{x} =$		^2 =	
8		$- \bar{x} =$		^2 =	
9		$- \bar{x} =$		^2 =	
10		$- \bar{x} =$		^2 =	
11		$- \bar{x} =$		^2 =	
12		$- \bar{x} =$		^2 =	
13		$- \bar{x} =$		^2 =	
14		$- \bar{x} =$		^2 =	
15		$- \bar{x} =$		^2 =	
16		$- \bar{x} =$		^2 =	
17		$- \bar{x} =$		^2 =	
18		$- \bar{x} =$		^2 =	
19		$- \bar{x} =$		^2 =	
n = 20		$- \bar{x} =$		^2 =	
Total # organisms $\Sigma (x_i) =$		**Sum of Squared Deviations** $\Sigma (d^2)_i =$			
Mean $\Sigma (x_i)/n =$		**Sample Variance** $s^2 = \Sigma (d^2)_i/(n-1) =$			
	Variance/Mean $(s^2/\bar{x}) =$				

Questions for Methods A, B, and C

1. Based on the variance/mean ratio, what can you conclude about the spatial pattern of your population? How might you explain this pattern, given observations you made as you were sampling?

2. Random sampling is very important if the data you collected are meant to represent a larger population. In retrospect, do you have any questions or concerns about the validity of the sampling method? If bias exists, how might you alter your method to randomize your samples?

3. An index of aggregation is maximized in patchy distributions if the size of the quadrat is the same as the size of the organism's aggregations. Might a larger or smaller sampling unit (or a different sized resource unit) have affected your results?

4. Would you expect another organism from the same biological community to exhibit a similar index of dispersion? Is spatial pattern a property of the organism, or of its habitat?

5. Lesser horseshoe bats (Figure 7.6) and many other bat species are increasingly rare. How does a highly aggregated distribution, for at least part of the life cycle, influence the status of endangered species?