

CHAPTER 14

NICHE MEASURES AND RESOURCE PREFERENCES

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The analysis of community dynamics depends in part on the measurement of how organisms utilize their environment. One way to do this is to measure the *niche* parameters of a population and to compare the niche of one population with that of another. Since food is one of the most important dimensions of the niche, the analysis of animal diets is closely related to the problem of niche specifications. In this chapter I will review niche metrics and the related measurement of dietary overlap and dietary preferences.

Before you decide on the appropriate measures of niche size and dietary preference, you must think carefully about the exact questions you wish to answer with these measures. The hypothesis must drive the measurements and the ways in which the raw data will be summarized. As in all ecological work it is important to think before you leap into analysis.

Research on ecological niches has moved in two directions. The first has been to quantify niches in order to investigate potential competition at the local scale between similar species. This is often termed the *Eltonian niche* concept, and the methods developed for its measurement is largely covered in this chapter. The second more recent and perhaps more important direction has been to use GIS-based approaches to estimate spatial niches in order to estimate geographical distributions of species and in particular to try to relate possible changes to ongoing climate change. This approach to niche definition has been called the *Grinnellian niche*, since Joseph Grinnell (1917{ #16376}) was concerned about determining the geographical ranges of species. This second direction is covered in detail in the book by Peterson et al. (2011{#16358}) and I will discuss it briefly in the latter part of this chapter. The literature on niche theory is very large and I concentrate here on how to measure aspects of the ecological niche on a local scale.

14.1 WHAT IS A RESOURCE?

The measurement of niche parameters is fairly straightforward, once the decision about what resources to include has been made. The question of defining a resource state can be subdivided into three questions (Colwell and Futuyma 1971). First, what *range* of resource states should be included? Second, how should

samples be taken across this range? And third, how can non-linear niche dimensions be analyzed? Figure 14.1 illustrates some of these questions graphically.

Resource states may be defined in a variety of ways:

1. *Food resources*: the taxonomic identity of the food taken may be used as a resource state, or the size category of the food items (without regard to taxonomy) could be defined as the resource state.
2. *Habitat resources*: habitats for animals may be defined botanically or from physical-chemical data into a series of resource states.
3. *Natural sampling units*: sampling units like lakes or leaves or individual fruits may be defined as resource states.
4. *Artificial sampling units*: a set of random quadrats may be considered different resource states.

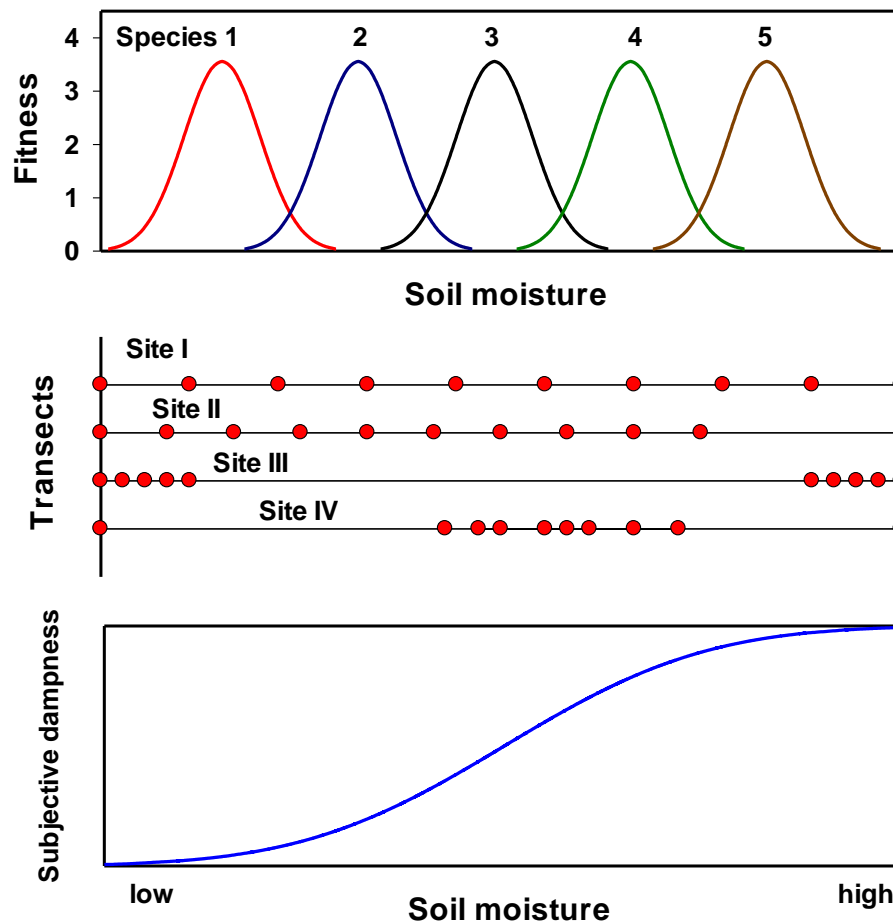


Figure 14.1 Hypothetical example to illustrate some problems in the measurement of niche breadth and niche overlap. The horizontal axis is a gradient of soil moisture from dry hillside (left) to moist stream bank (right). Consider 5 species of plants, each adapted to different soil moisture levels (top). The same moisture gradient exists at each of four different study sites (I, II, III, IV), but the sampling quadrats (large red dots) are placed in different patterns relative to soil moisture. Estimates of niche breadth and overlap will vary at the different sites because of the patterns of spacing of the quadrats and the total range of soil moisture covered. (Source: Colwell and Futuyma 1971). { #4965}

Clearly the idea of a resource state is very broad and depends on the type of organism being studied and the purpose of the study. Resource states based on clearly significant resources like food or habitat seem preferable to more arbitrarily defined states (like 3 and 4 above). It is important to specify the type of resources being utilized in niche measurements so that we quantify the 'food niche' or the 'temperature niche'. The large number of resources critical to any organism means that the entire niche can never be measured, and we must deal with the parts of the niche that are relevant to the questions being investigated.

In analyzing the comparative use of resource states by a group of species, it is important to include the extreme values found for all the species combined as upper and lower bounds for your measurements (Colwell and Futuyma 1971). Only if the complete range of possible resource states is used will the niche measurements be valid on an absolute scale. Conversely, you should not measure beyond the extreme values for the set of species, or you will waste time and money in measuring resource states that are not occupied.

If samples are taken across the full range of resource states, there is still a problem of "spacing". Compare the sampling at hypothetical sites I, III and IV in Figure 14.1. All these sampling schemes range over the same extreme limits of soil moisture, but niche breadths calculated for each species would differ depending on the spacing of the samples. If all resource states are ecologically distinct to the same degree, the problem of "spacing" is not serious. But this is rarely the case in a community in nature. The important point is to sample evenly across all the resource states as much as possible.

Resource states may be easily quantified on an absolute scale if they are physical or chemical parameters like soil moisture. But the effects of soil moisture or any other physical-chemical parameter on the abundance of a species is never a simple straight line (Hanski, 1978; Green 1979). Colwell and Futuyma (1971) made the first attempt to weight resource states by their level of distinctness. Hanski (1978) provided a second method for weighting resource states, but neither of these two methods seems to have solved the problem of non-linear niche dimensions. In practice we can do little to correct for this problem except to recognize that it is present in our data.

A related problem is how resource states are recognized by organisms and by field ecologists. If an ecologist recognizes more resource states than the organism, there is no problem in calculating niche breadth and overlap, assuming a suitable niche metric (Abrams 1980). Many measures of niche overlap show increased bias as the number of resource states increases (see page 000), so that one must be careful in picking a suitable niche measure. But if the ecologist does not recognize resource states that organisms do, there is a potential for misleading comparisons of species in different communities. There is no simple resolution of this difficulty, and it points again to the necessity of having a detailed knowledge of the natural history of the organisms being studied in order to minimize such distortions. In most studies of food niches, food items can be classified to species and we presume that herbivores or predators do not subdivide resources more finely, although clearly animals may select different age-classes or growth-stages within a species. Microhabitat resource states are more difficult to define. Schoener (1970), for example, on the basis of detailed natural history observations recognized 3 perch diameter classes and 3 perch height classes in sun or in shade for *Anolis* lizards in Bermuda. These classes were sufficient to show microhabitat segregation in *Anolis* and thus a finer subdivision was not necessary. There is an important message here that you must know the natural history of your organisms to quantify niche parameters in an ecologically useful way.

14.2 NICHE BREADTH

Some plants and animals are more specialized than others and measures of *niche breadth* attempt to measure this quantitatively. Niche breadth has also been called *niche width* or *niche size* by ecologists. Niche breadth can be measured by observing the distribution of individual organisms within a set of resource states. The table formed by assigning species to the rows and resource states to the columns is called the *resource matrix* (Colwell and Futuyma 1971). Table 14.1 illustrates a resource matrix for lizards in the southwestern United States in which microhabitats are divided into 14 resource states.

Three measures of niche breadth are commonly applied to the resource matrix.

14.2.1 Levins' Measure

Levins (1968) proposed that niche breadth be estimated by measuring the uniformity of distribution of individuals among the resource states. He suggested one way to measure this was:

$$\hat{B} = \frac{1}{\sum \hat{p}_j^2} \quad (14.1)$$

which can also be written as:

$$\hat{B} = \frac{Y^2}{\sum N_j^2}$$

where:

- \hat{B} = Levins' measure of niche breadth
- \hat{p}_j = Proportion of individuals found in or using resource state j ,
or fraction of items in the diet that are of food category j
(estimated by N_j / Y) ($\sum \hat{p}_j = 1.0$)
- N_j = Number of individuals found in or using resource state j
- $Y = \sum N_j$ = Total number of individuals sampled

TABLE 14.1 EXAMPLE OF A RESOURCE MATRIX FOR LIZARD MICROHABITATS IN THE SOUTHWESTERN USA^a

	Terrestrial										Arboreal				Sample size, N	Levins' <i>B</i> (niche breadth)
	Open	Grass	Bush	Tree	Oth	Open	Grass	Bush	Tree	Other	Low	Low	High	High		
Species	sun	sun	sun	sun	sun	shade	shade	shade	shade	shade	sun	shade	sun	shade		
<i>Cnemidophorus tigris</i>	47.5	2.5	34.6	2.5	2.5	.0.	0.0	7.8	0.0	2.5	0.1	0.0	0.0	0.0	1801	2.82
<i>Uta stansburiana</i>	27.1	4.6	41.3	4.6	4.6	0.8	0.0	6.0	0.0	3.9	5.3	0.1	1.8	0.0	768	3.87
<i>Phrynosoma platyrhinos</i>	92.6	0.0	2.5	0.0	0.0	2.5	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	121	1.17
<i>Crotaphytus wislizeni</i>	59.1	0.7	22.6	0.7	0.7	2.2	0.0	9.5	0.0	0.0	2.2	0.0	2.2	0.0	137	2.43
<i>Callisaurus draconoides</i>	80.7	2.0	4.3	3.9	2.0	0.7	0.4	0.9	0.4	0.4	3.2	0.0	1.1	0.0	538	1.52
<i>Sceloporus magister</i>	0.0	0.0	1.2	1.2	3.5	0.0	0.0	3.5	1.2	1.2	10.0	5.9	38.2	34.1	85	3.58
<i>Urosaurus graciosus</i>	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	1.1	39.6	49.5	46	2.45
<i>Dipsosaurus dorsalis</i>	46.3	1.5	40.3	1.5	1.5	0.0	0.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	67	2.60
<i>Uma scoparia</i>	80.5	0.8	7.3	0.8	0.8	2.4	0.0	7.3	0.0	0.0	0.0	0.0	0.0	0.0	41	1.52
<i>Coleonyx variegatus</i>	0.0	0.0	0.0	0.0	0.0	95.3	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	43	1.10
<i>Xantusia vigilis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	27	1.00

^a The percentage utilization of 14 microhabitats by 11 lizard species from the deserts of the southwestern United States was determined by recording where each individual was sitting when first sighted. This table is based on 3674 sightings. *Source:* Pianka, 1986, pp. 160-161.

Note that B is the reciprocal of Simpson's index of diversity (Chapter 13, page 000). Like the reciprocal of Simpson's index, B is maximum when an equal number of individuals occur in each resource state, so that the species does not discriminate among the resource states and has the broadest possible niche. Levins' B is minimal when all the individuals occur in only one resource state (minimum niche breadth, maximum specialization). The range of B is from 1 to n , where n is the total number of resource states.

It is often useful to standardize niche breadth to express it on a scale from 0 to 1.0. This can be done easily for Levins' measure by dividing B by the total number of resource states after correcting for a finite number of resources. Hurlbert (1978) suggests the following measure for standardized niche breadth:

$$\hat{B}_A = \frac{\hat{B} - 1}{n - 1} \quad (14.2)$$

where:

\hat{B}_A = Levins' standardized niche breadth

\hat{B} = Levins' measure of niche breadth

n = Number of possible resource states

Box 14.1 illustrates the calculations of Levins' niche breadth.

Box 14.1 CALCULATION OF NICHE BREADTH FOR DESERT LIZARDS

Pianka (1986) gives the percentage utilization of 19 food sources for two common lizards of southwestern United States as follows:

	<i>Cnemidophorus tigris</i> (whiptail lizard)	<i>Uta stansburiana</i> (side-blotched lizard)
Spiders	1.9	3.9
Scorpions	1.3	0
Solpugids	2.1	0.5
Ants	0.4	10.3
Wasps	0.4	1.3
Grasshoppers	11.1	18.1
Roaches	4.8	1.5

Mantids	1.0	0.9
Ant lions	0.3	0.4
Beetles	17.2	23.5
Termites	30.0	14.7
Hemiptera and Homoptera	0.6	5.8
Diptera	0.4	2.3
Lepidoptera	3.8	1.0
Insect eggs and pupae	0.4	0.1
Insect larvae	18.1	7.4
Miscellaneous arthropods	2.6	6.5
Vertebrates	3.6	0.2
Plants	0.1	1.6
Total	100.1	100.0
No. of individual lizards	1975	944

Levin's Measure of Niche Breadth

For the whiptail lizard, from equation (14.1):

$$B = \frac{1}{\sum p_j^2}$$

$$= \frac{1}{0.019^2 + 0.013^2 + 0.021^2 + 0.004^2 + 0.004^2 + 0.111^2 + \dots}$$

$$= \frac{1}{0.171567} = 5.829$$

To standardize this measure of niche breadth on a scale of 0 to 1, calculate Levins' measure of standardized niche breadth (equation 14.2):

$$B_A = \frac{B - 1}{n - 1}$$

$$= \frac{5.829 - 1}{19 - 1} = 0.2683$$

Shannon-Wiener Measure

For the whiptail lizard, using equation (14.7) and logs to the base e:

$$\begin{aligned}
 H' &= -\sum p_j \log p_j \\
 &= -[(0.019) \log 0.019 + (0.013) \log 0.013 + (0.021) \log 0.021 + \\
 &\quad (0.004) \log 0.004 + 0.004 \log 0.004 + (0.111) \log 0.111 + \dots] \\
 &= 2.103 \text{ nits per individual}
 \end{aligned}$$

To express this in the slightly more familiar units of *bits*:

$$\begin{aligned}
 H' \text{ (bits)} &= 1.442695 H' \text{ (nits)} \\
 &= (2.103)(1.442695) = 3.034 \text{ bits/individual}
 \end{aligned}$$

To standardize this measure, calculate evenness from equation (14.8):

$$\begin{aligned}
 J' &= \frac{H'}{\log n} \\
 &= \frac{2.103}{\log (19)} = 0.714
 \end{aligned}$$

Smith's Measure

For the whiptail lizard data, by the use of equation (14.9):,

$$FT = \sum (\sqrt{p_j a_j})$$

and assuming all 19 resources have equal abundance (each as a proportion 0.0526)

$$\begin{aligned}
 FT &= \sqrt{(0.019)(0.0526)} + \sqrt{(0.013)(0.0526)} + \sqrt{(0.021)(0.0526)} + \dots \\
 &= 0.78
 \end{aligned}$$

The 95% confidence interval is given by equations (14.10) and (14.11):

$$\begin{aligned}
 \text{Lower 95\% confidence limit} &= \sin \left[\arcsin (0.78) - \frac{1.96}{2\sqrt{1975}} \right] \\
 &= \sin (0.8726) = 0.766 \\
 \text{Upper 95\% confidence limit} &= \sin \left[\arcsin (0.78) + \frac{1.96}{2\sqrt{1975}} \right] \\
 &= \sin (0.9167) = 0.794
 \end{aligned}$$

Number of Frequently Used Resources

If we adopt 5% as the minimum cutoff, the whiptail lizard uses four resources frequently (grasshoppers, beetles, termites, and insect larvae).

These measures of niche breadth can all be calculated by Program NICHE (Appendix

2, page 000)

Levins' measure of niche breadth does not allow for the possibility that resources vary in abundance. Hurlbert (1978) argues that in many cases ecologists should allow for the fact that some resources are very abundant and common, and other resources are uncommon or rare. The usage of resources ought to be scaled to their availability. If we add to the resource matrix a measure of the proportional abundance of each resource state, we can use the following measure of niche breadth:

$$\hat{B} = \frac{1}{\sum \left(\hat{p}_j^2 / \hat{a}_j \right)} \quad (14.3)$$

where

B' = Hurlbert's niche breadth

p_j = proportion of individuals found in or using resource j ($\sum p_i = 1.0$)

a_j = proportion of the total available resources consisting of resource j
($\sum a_i = 1.0$)

B' can take on values from $1/n$ to 1.0 and should be standardized for easier comprehension. To standardize Hurlbert's niche breadth to a scale of 0-1, use the equation:

$$\hat{B}_A = \frac{\hat{B} - a_{\min}}{1 - a_{\min}} \quad (14.4)$$

where

B_A' = Hurlbert's standardized niche breadth

B' = Hurlbert's niche breadth (equation 14.3)

a_{\min} = smallest observed proportion of all the resources (minimum a_j)

Note that when all resource states are equally abundant, the a_j are all equal to $1/n$, and Levins' standardized niche breadth (equation 14.2) and Hurlbert's standardized niche breadth (equation 14.4) are identical.

The variance of Levins' niche breadth and Hurlbert's niche breadth can be estimated by the delta method (Smith 1982), as follows:

$$\text{var}(\hat{B}) = \frac{4\hat{B}^4 \left[\sum \left(\frac{\hat{p}_j^3}{\hat{a}_j^3} \right) - \left(\frac{1}{\hat{B}} \right)^2 \right]}{Y} \quad (14.5)$$

where

$\text{var}(\hat{B})$ = variance of Levins' or Hurlbert's measure of niche breadth (B or B')

p_j = proportion of individuals found in or using resource state j ($\sum p_j = 1.0$)

a_j = proportion resource j is of the total resources ($\sum a_j = 1.0$)

Y = total number of individuals studied = $\sum N_j$

This variance, which assumes a multinomial sampling distribution, can be used to set confidence limits for these measures of niche breadth, if sample sizes are large, in the usual way: e.g.

$$B' \pm 1.96 \sqrt{\text{var}(B')} \quad (14.6)$$

would give an approximate 95% confidence intervals for Hurlbert's niche breadth.

In measuring niche breadth or niche overlap for food resources an ecologist typically has two counts available: the number of *individual animals* and the number of *resource items*. For example, a single lizard specimen might have several hundred insects in its stomach. The sampling unit is usually the individual animal and one must assume these individuals constitute a random sample. It is this sample size, of individual animals, that is used to calculate confidence limits (equation 14.6). The resource items in the stomach of each individual are *not* independent samples, and they should be counted only to provide an estimate of the dietary proportions for that individual. If resource items are pooled over all individuals, the problem of sacrificial pseudoreplication occurs (see Chapter 10, page 000). If one fox has eaten one hare and a second fox has eaten 99 mice, the diet of foxes is 50% hares, not 1% hares.

14.2.2 Shannon-Wiener Measure

Colwell and Futuyma (1971) suggested using the Shannon-Wiener formula from information theory to measure niche breadth. Given the resource matrix, the formula is:

$$H' = - \sum \hat{p}_j \log \hat{p}_j \quad (14.7)$$

where

H' = Shannon-Wiener measure of niche breadth

p_j = proportion of individuals found in or using resource j ($j = 1, 2, 3 \dots n$)

n = total number of resource states

and any base of logarithms may be used (see page 000). Since the Shannon-Wiener measure can range from 0 to ∞ , one may wish to standardize it on a 0-1 scale. This can be done simply by using the evenness measure J' :

$$J' = \frac{\text{Observed Shannon measure of niche breadth}}{\text{Maximum possible Shannon measure}} \quad (14.8)$$

$$= \frac{H'}{\log n}$$

where

J' = Evenness measure of the Shannon-Wiener function

n = Total number of possible resource states

and the same base of logarithms is used in equations (14.7) and (14.8). The Shannon-Wiener function is used less frequently than Levins' measure for niche breadth. Hurlbert (1978) argues against the use of the Shannon measure because it has no simple ecological interpretation and for the use of Levins' measure of niche breadth. The Shannon measure will give relatively more weight to the rare resources used by a species, and conversely the Levins' measure will give more weight to the abundant resources used.

Box 14.1 illustrates the calculation of Shannon's measure of niche breadth.

14.2.3 Smith's Measure

Smith (1982) proposed another measure of niche breadth. It is similar to Hurlbert's measure (equation 14.3) in that it allows you to take resource availability into account. The measure is:

$$FT = \sum (\sqrt{p_j a_j}) \quad (14.9)$$

where

FT = Smith's measure of niche breadth

p_j = Proportion of individuals found in or using resource state j

a_j = Proportion resource j is of the total resources

n = Total number of possible resource states

For large sample sizes, an approximate 95% confidence interval for FT can be obtained using the arcsine transformation as follows:

$$\text{Lower 95\% confidence limit} = \sin \left[x - \frac{1.96}{2\sqrt{Y}} \right] \quad (14.10)$$

$$\text{Upper 95\% confidence limit} = \sin \left[x + \frac{1.96}{2\sqrt{Y}} \right] \quad (14.11)$$

where

$$x = \text{Arcsin}(FT)$$

$$Y = \text{Total number of individuals studied} = \sum N_j$$

and the arguments of the trigonometric functions are in radians (not in degrees!).

Smith's measure of niche breadth varies from 0 (minimal) to 1.0 (maximal) and is thus a standardized measure. It is a convenient measure to use because its sampling distribution is known (Smith 1982).

Smith (1982) argues that his measure FT is the best measure of niche breadth that takes resource availability into account. Hurlbert's measure B' (equation 14.3) is very sensitive to the selectivity of rare resources, which are more heavily weighted in the calculation of B' . Smith's FT measure is much less sensitive to selectivity of rare resources.

All niche breadth measures that consider resource availability estimate the overlap between the two frequency distributions of use and availability. The choice of the niche breadth measure to use in these situations depends upon how you wish to weight the differences. One simple measure is the percentage similarity measure (PS , see Chap. 11, page 000), suggested as a measure of niche breadth by Feinsinger *et al.* (1981) and Schluter (1982). The percentage similarity measure of niche breadth is the opposite of Hurlbert's B' because it gives greater weight to the abundant resources and little weight to rare resources. For this reason Smith (1982) recommended against the use of percentage similarity as a measure of niche breadth. The decision about which measure is best depends completely on whether you wish for ecological reasons to emphasize dominant or rare resources in the niche breadth measure.

Box 14.1 illustrates the calculation of Smith's measure of niche breadth.

14.2.4 Number of Frequently Used Resources

The simplest measure of niche breadth is to count the number of resources used more than some minimal amount (Schluter, pers. comm.). The choice of the cutoff for frequent resource use is completely arbitrary, but if it is too high ($> 10\%$) the number of frequently-used resources is constrained to be small. A reasonable value for the cutoff for many species might be 5%, so that the number of frequently-used resources would always be 20 or less.

This simple measure of niche breadth may be adequate for many descriptive purposes. Figure 14.2 illustrates how closely it is correlated with Levins' measure of niche breadth for some of Pianka's lizard food niche data.

If resources are subdivided in great detail, the minimal cutoff for the calculation of the number of frequently-used resources will have to be reduced. As a rule of thumb, the cutoff should be approximately equal to the reciprocal of the number of resources, but never above 10%.

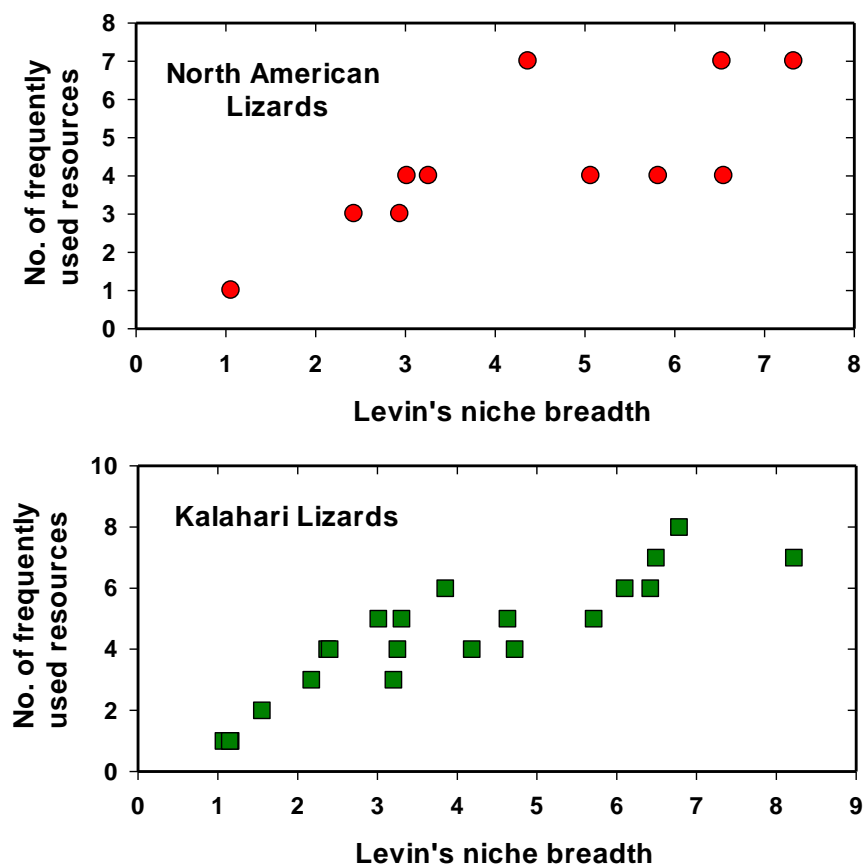


Figure 14.2 Relationship between two measures of niche breadth for desert lizard communities. (a) Diet niche breadths for North American lizards, 11 species, $r = 0.74$. (b) Diet niche breadths for Kalahari lizards, 21 species, $r = 0.84$. (Data from Pianka 1986). The simple measure of number of frequently used resources (>5%) is highly correlated with the more complex Levin's niche breadth measure for diets of these lizards. { #4966 }

14.3 NICHE OVERLAP

One step to understanding community organization is to measure the overlap in resource use among the different species in a community guild. The most common resources measured in order to calculate overlap are *food* and *space* (or microhabitat). Several measures of niche overlap have been proposed and there is considerable controversy about which is best (Hurlbert 1978, Abrams 1980, Linton *et al.* 1981). The general problem of measuring niche overlap is very similar to the problem of measuring similarity (Chapter 11, page 000) and some of the measures of niche overlap are identical to those we have already discussed for measuring community similarity.

14.3.1 MacArthur and Levins' Measure

One of the first measures proposed for niche overlap was that of MacArthur and Levins (1967):

$$\hat{M}_{jk} = \frac{\sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sum_i^n \hat{p}_{ij}^2} \quad (14.12)$$

where

- M_{jk} = MacArthur and Levins' niche overlap of species k on species j
- p_{ij} = proportion that resource i is of the total resources used by species j
- p_{ik} = proportion that resource i is of the total resources used by species k
- n = total number of resource states

Note that the MacArthur-Levins measure of overlap is *not* symmetrical between species j and species k as you might intuitively expect. The MacArthur and Levins' measure estimates the extent to which the niche space of species k overlaps that of species j . If species A specializes on a subset of foods eaten by a generalist species B, then from species A's viewpoint overlap is total but from species B's viewpoint overlap is only partial. This formulation was devised to mimic the competition coefficients of the Lotka-Volterra equations (MacArthur 1972). Since most ecologists

now agree that overlap measures cannot be used as competition coefficients (Hurlbert 1978, Abrams 1980, Holt 1987) the MacArthur-Levins measure has been largely replaced by a very similar but symmetrical measure first used by Pianka (1973):

$$\hat{O}_{jk} = \frac{\sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sqrt{\sum_i^n \hat{p}_{ij}^2 \sum_i^n \hat{p}_{ik}^2}} \quad (14.13)$$

where

O_{jk} = Pianka's measure of niche overlap between species j and species k
 p_{ij} = Proportion resource i is of the total resources used by species j
 p_{ik} = Proportion resource i is of the total resources used by species k
 n = Total number of resources states

This is a symmetric measure of overlap so that overlap between species A and species B is identical to overlap between species B and species A.

This measure of overlap ranges from 0 (no resources used in common) to 1.0 (complete overlap). It has been used by Pianka (1986) for his comparison of desert lizard communities.

Box 14.2 illustrates the calculation of niche overlap with the MacArthur-Levins measure and the Pianka measure.

Box 14.2 CALCULATION OF NICHE OVERLAP FOR AFRICAN FINCHES

Dolph Schluter measured the diet of two seed-eating finches in Kenya in 1985 from stomach samples and obtained the following results, expressed as number of seeds in stomachs and proportions (in parentheses):

Seed species	Green-winged Pytilia (<i>Pytilia melba</i>)	Vitelline masked weaver (<i>Ploceus velatus</i>)
Sedge # 1	7 (0.019)	0 (0)
Sedge # 2	1 (0.003)	0 (0)
<i>Setaria</i> spp. (grass)	286 (0.784)	38 (0.160)
Grass # 2	71 (0.194)	24 (0.101)
<i>Amaranth</i> spp.	0 (0)	30 (0.127)
<i>Commelina</i> # 1	0 (0)	140 (0.591)

Commelina # 2

0 (0)

5 (0.021)

Total

365 food items

237 food items

MacArthur and Levins' Measure

From equation (14.12):

$$\hat{M}_{jk} = \frac{\sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sum_i \hat{p}_{ij}^2}$$

$$\sum \hat{p}_{ij} \hat{p}_{ik} = (0.019)(0) + (0.003)(0) + (0.784)(0.160) + (0.194)(0.101) + (0)(0.127) + \dots = 0.1453325$$

$$\sum \hat{p}_{ij}^2 = 0.019^2 + 0.003^2 + 0.784^2 + 0.194^2 = 0.652662$$

$$\sum \hat{p}_{ik}^2 = 0.160^2 + 0.101^2 + 0.127^2 + 0.591^2 + 0.021^2 = 0.401652$$

$$\hat{M}_{jk} = \frac{0.14533}{0.6527} = 0.223 \quad \left(\begin{array}{l} \text{extent to which } Pytilia \text{ is} \\ \text{overlapped by } Ploceus \end{array} \right)$$

$$\hat{M}_{kj} = \frac{0.14533}{0.40165} = 0.362 \quad \left(\begin{array}{l} \text{extent to which } Ploceus \text{ is} \\ \text{overlapped by } Pytilia \end{array} \right)$$

Note that these overlaps are not symmetrical, and for this reason this measure is rarely used by ecologists.

Pianka's modification of the MacArthur-Levins measure gives a symmetric measure of overlap that is preferred (equation 14.13):

$$\hat{O}_{jk} = \frac{\sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sqrt{\sum_i^n \hat{p}_{ij}^2 \sum_i^n \hat{p}_{ik}^2}}$$

$$\hat{O}_{jk} = \frac{0.1453325}{\sqrt{(0.6527)(0.40165)}} = 0.284$$

Note that this measure of overlap is just the geometric mean of the two MacArthur and Levins overlaps:

$$\text{Pianka's } O_{jk} = \sqrt{\text{MacArthur and Levins' } M_{jk} M_{kj}}$$

Percentage Overlap

From equation (14.14):

$$\begin{aligned}\hat{P}_{jk} &= \left[\sum_{i=1}^n (\text{minimum } \hat{p}_{ij}, \hat{p}_{ik}) \right] 100 \\ &= (0 + 0 + 0.1603 + 0.1013 + 0 + 0 + 0) 100 = 26.2 \%\end{aligned}$$

Morisita's Measure

From equation (14.15):

$$\hat{C} = \frac{2 \sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sum_i^n \hat{p}_{ij} \left[\frac{(n_{ij}-1)}{(N_j-1)} \right] + \sum_i^n \hat{p}_{ik} \left[\frac{(n_{ik}-1)}{(N_k-1)} \right]}$$

From the calculations given above:

$$\sum \hat{p}_{ij} \hat{p}_{ik} = 0.14533$$

$$\sum \hat{p}_{ij} \left[\frac{(n_{ij}-1)}{N_j-1} \right] = 0.019 \left(\frac{7-1}{365-1} \right) + 0.003 \left(\frac{1-1}{365-1} \right) +$$

$$0.784 \left(\frac{286-1}{365-1} \right) + \dots = 0.6514668$$

$$\sum \hat{p}_{ik} \left[\frac{(n_{ik}-1)}{N_k-1} \right] = 0.160 \left(\frac{38-1}{237-1} \right) + 0.101 \left(\frac{24-1}{237-1} \right) +$$

$$0.127 \left(\frac{30-1}{237-1} \right) + \dots = 0.3989786$$

$$\hat{C} = \frac{2(0.14533)}{0.6514668 + 0.3989786} = 0.277$$

Simplified Morisita Index

From equation (14.16):

$$\hat{C}_H = \frac{2 \sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sum_i^n \hat{p}_{ij}^2 + \sum_i^n \hat{p}_{ik}^2}$$

These summation terms were calculated above for the MacArthur and Levins measures; thus,

$$\hat{C}_H = \frac{2(0.1453325)}{0.652662 + 0.401652} = 0.276$$

Note that the Simplified Morisita index is very nearly equal to the original Morisita measure and to the Pianka modification of the MacArthur-Levins measure.

Horn's Index

From equation (14.17):

$$\hat{R}_o = \frac{\sum (\hat{p}_{ij} + \hat{p}_{ik}) \log(\hat{p}_{ij} + \hat{p}_{ik}) - \sum \hat{p}_{ij} \log \hat{p}_{ij} - \sum \hat{p}_{ik} \log \hat{p}_{ik}}{2 \log 2}$$

Using logs to base e:

$$\begin{aligned} \sum (\hat{p}_{ij} + \hat{p}_{ik}) \log(\hat{p}_{ij} + \hat{p}_{ik}) &= (0.019 + 0) \log(0.019 + 0) + (0.003 + 0) \log(0.003 + 0) \\ &\quad + (0.784 + 0.160) \log(0.784 + 0.160) + \dots = -1.16129 \end{aligned}$$

$$\sum \hat{p}_{ij} \log \hat{p}_{ij} = (0.019) \log 0.019 + (0.003) \log 0.003 + (0.784) \log 0.784 + \dots = -0.60165$$

$$\sum \hat{p}_{ik} \log \hat{p}_{ik} = (0.160) \log 0.160 + (0.101) \log 0.101 + (0.127) \log 0.127 + \dots = -1.17880$$

$$\hat{R}_o = \frac{-1.16129 + 0.60165 + 1.17880}{2 \log 2} = 0.4466$$

Hurlbert's Index

From equation (14.18):

$$\hat{L} = \sum_i^n \left(\frac{\hat{p}_{ij} \hat{p}_{ik}}{a_i} \right)$$

If we assume that all seven seed species are equally abundant ($a_i = 1/7$ for all), we obtain:

$$\hat{L} = \frac{(0.019)(0)}{0.1429} + \frac{(0.003)(0)}{0.1429} + \frac{(0.784)(0.160)}{0.1429} + \dots = 1.015$$

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

14.3.2 Percentage Overlap

This is identical with the *percentage similarity* measure proposed by Renkonen (1938) and is one of the simplest and most attractive measures of niche overlap.

This measure is calculated as a *percentage* (see Chapter 11, page 000) and is given by:

$$\hat{P}_{jk} = \left[\sum_{i=1}^n (\text{minimum } \hat{p}_{ij}, \hat{p}_{ik}) \right] 100 \quad (14.14)$$

where

P_{jk} = Percentage overlap between species j and species k

p_{ij} = Proportion resource i is of the total resources used by species j

p_{ik} = Proportion resource i is of the total resources used by species k

n = Total number of resource states

Percentage overlap is the simplest measure of niche overlap to interpret because it is a measure of the actual area of overlap of the resource utilization curves of the two species. This overlap measure was used by Schoener (1970) and has been labeled the Schoener overlap index (Hurlbert 1978). It would seem preferable to call it the Renkonen index or, more simply, percentage overlap. Abrams (1980) recommends this measure as the best of the measures of niche overlap. One strength of the Renkonen measure is that it is not sensitive to how one divides up the resource states. Human observers may recognize resource categories that animals or plants do not, and conversely organisms may distinguish resources lumped together by human observers. The first difficulty will affect the calculated value of MacArthur and Levins' measure of overlap, but should not affect the percentage overlap measure if sample size is large. The second difficulty is implicit in all niche measurements and emphasizes the need for sound natural history data on the organisms under study.

Box 14.2 illustrates the calculation of the percentage overlap measure of niche overlap.

14.3.3 Morisita's Measure

Morisita's index of similarity (Chapter 11, page 000) first suggested by Morisita (1959) can also be used as a measure of niche overlap. It is calculated from the formula:

$$\hat{C} = \frac{2 \sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sum_i^n \hat{p}_{ij} \left[\frac{(n_{ij}-1)}{(N_j-1)} \right] + \sum_i^n \hat{p}_{ik} \left[\frac{(n_{ik}-1)}{(N_k-1)} \right]} \quad (14.15)$$

where

C = Morisita's index of niche overlap between species j and k
 p_{ij} = Proportion resource i is of the total resources used by species j
 p_{ik} = Proportion resource i is of the total resources used by species k
 n_{ij} = Number of individuals of species j that use resource category i
 n_{ik} = Number of individuals of species k that use resource category i
 N_j, N_k = Total number of individuals of each species in sample

$$\sum_{i=1}^n n_{ij} = N_j, \quad \sum_{i=1}^n n_{ik} = N_k$$

Box 14.2 illustrates the calculation of the Morisita index of niche overlap.

Morisita's measure was formulated for counts of individuals and not for other measures of usage like proportions or biomass. If your data are not formulated as numbers of individuals, you can use the next measure of niche overlap, the Simplified Morisita Index, which is very similar to Morisita's original measure.

14.3.4 Simplified Morisita Index

The simplified Morisita index proposed by Horn (1966) is another similarity index that can be used to measure niche overlap. It is sometimes called the *Morisita-Horn index*. It is calculated as outlined in Box 14.2 (page 000), from the formula:

$$\hat{C}_H = \frac{2 \sum_i^n \hat{p}_{ij} \hat{p}_{ik}}{\sum_i^n \hat{p}_{ij}^2 + \sum_i^n \hat{p}_{ik}^2} \quad (14.16)$$

where

C_H = Simplified Morisita Index of overlap (Horn 1966) between species j and species k

p_{ij} = Proportion resource i is of the total resources used by species j
 p_{ik} = Proportion resource i is of the total resources used by species k
 n = Total number of resource states ($i = 1, 2, 3, \dots, n$)

The Simplified Morisita index is very similar to the Pianka modification of the MacArthur and Levins measure of niche overlap, as can be seen by comparing equations (14.13) and (14.16). Linton *et al.* (1981) showed that for a wide range of simulated populations, the values obtained for overlap were nearly identical for the Simplified Morisita and the Pianka measures. In general for simulated populations Linton *et al.* (1981) found that the Pianka measure was slightly less precise (larger standard errors) than the Simplified Morisita index in replicated random samples from two hypothetical distributions, and they recommended the Simplified Morisita index as better.

14.3.5 Horn's Index of Overlap

Horn (1966) suggested an index of similarity or overlap based on information theory. It is calculated as outlined in Chapter 11 (page 000).

$$\hat{R}_o = \frac{\sum (\hat{p}_{ij} + \hat{p}_{ik}) \log(\hat{p}_{ij} + \hat{p}_{ik}) - \sum \hat{p}_{ij} \log \hat{p}_{ij} - \sum \hat{p}_{ik} \log \hat{p}_{ik}}{2 \log 2} \quad (14.17)$$

where

R_o = Horn's index of overlap for species j and k
 p_{ij} = Proportion resource i is of the total resources utilized by species j
 p_{ik} = Proportion resource i is of the total resources utilized by species k and
 any base of logarithms may be used.

Box 14.2 illustrates these calculation for Horn's index of overlap.

14.3.6 Hurlbert's Index

None of the previous four measures of niche overlap recognize that the resource states may vary in abundance. Hurlbert (1978) defined niche overlap as *the degree to which the frequency of encounter between two species is higher or lower than it would be if each species utilized each resource state in proportion to the abundance of that resource state*. The appropriate measure of niche overlap that allows resource states to vary in size is as follows:

$$\hat{L} = \sum_i^n \left(\frac{\hat{p}_{ij} \hat{p}_{ik}}{\hat{a}_i} \right) \quad (14.18)$$

where

L = Hurlbert's measure of niche overlap between species j and species k

p_{ij} = Proportion resource i is of the total resources utilized by species j

p_{ik} = Proportion resource i is of the total resources utilized by species k

a_i = Proportional amount or size of resource state i ($\sum a_i = 1.0$)

Hurlbert's overlap measure is not like other overlap indices in ranging from 0 to 1. It is 1.0 when both species utilize each resource state in proportion to its abundance, 0 when the two species share no resources, and > 1.0 when the two species both use certain resource states more intensively than others and the preferences of the two species for resources tend to coincide.

Hurlbert's index L has been criticized by Abrams (1980) because its value changes when resource states used by neither one of the two species are added to the resource matrix. Hurlbert (1978) considers this an advantage of his index because it raised the critical question of what resource states one should include in the resource matrix.

Box 14.2 illustrates the calculation of Hurlbert's index of overlap.

14.3.7 Which Overlap Index is Best?

The wide variety of indices available to estimate niche overlap has led many ecologists to argue that the particular index used is relatively unimportant, since they all give the same general result (Pianka 1974).

One way to evaluate overlap indices is to apply them to artificial populations with known overlaps. Three studies have used simulation techniques to investigate the bias of niche overlap measures and their sensitivity to sample size. Ricklefs and Lau (1980) analyzed four indices of niche overlap. Smith and Zaret (1982) analyzed 7 measures of niche overlap.

Ricklefs and Lau (1980) showed by computer simulation that the sampling distribution of all measures of niche overlap are strongly affected by sample size (Figure 14.3). When niche overlap is complete, there is a negative bias in the

percentage overlap measure, and this negative bias is reduced but not eliminated as sample size increases (Figure 14.3). This negative bias at high levels of overlap seems to be true of all measures of niche overlap (Ricklefs and Lau 1980, Linton *et al.* 1981).

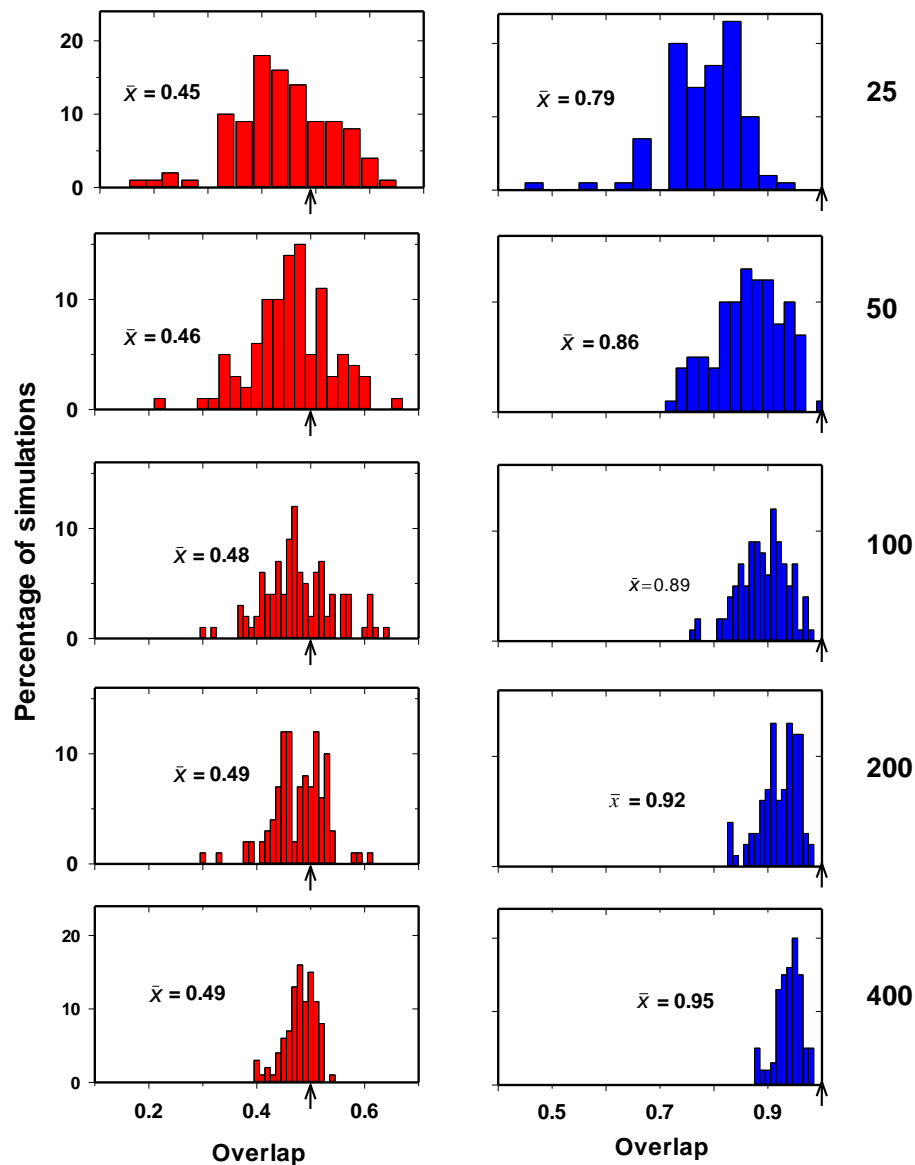


Figure 14.3 Sampling distributions of the percentage overlap measure of niche breadth (equation 14.14) for probability distributions having five resource categories. Sample sizes were varied from $n = 25$ at top to $n = 400$ at the bottom. The expected values of niche overlap are marked by the arrows (0.5 for the left side and 1.0 for the right side). Simulations were done 100 times for each example. (After Ricklefs and Lau 1980).

Smith and Zaret (1982) have presented the most penetrating analysis of bias in estimating niche overlap. Figure 14.4 shows the results of their simulations. Bias (= true value – estimated value) increases in all measures of overlap as the number of resources increases, and overlap is always underestimated. This effect is particularly strong for the percentage overlap measure. The amount of bias can be quite large when the number of resource categories is large, even if sample size is reasonably large ($N = 200$) (Fig. 14.4(a)). All niche overlap measures show decreased bias as sample size goes up (Fig. 14.4(b)). Increasing the smaller sample size has a much greater effect than increasing the larger sample size. The bias is minimized when both species are sampled equally ($N_1 = N_2$). As evenness of resource use increases, bias increases only for the percentage overlap measure and the Simplified Morisita index (Fig. 14.4(c)).

The percentage overlap measure (eq. 14.14) and the Simplified Morisita Index (eq. 14.16) are the two most commonly used measures of niche overlap, yet they are the two measures that Smith and Zaret (1982) found to be most biased under changing numbers of resources, sample size, and resource evenness (Fig. 14.4). The best overlap measure found by Smith and Zaret (1982) is Morisita's measure (equation 14.15), which is not graphed in Figure 14.4 because it has nearly zero bias at all sample sizes and also when there are a large number of resources. The recommendation to minimize bias is thus to use Morisita's measure to assess niche overlap. If resource use cannot be expressed as numbers of individuals (which Morisita's measure requires), the next best measure of overlap appears to be Horn's index (Smith and Zaret 1982, Ricklefs and Lau 1980).

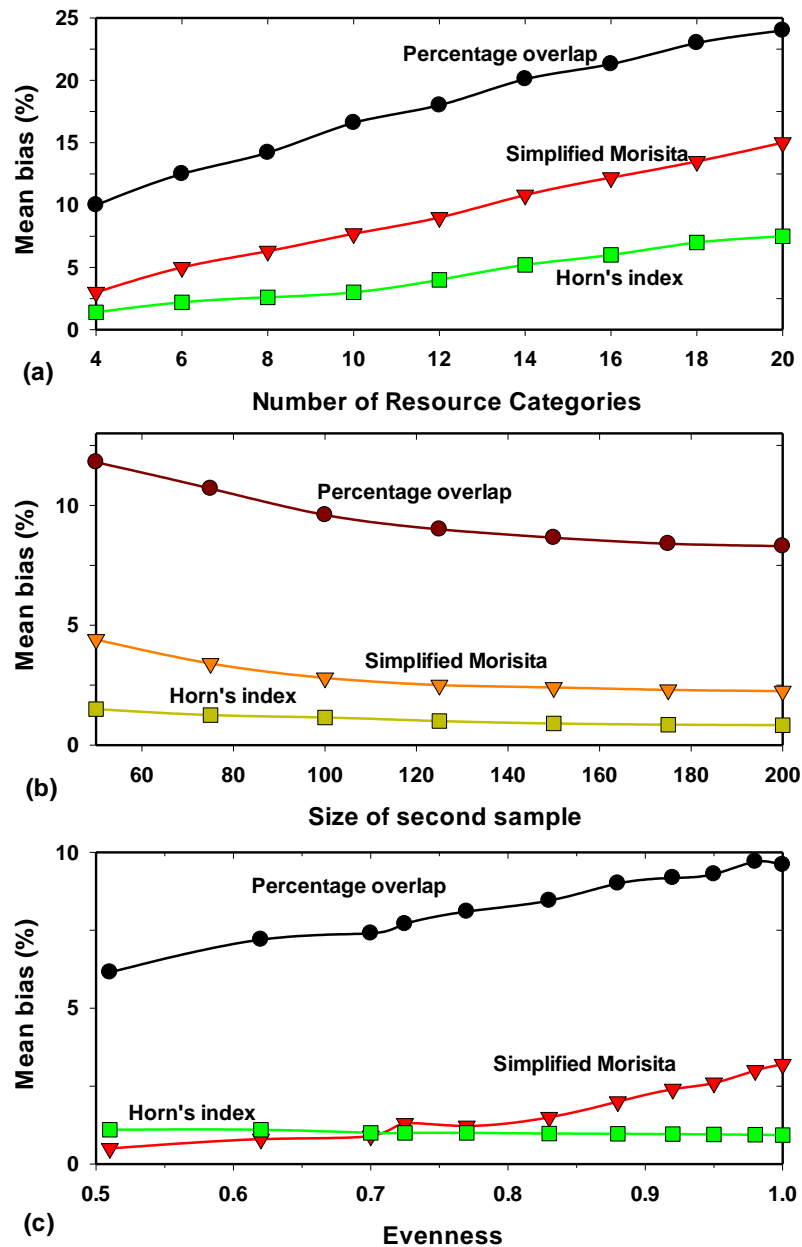


Figure 14.4 Bias in niche overlap measures. Bias is measured as (true value–estimated value) expressed as a percentage. All overlap bias results in an underestimation of the overlap. (a) Effect of changing the number of resource categories on the bias of the percentage overlap measure (eq. 13.14), the simplified Morisita measure (eq. 13.16), and the Horn index (eq. 13.17). Simulations were run with equal sample sizes for the two species. (b) Effect of the size of the second sample on bias. The first sample was $n_1 = 100$ and four resource categories were used. (c) Effect of evenness of resource use on the bias of measures of niche overlap. Evenness is 1.0 when all four resource categories are used equally. Sample sizes for both species were 100 in these simulations. (Source: Smith and Zaret 1982)

If confidence intervals or tests of significance are needed for niche overlap measures, two approaches may be used: first, obtain replicate sets of samples, calculate the niche overlap for each set, and calculate the confidence limits or statistical tests from these replicate values (Horn 1966, Hurlbert 1978). Or alternatively, use statistical procedures to estimate standard errors for these indices.

Three statistical procedures can be used to generate confidence intervals for measures of niche overlap (Mueller and Altenberg 1985, Maurer 1982, Ricklefs and Lau 1980): the delta method, the jackknife method, and the bootstrap. The delta method is the standard analytical method used in mathematical statistics for deriving standard errors of any estimated parameter. Standard errors estimated by the delta method are not always useful to ecologists because they are difficult to derive for complex ecological measures and they cannot be used to estimate confidence limits that are accurate when sample sizes are small and variables do not have simple statistical distributions. For this reason the jackknife and bootstrap methods — resampling methods most practical with a computer — are of great interest to ecologists (see Chapter 15, page 000). Mueller and Altenberg (1985) argue that in many cases the populations being sampled may be composed of several unrecognized subpopulations (e.g. based on sex or age differences). If this is the case, the bootstrap method is the best to use. We will discuss the bootstrap method in Chapter 16 (page 000). See Mueller and Altenberg (1985) for a discussion of the application of the bootstrap to generating confidence limits for niche overlap measures.

The original goal of measuring niche overlap was to infer interspecific competition (Schoener 1974). But the relationship between niche overlap and competition is poorly defined in the literature. The particular resources being studied may not always be limiting populations, and species may overlap with no competition. Conversely, MacArthur (1968) pointed out that zero niche overlap did not mean that interspecific competition was absent. Abrams (1980) pointed out that niche overlap does not always imply competition, and that in many cases niche overlap should be used as a descriptive measure of community organization. The relationship between competition and niche overlap is complex (Holt 1987).

14.4 MEASUREMENT OF HABITAT AND DIETARY PREFERENCES

If an animal is faced with a variety of possible food types, it will prefer to eat some and will avoid others. We ought to be able to measure "preference" very simply by comparing usage and availability. Manly *et al.* (1993) have recently reviewed the problem of resource selection by animals and they provide a detailed statistical discussion of the problems of measuring preferences. Note that resource selection may involve habitat preferences, food preferences, or nest site preferences. We will discuss here more cases of diet preference but the principles are the same for any resource selection problem.

Three general study designs for measuring preferences are reviewed by Manly *et al.* (1993):

- **Design I:** With this design all measurements are made at the population level and individual animals are not recognized. Used and unused resources are sampled for the entire study area with no regard for individuals. For example, fecal pellets are recorded as present or absent on a series of quadrats.
- **Design II:** Individual animals are identified and the use of resources measured for each individual, but the availability of resources is measured at the population level for the entire study zone. For example, stomach contents of individuals can be measured and compared with the food available on the study area.
- **Design III:** Individual animals are measured as in Design II but in addition the resources available for each individual are measured. For example, habitat locations can be measured for a set of radio-collared individuals and these can be compared to the habitats available within the home range of each individual.

Clearly Designs II and III are most desirable, since they allow us to measure resource preferences for each individual. If the animals studied are a random sample of the population, we can infer the average preference of the entire population, as in Design I. But in addition we can ask questions about preferences of different age or sex groups in the population.

The key problem in all these designs is to estimate the resource selection probability function, defined as the probability of use of resources of different types. In many cases we cannot estimate these probabilities in an absolute sense but we can estimate a set of preferences that are proportional to these probabilities. We can

thus conclude, for example, that moose prefer to eat the willow *Salix glauca* without knowing exactly what fraction of the willows are in fact eaten by the moose in an area.

Several methods have been suggested for measuring preferences (Chesson 1978, Cock 1978, Johnson 1980, Manly *et al.* 1993). The terminology for all the indices of preference is the same, and can be described as follows: Assume an array of n types of food (or other resources) in the environment, and that each food type has m_i items or individuals ($i = 1, 2 \dots n$), and the total abundance of food items is:

$$M = \sum_{i=1}^n m_i \quad (14.19)$$

where M = total number of food items available

Let u_i be the number of food items of species i in the diet so that we have a second array of items selected by the species of interest. The total diet is given by:

$$U = \sum_{i=1}^n u_i \quad (14.20)$$

where U = total number of food items in the diet

In most cases the array of items in the environment and the array of food items in the diet are expressed directly as proportions or percentages. Table 14.2 gives an example of dietary data in meadow voles.

Most measures of "preference" assume that the density of the food items available is constant. Unless food items are replaced as they are eaten, food densities will decrease. If any preference is shown, the relative proportion of the food types will thus change under exploitation. If the number of food items is very large, or food can be replaced as in a laboratory test, this problem of exploitation is unimportant. Otherwise you must be careful in choosing a measure of preference (Cock 1978).

TABLE 14.2 INDEX OF ABUNDANCE OF 15 GRASSES AND HERBS IN AN INDIANA GRASSLAND AND PERCENTAGE OF THE DIET OF THE MEADOW VOLE *Microtus pennsylvanicus* (BY VOLUME) ESTIMATED

FROM STOMACH SAMPLES.

Plant	Grassland		Diet	
	Index of abundance	Proportion of total	Percent of total volume	Percent of plant volume
<i>Poa</i>	6.70	26.8	32.1	36.9
<i>Muhlenbergia</i>	6.30	25.2	14.6	16.8
<i>Panicum</i>	2.90	11.6	24.7	28.4
<i>Achillea</i>	2.90	11.6	4.7	5.4
<i>Plantago</i>	2.25	9.0	5.8	6.7
<i>Daucus</i>	0.70	2.8	0	0
<i>Aster</i>	0.55	2.2	0	0
<i>Solidago</i>	0.55	2.2	0	0
<i>Bromus</i>	0.50	2.0	0	0
<i>Ambrosia</i>	0.40	1.6	0	0
<i>Rumex</i>	0.35	1.4	0	0
<i>Taraxacum</i>	0.30	1.2	2.1	2.4
<i>Phleum</i>	0.20	0.8	1.4	1.6
<i>Asclepias</i>	0.20	0.8	0	0
<i>Oxalis</i>	0.20	0.8	1.6	1.8
Total	25.00	100.0	87.0	100.0
Other items (roots, fungi, insects)			13.0	

Source: Zimmerman, 1965. { #4975 }

How can we judge the utility of measures of preference? Cock (1978) has suggested that three criteria should be considered in deciding on the suitability of an index of preference:

(1) *scale* of the index: it is best to have both negative and positive preference scales of equal size, symmetric about 0.

(2) *adaptability* of the index: it is better to have the ability to include more than two food types in the index.

(3) *range* of the index: it is best if maximum index values are attainable at all combinations of food densities.

I will now consider several possible measures of "preference" and evaluate their suitability on the basis of these criteria.

14.4.1 Forage Ratio

The simplest measure of preference is the *forage ratio* first suggested by Savage (1931) and by Williams and Marshall (1938):

$$\hat{w}_i = \frac{\hat{o}_i}{\hat{p}_i} \quad (14.21)$$

where

w_i = Forage ratio for species i (Index 2 of Cock (1978))

o_i = Proportion or percentage of species i in the diet

p_i = Proportion or percentage of species i available in the environment

The forage ratio is more generally called the *selection index* by Manly *et al.* (1993), since not all resource selection problems involve food. One example will illustrate the forage ratio. Lindroth and Batzli (1984) found that *Bromus inermis* comprised 3.6% of the diet of meadow voles in bluegrass fields when this grass comprised 0.3% of the vegetation in the field. Thus the forage ratio or selection index for *Bromus inermis* is:

$$\hat{w}_i = \frac{3.6}{0.3} = 12.0$$

Selection indices above 1.0 indicate preference, values less than 1.0 indicate avoidance. Selection indices may range from 0 to ∞ , which is a nuisance and consequently Manly *et al.* (1993) suggest presenting forage ratios or selection indices as standardized ratios which sum to 1.0 for all resource types:

$$\hat{B}_i = \frac{\hat{w}_i}{\sum_{i=1}^n \hat{w}_i} \quad (14.22)$$

where:

\hat{B}_i = Standardized selection index for species i

\hat{w}_i = Forage ratio for species i (eq. 14.19)

Standardized ratios of (1/number of resources) indicate no preference. Values below this indicate relative avoidance, values above indicate relative preference.

Table 14.3 illustrates data on selection indices from a Design I type study of habitat selection by moose in Minnesota.

TABLE 14.3 SELECTION INDICES FOR MOOSE TRACKS IN FOUR HABITAT TYPES ON 134 SQUARE KILOMETERS OF THE LITTLE SIOUX BURN IN MINNESOTA DURING THE WINTER OF 1971-72.¹

Habitat	Proportion available (p_i)	No. of moose tracks (u_i)	Proportion of tracks in habitat (o_i)	Selection index (w_i)	Standardized selection index ² (B_i)
Interior burn	0.340	25	0.214	0.629	0.110
Edge burn	0.101	22	0.188	1.866	0.326
Forest edge	0.104	30	0.256	2.473	0.433
Forest	0.455	40	0.342	0.750	0.131
Total	1.000	117	1.000	5.718	1.000

¹ Data from Neu *et al.* (1974)

² Standardized selection indices above $\left(\frac{1}{\text{number of resources}}\right)$ or 0.25 in this case indicate preference.

Statistical tests of selection indices depend on whether the available resources are censused completely or estimated with a sample. In many cases of habitat selection, air photo maps are used to measure the area of different habitat types, so that there is a complete census with (in theory) no errors of estimation. Or in laboratory studies of food preference, the exact ratios of the foods made available are set by the experimenter. In other cases sampling is carried out to estimate the available resources, and these availability ratios are subject to sampling errors.

Let us consider the first case of a complete census of available resources so that there is no error in the proportions available (p_i). To test the null hypothesis that animals are selecting resources at random, Manly *et al.* (1993) recommend the G-test:

$$\chi^2 = 2 \sum_{i=1}^n \left[u_i \ln \left(\frac{u_i}{U p_i} \right) \right] \quad (14.23)$$

where

- u_i = Number of observations using resource i
 U = Total number of observations of use = $\sum u_i$
 χ^2 = Chi-square value with $(n-1)$ degrees of freedom
 $(H_0 : \text{random selection})$
 n = Number of resource categories

The standard error of a selection ratio can be approximated by:

$$s_{\hat{w}_i} = \sqrt{\frac{\hat{o}_i(1-\hat{o}_i)}{U\hat{p}_i^2}} \quad (14.24)$$

where

- $\hat{s}_{\hat{w}_i}$ = Standard error of the selection ratio for resource i
 \hat{o}_i = Observed proportion of use of resource i
 U = Total number of observations of use
 \hat{p}_i = Proportion of type i resources that are available in study area

The confidence limits for a single selection ratio is the usual one:

$$\hat{w}_i \pm z_\alpha \hat{s}_{\hat{w}_i} \quad (14.25)$$

where z_α is the standard normal deviate (1.96 for 95% confidence, 2.576 for 99%, and 1.645 for 90% confidence).

Two selection ratios can be compared to see if they are significantly different with the following test from Manly *et al.* (1993, p.48):

$$\chi^2 = \frac{(\hat{w}_i - \hat{w}_j)^2}{\text{variance}(\hat{w}_i - \hat{w}_j)} \quad (14.26)$$

where

$$\text{variance}(\hat{w}_i - \hat{w}_j) = \frac{o_i(1-o_i)}{Up_i^2} - \frac{2o_i o_j}{Up_i p_j} + \frac{o_j(1-o_j)}{Up_j^2}$$

- χ^2 = Chi-square value with 1 degree of freedom ($H_0 : \hat{w}_i = \hat{w}_j$)
 \hat{o}_i, \hat{o}_j = Observed proportion of use of resource i or j
 U = Total number of observations of use
 \hat{p}_i, \hat{p}_j = Proportion of type i or j resources that are available in study area

Box 14.3 illustrates the calculation of selection indices and their confidence limits for the moose data in Table 14.3.

Box 14.3 CALCULATION OF SELECTION INDICES FOR MOOSE IN FOUR HABITAT TYPES

Neu *et al.* (1974) provided these data for moose in Minnesota:

Habitat	Proportion available (p_i)	No. of moose tracks (u_i)	Proportion of tracks in habitat (o_i)
Interior burn	0.340	25	0.214
Edge burn	0.101	22	0.188
Forest edge	0.104	30	0.256
Forest	0.455	40	0.342
Total	1.000	117	1.000

This is an example of Design I type data in which only population-level information is available. Since the proportion available was measured from aerial photos, we assume it is measured exactly without error.

The selection index is calculated from equation (14.21):

$$\hat{w}_i = \frac{\hat{o}_i}{\hat{p}_i}$$

For the interior burn habitat:

$$\hat{w}_1 = \frac{o_1}{p_1} = \frac{25/117}{0.340} = 0.629$$

Similarly for the other habitats:

$$\begin{aligned}\hat{w}_2 &= \frac{22/117}{0.101} = 1.866 \\ \hat{w}_3 &= 2.473 \\ \hat{w}_4 &= 0.750\end{aligned}$$

We can test the hypothesis of equal use of all four habitats with equation (14.23):

$$\begin{aligned}
\chi^2 &= 2 \sum_{i=1}^n \left[\hat{u}_i \ln \left(\frac{u_i}{U \hat{p}_i} \right) \right] \\
&= 2 \left[25 \left(\log_e \left(\frac{25}{117(0.340)} \right) \right) + 22 \left\{ \log_e \left(\frac{22}{117(0.101)} \right) \right\} + \dots \right] \\
&= 35.40 \text{ with 3.d.f. } (p < 0.01)
\end{aligned}$$

This value of chi-square is considerably larger than the critical value of 3.84 at $\alpha = 5\%$, so we reject the null hypothesis that moose use all these habitats equally.

We can compute the confidence limits for these selection indices from equation (14.24) and (14.25). For the interior burn habitat:

$$\hat{s}_{\bar{w}_1} = \sqrt{\frac{\hat{o}_1(1-\hat{o}_1)}{U \hat{p}_1^2}} = \sqrt{\frac{0.214(1-0.214)}{117(0.340^2)}} = 0.112$$

The 95% confidence limits for this selection index must be corrected using the Bonferroni correction for (α/n) are given by:

$$\begin{aligned}
&\hat{w}_i \pm z_{\alpha} \hat{s}_{\bar{w}_i} \\
&0.629 \pm z_{0.0125} (0.112) \text{ or } 0.629 \pm 2.498(0.112) \text{ or } 0.350 \text{ to } 0.907
\end{aligned}$$

The Bonferroni correction corrects for multiple comparisons to maintain a consistent overall error rate by reducing the α value to α/n and thus in this example using $z_{0.0125}$ instead of $z_{0.05}$.

Similar calculations can be done for the confidence limits for the edge burn (0.968 to 2.756). Since these two confidence belts do not overlap we suspect that these two habitats are selected differently.

We can now test if the selection index for the interior burn habitat differs significantly from that for the edge burn habitat. From equation (14.26):

$$\chi^2 = \frac{(\hat{w}_i - \hat{w}_j)^2}{\text{variance}(\hat{w}_i - \hat{w}_j)}$$

The variance of the difference is calculated from:

$$\begin{aligned}
\text{variance}(\hat{w}_i - \hat{w}_j) &= \frac{\hat{o}_i(1-\hat{o}_i)}{U \hat{p}_i^2} - \frac{2 \hat{o}_i \hat{o}_j}{U \hat{p}_i \hat{p}_j} + \frac{\hat{o}_j(1-\hat{o}_j)}{U \hat{p}_j^2} \\
&= \frac{0.214(1-0.214)}{117(0.340^2)} - \frac{2(0.214)(0.188)}{117(0.340)(0.101)} + \frac{0.188(1-0.188)}{117(0.101^2)} \\
&= 0.1203
\end{aligned}$$

Thus:

$$\chi^2 = \frac{(\hat{w}_i - \hat{w}_j)^2}{\text{variance}(\hat{w}_i - \hat{w}_j)} = \frac{(0.629 - 1.866)^2}{0.1203} = 12.72 \quad (p < 0.01)$$

This chi-square has 1 d.f., and we conclude that these two selection indices are significantly different, edge burn being the preferred habitat..

These calculations can be carried out by Program SELECT (Appendix 2, page 000).

In the second case in which the resources available must be estimated from samples (and hence have some possible error), the statistical procedures are slightly altered. To test the null hypothesis of no selection, we compute the G-test in a manner similar to that of equation (14.23):

$$\chi^2 = 2 \sum_{i=1}^n \left[\hat{u}_i \ln \left(\frac{\hat{u}_i}{U \hat{p}_i} \right) + \hat{m}_i \ln \left(\frac{\hat{m}_i}{(\hat{m}_i + \hat{u}_i M / (U + M))} \right) \right] \quad (14.27)$$

where

- \hat{u}_i = Number of observations using resource i
- \hat{m}_i = Number of observations of available resource i
- U = Total number of observations of use = $\sum u_i$
- M = Total number of observations of availability = $\sum m_i$
- χ^2 = Chi-square value with $(n-1)$ degrees of freedom (H_0 : random selection)
- n = Number of resource categories

Similarly, to estimate a confidence interval for the selection ratio when availability is sampled, we estimate the standard error of the selection ratio as :

$$\hat{s}_{\bar{w}_i} = \sqrt{\frac{(1 - \hat{o}_i)}{U \hat{o}_i} + \frac{(1 - \hat{p}_i)}{\hat{p}_i M}} \quad (14.28)$$

where all the terms are defined above. Given this standard error, the confidence limits for the selection index are determined in the usual way (equation 14.25).

We have discussed so far only Design I type studies. Design II studies in which individuals are recognized allow a finer level of analysis of resource selection. The general principles are similar to those just provided for Design I studies, and details of the calculations are given in Manly *et al.* (1993, Chapter 4).

When a whole set of confidence intervals are to be computed for a set of proportions of habitats utilized, one should not use the simple binomial formula because the anticipated confidence level (e.g. 95%) is often not achieved in this multinomial situation (Cherry 1996). Cherry (1996) showed through simulation that acceptable confidence limits for the proportions of resources utilized could be obtained with Goodman's (1965) formulas as follows:

$$\hat{L}_{o_i} = \frac{C + 2(\hat{u}_i - 0.5) - \sqrt{C(C + 4(\hat{u}_i - 0.5)(U - \hat{u}_i + 0.5))}}{2(C + U)} \quad (14.29)$$

$$\hat{U}_{o_i} = \frac{C + 2(\hat{u}_i + 0.5) - \sqrt{C(C + 4(\hat{u}_i + 0.5)(U - \hat{u}_i - 0.5))}}{2(C + U)} \quad (14.30)$$

where

\hat{L}_{o_i} = Lower confidence limit for the proportion of habitat i used

\hat{U}_{o_i} = Upper confidence limit for the proportion of habitat i used

C = Upper α/n percentile of the χ^2 distribution with 1 d.f.

\hat{u}_i = Number of observations of resource i being used

U = Total number of observation of resource use

n = Number of habitats available or number of resource states

These confidence limits can be calculated in Program SELECT (Appendix 2, page 000)

14.4.2 Murdoch's Index

A number of indices of preference are available for the 2-prey case in which an animal is choosing whether to eat prey species a or prey species b . Murdoch (1969) suggested the index C such that:

$$\frac{\hat{r}_a}{\hat{r}_b} = C \left(\frac{\hat{n}_a}{\hat{n}_b} \right) \quad \text{or} \quad C = \left(\frac{\hat{r}_a}{\hat{r}_b} \right) \left(\frac{\hat{n}_b}{\hat{n}_a} \right) \quad (14.31)$$

where C = Murdoch's Index of preference (Index 4 of Cock (1978))

r_a, r_b = Proportion of prey species a, b in diet

n_a, n_b = Proportion of prey species a, b in the environment

Murdoch's index is similar to the instantaneous selective coefficient of Cook (1971) and the survival ratio of Paulik and Robson (1969), and was used earlier by Cain and Sheppard (1950) and Tinbergen (1960). Murdoch's index is limited to comparisons of the relative preference of two prey species, although it can be adapted to the multiprey case by pooling prey into two categories: species A and all-other-species.

Murdoch's index has the same scale problem as the forage ratio - ranging from 0 to 1.0 for negative preference and from 1.0 to infinity for positive preference. Jacobs (1974) pointed out that by using the logarithm of Murdoch's index, symmetrical scales for positive and negative preference can be achieved. Murdoch's index has the desirable attribute that actual food densities do not affect the maximum attainable value of the index C.

14.4.3 Manly's α

A simple measure of preference can be derived from probability theory using the probability of encounter of a predator with a prey and the probability of capture upon encounter (Manly *et al.* 1972, Chesson 1978). Chesson (1978) argues strongly against Rapport and Turner (1970) who attempted to separate *availability* and *preference*. Preference, according to Chesson (1978) reflects any deviation from random sampling of the prey, and therefore includes all the biological factors that affect encounter rates and capture rates, including availability.

Two situations must be distinguished to calculate Manly's α as a preference index (Chesson 1978).

Constant Prey Populations

When the number of prey eaten is very small in relation to the total (or when replacement prey are added in the laboratory) the formula for estimating α is:

$$\hat{\alpha}_i = \frac{\hat{r}_i}{\hat{n}_i} \left(\frac{1}{\sum \left(\frac{\hat{r}_j}{\hat{n}_j} \right)} \right) \quad (14.32)$$

where α_i = Manly's alpha (preference index) for prey type i
 r_i, r_j = proportion of prey type i or j in the diet (i and $j = 1, 2, 3 \dots m$)
 n_i, n_j = proportion of prey type i or j in the environment
 m = number of prey types possible

Note that the alpha values are normalized so that

$$\sum_{i=1}^m \hat{\alpha}_i = 1.0 \quad (14.33)$$

When selective feeding does not occur, $\alpha_i = 1/m$ (m = total number of prey types). If α_i is greater than $(1/m)$, then prey species i is preferred in the diet. Conversely, if α_i is less than $(1/m)$, prey species i is avoided in the diet.

Given estimates of Manly's α for a series of prey types, it is easy to eliminate one or more prey species and obtain a relative preference for those remaining (Chesson 1978). For example, if 4 prey species are present, and you desire a new estimate for the alphas without species 2 present, the new alpha values are simply:

$$\alpha_1 = \frac{\alpha_1}{\alpha_1 + \alpha_3 + \alpha_4} \quad (14.34)$$

and similarly for the new α_3 and α_4 . One important consequence of this property is that you should not compare α values from two experiments with different number of prey types, since their expected values differ.

Variable Prey Populations.

When a herbivore or a predator consumes a substantial fraction of the prey available, or in laboratory studies in which it is not possible to replace prey as they are consumed, one must take into account the changing numbers of the prey species in estimating alphas. This is a much more complex problem than that outlined above for the constant prey case. Chesson (1978) describes one method of estimation. Manly (1974) showed that an approximate estimate of the preference index for experiments in which prey numbers are declining is given by:

$$\hat{\alpha}_i = \frac{\log \hat{p}_i}{\sum_{j=1}^m \hat{p}_j} \quad (14.35)$$

where α_i = Manly's alpha (preference index) for prey type i
 p_i, p_j = Proportion of prey i or j remaining at the end of the experiment ($i = 1, 2, 3 \dots m$) ($j = 1, 2, 3, m$) = e_i / n_i
 e_i = Number of prey type i remaining uneaten at end of experiment
 n_i = Initial number of prey type i in experiment
 m = Number of prey types

Any base of logarithms may be used and will yield the same final result. Manly (1974) gives formulas for calculating the standard error of these α values. Manly (1974) suggested that equation (14.35) provided a good approximation to the true values of α when the number of individuals eaten *and* the number remaining uneaten at the end were all larger than 10.

There is a general problem in experimental design in estimating Manly's α for a variable prey population. If a variable prey experiment is stopped before too many individuals have been eaten, it may be analyzed as a constant prey experiment with little loss in accuracy. But otherwise the stopping rule should be that for all prey species both the number eaten and the number left uneaten should be greater than 10 at the end of the experiment.

Manly's α is also called Chesson's index in the literature. Manly's α is strongly affected by the values observed for rare resource items and is affected by the number of resource types used in a study (Confer and Moore 1987).

Box 14.4 illustrates the calculation of Manly's alpha. Program PREFER (Appendix 11, page 000) does these calculations.

Box 14.4 CALCULATION OF MANLY'S ALPHA AS AN INDEX OF PREFERENCE

1. Constant Prey Population

Three color-phases of prey were presented to a fish predator in a large aquarium. As each prey was eaten, it was immediately replaced with another individual. One experiment produced these results:

	Type 1 Prey	Type 2 prey	Type 3 prey
No. of prey present in the environment at all times	4	4	4

Proportion present, n_i	0.333	0.333	0.333
Total number eaten during experiment	105	67	28
Proportion eaten, r_i	0.525	0.335	0.140

From equation (14.32):

$$\hat{\alpha}_i = \frac{\hat{r}_i}{\hat{n}_i} \left(\frac{1}{\sum \left(\frac{\hat{r}_j}{\hat{n}_j} \right)} \right)$$

$$\hat{\alpha}_1 = \frac{0.525}{0.333} \left[\frac{1}{(0.525/0.333) + (0.335/0.333) + (0.140/0.333)} \right] = 0.52$$

(preference for type 1 prey)

$$\hat{\alpha}_2 = \frac{0.335}{0.333} \left(\frac{1}{3.00} \right) = 0.34 \text{ (preference for type 2 prey)}$$

$$\hat{\alpha}_3 = \frac{0.140}{0.333} \left(\frac{1}{3.00} \right) = 0.14 \text{ (preference for type 3 prey)}$$

The α values measure the probability that an individual prey item is selected from a particular prey class when all prey species are equally available.

Since there are 3 prey types, α values of 0.33 indicate no preference. In this example prey type 1 is highly preferred and prey type 3 is avoided.

2. Variable Prey Population

The same color-phases were presented to a fish predator in a larger aquarium but no prey items were replaced after one was eaten, so the prey numbers declined during the experiment. The results obtained were:

	Type 1 prey	Type 2 prey	Type 3 prey
No. of prey present at start of experiment, n_i	98	104	54
No. of prey alive at end of experiment, e_i	45	66	43
Proportion of prey alive at end of experiment, p_i	0.459	0.635	0.796

From equation (14.35):

$$\hat{\alpha}_i = \frac{\log \hat{p}_i}{\sum_{j=1}^m \hat{p}_j}$$

Using logs to base e, we obtain:

$$\hat{\alpha}_1 = \frac{\log_e(0.459)}{\log_e(0.459) + \log_e(0.635) + \log_e(0.796)} = \frac{-0.7783}{-1.4608} = 0.53$$

$$\hat{\alpha}_2 = \frac{\log_e(0.635)}{-1.4608} = 0.31$$

$$\hat{\alpha}_3 = \frac{\log_e(0.796)}{-1.4608} = 0.16$$

As in the previous experiment, since there are 3 prey types, α values of 0.33 indicate no preference. Prey type 1 is highly preferred and prey type 3 is avoided.

Manly (1974) shows how the standard errors of these α values can be estimated.

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

14.4.4 Rank Preference Index

The calculation of preference indices is critically dependent upon the array of resources that the investigator includes as part of the "available" food supply (Johnson 1980). Table 14.4 illustrates this with a hypothetical example. When a common but seldom-eaten food species is included or excluded in the calculations, a complete reversal of which food species are preferred may arise.

TABLE 14.4 HYPOTHETICAL EXAMPLE OF HOW THE INCLUSION OF A COMMON BUT SELDOM-USED FOOD ITEM WILL AFFECT THE PREFERENCE CLASSIFICATION OF A FOOD SPECIES

Food species	Percent in diet	Percent in environment	Classification
Case A - species x included			
x	2	60	Avoided
y	43	30	Preferred

z	55	10	Preferred
Case B - species x not included			
y	44	75	Avoided
z	56	25	Preferred
Source: Johnson, 1980.			

One way to avoid this problem is to *rank* both the utilization of a food resource and the availability of that resource, and then to use the difference in these ranks as a measure of relative preference. Johnson (1980) emphasized that this method will produce only a ranking of *relative* preferences, and that all statements of absolute preference should be avoided. The major argument in favor of the ranking method of Johnson (1980) is that the analysis is usually not affected by the inclusion or exclusion of food items that are rare in the diet. Johnson's method is applied to individuals and can thus be applied to Design II and Design III type studies of how individuals select resources.

To calculate the rank preference index, proceed as follows:

1. Determine for each individual the rank of usage (r_i) of the food items from 1 (most used) to m (least used), where m is the number of species of food resources
2. Determine for each individual the rank of availability (s_i) of the m species in the environment; these ranks might be the same for all individuals or be specific for each individual
3. Calculate the rank difference for each of the m species

$$t_i = r_i - s_i \quad (14.36)$$

where t_i = Rank difference (measure of relative preference)

r_i = Rank of usage of resource type i ($i = 1, 2, 3 \dots m$)

s_i = Rank of availability of resource type i

4. Average all the rank differences across all the individuals sampled, and rank these averages to give an order of relative preference for all the species in the diet.

Box 14.5 illustrates these calculations of the rank preference index, and Program RANK provided by Johnson (1980) (Appendix 2, page 000) can do these calculations.

Box 14.5 CALCULATION OF RANK PREFERENCE INDICES

Johnson (1980) gave data on the habitat preferences of two mallard ducks, as follows:

	Bird 5198		Bird 5205		
Wetland class	Usage ¹	Availability ²	Usage	Availability	
I	0.0	0.1	0.0	0.4	
II	10.7	1.2	0.0	1.4	
III	4.7	2.9	21.0	3.5	
IV	20.1	0.8	0.0	0.4	
V	22.1	20.1	5.3	1.2	
VI	0.0	1.4	10.5	4.9	
VII	2.7	12.6	0.0	1.0	
VIII	29.5	4.7	15.8	5.1	
IX	0.0	0.0	10.5	0.7	
X	2.7	0.2	36.8	1.8	
XI	7.4	1.1	0.0	1.2	
Open water	0.0	54.9	0.0	78.3	
Total	99.9	100.0	99.9	99.9	

¹ Usage = percentage of recorded locations in each wetland class (r_i)

² Availability = percentage of wetland area in a bird's home range in each wetland class (s_i)

1. Rank the usage values (r_i) from 1 (most used) to 12 (least used), assigning average ranks to ties. Thus wetland class VIII has the highest usage score (29.5) for duck 5198 so it is assigned rank 1. Wetland class I, VI, IX, and open water all have 0.0 for duck 5198 so these tie for ranks 9, 10, 11, and 12 and hence are assigned average rank of 10.5. The results are given below.

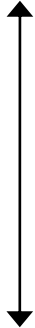
2. Rank the available resources (s_i) in the same manner from open water (rank 1) to the lowest availability (class IX for bird 5198, class I for bird 5205). Note that because this is a Design III type study, in which individuals are scored for both availability and usage, we must rank each individual separately. The resulting rankis for these two mallards are as follows:

Rank					
	Bird 5198		Bird 5205		
Wetland class	Usage	Availability	Usage	Availability	
I	10.5	11	9.5	12	

II	4	7	9.5	6	
III	6	5	2	4	
IV	3	9	9.5	11	
V	2	2	6	7.5	
VI	10.5	6	4.5	3	
VII	7.5	3	9.5	9	
VIII	1	4	3	2	
IX	10.5	12	4.5	10	
X	7.5	10	1	5	
XI	5	8	9.5	7.5	
Open water	10.5	1	9.5	1	

3. Calculate the differences in ranks for each individual to get a relative measure of preference, $t_i = r_i - s_i$

Wetland class	Bird 5198	Bird 5205	Average rank difference		
I	-0.5	-2.5	-1.5		
II	-3	+3.5	+0.25		
III	+1	-2	-0.5		
IV	-6	-1.5	-3.7		
V	0	-1.5	-0.7		
VI	+4.5	+1.5	+3.0		
VII	+4.5	+0.5	+2.5		
VIII	-3	+1	-1.0		
IX	-1.5	-5.5	-3.5		
X	-2.5	-4	-3.2		
XI	-3	+2	-0.5		
Open water	+9.5	+8.5	+9.0		

The smallest average rank indicates the most preferred resource. For these ducks we can rank the wetland habitats as:					
	IV				
	IX				
	X				
	I				
	VIII				
	V				
	III				
	XI				
	II				
	VII				
	VI				
	Open water	Least preferred habitat			
Johnson (1980) discusses a method by which the significance of these preferences can be evaluated. Note that statistical tests cannot be done unless the number of individuals is equal to or greater than the number of preference categories (habitats). This simple case with 2 ducks was used here for illustration only.					
These rank preferences can be obtained with Program RANK (see Appendix 2, page 000), provided by Johnson (1980).					

14.4.5 Rodgers' Index For Cafeteria Experiments

In cafeteria experiments an array of food types is presented to an animal in equal abundance so that availability does not enter directly into the measurement of preference. But in many cases food types cannot be easily replenished as they are eaten and consequently the most preferred foods are eaten first. Figure 14.5 illustrates one such cafeteria experiment on the collared lemming (*Dicrostonyx groenlandicus*). Rodgers (1985) argues that if the total amount eaten at the end of the trial is used (as in Manly's α , page 635), a misleading preference score can be obtained because species not eaten until later in the trial will have equal preference scores to those eaten first. Rodgers (1985) suggests that the most appropriate measure of preference is the *area* under each of the cumulative consumption curves in Figure 14.5, standardized to a maximum of 1.0. Rodgers' index is calculated as follows:

1. Measure the area under the curve for each of the species in the cafeteria trial. This can be done most simply by breaking the curve up into a series of triangles and trapezoids, and summing the area of these.

2. Standardize the preference scores to the range 0-1.0 by the formula:

$$R_i = \frac{A_i}{\max(A_i)} \quad (14.37)$$

where

R_i = Rodgers' index of preference for cafeteria experiments for species i

A_i = Area under the cumulative proportion eaten curve for species i

$\max(A_i)$ = The largest value of the A_i

Cafeteria-type experiments could also be analyzed using Manly's α for variable prey populations but this is not recommended. Note that Manly's α was designed for experiments in which some fraction of *each* of the food items remains uneaten at the end of the experiment, while Rodgers' index can be applied to experiments in which one or more food types are completely consumed during the course of the experiment. Manly *et al.* (1993, Chapter 6) provide a detailed discussion of additional, more comprehensive methods that can be used for time series observations of this type.

Box 14.6 illustrates the calculation of Rodgers' index of preference, and Program SELECT (Appendix 2, page 000) can do these calculations.

Box 14.6 CALCULATION OF RODGERS' INDICES OF PREFERENCE FROM CAFETERIA EXPERIMENTS

In one trial of a cafeteria experiment with snowshoe hares we obtained these results:

Time (hr)	Proportion eaten		
	<i>Betula glandulosa</i>	<i>Salix glauca</i>	<i>Picea glauca</i>
6	0.20	0.10	0.00
12	0.45	0.25	0.05
18	0.55	0.40	0.05
24	0.90	0.55	0.10
36	1.00	0.75	0.15
48	1.00	0.85	0.20

I will illustrate the calculations only for bog birch (*Betula glandulosa*).

1. Calculate the area under the cumulative consumption curve as a series of triangles and trapezoids:

(a) 0-6 hr:

$$\begin{aligned}\text{Triangle area} &= \frac{1}{2}(\text{base})(\text{height}) \\ &= \frac{1}{2}(6)(0.2) = 0.6\end{aligned}$$

(b) 6-12 hr:

Using the equation for the area of a trapezoid:

$$\begin{aligned}\text{Area} &= \text{base} \times \text{average height of trapezoid} \\ &= (12-6)\left(\frac{0.2+0.45}{2}\right) = 1.95\end{aligned}$$

(c) 12-18 hr: by the same rule

$$\text{Area} = (18-12)\left(\frac{0.45+0.55}{2}\right) = 3.00$$

(d) 18-24 hr: by the same rule

$$\text{Area} = (24-18)\left(\frac{0.55+0.90}{2}\right) = 4.35$$

(e) 24-36 hr: by the same rule

$$\text{Area} = (36-24)\left(\frac{0.90+1.00}{2}\right) = 11.40$$

(f) 36-48 hr: one piece:

$$\text{Rectangular area} = (48-36)(1.00) = 12.0$$

$$\begin{aligned}\text{Total area under the curve for } \textit{Betula} &= 0.6 + 1.95 + 3.0 + 4.35 + 11.40 + 12.00 \\ &= 33.3 \text{ units of area (hours} \times \text{proportion)}\end{aligned}$$

By a similar set of calculations we obtain:

Total area for *Salix* = 23.55 units of area

Total area for *Picea* = 4.50 units of area

2. Standardize the preference scores by the use of equation (13.37):

$$R_i = \frac{A_i}{\max(A_i)}$$

$$R_1 = \frac{33.3}{33.3} = 1.00$$

$$R_2 = \frac{23.55}{33.3} = 0.71$$

$$R_3 = \frac{4.50}{33.3} = 0.14$$

The most preferred food has preference score 1.0 and the smaller the standardized preference score the less preferred the food. In this experiment hares prefer to eat *Betula glandulosa* and they tend to avoid *Picea glauca* when they have a choice.

These calculations can be done by Program SELECT (Appendix 2, page 000).

14.4.6 Which Preference Index ?

There is no general agreement in the literature about which of these indices is the best measure of preference. No one has done a simulation study to look at the properties of these indices under a variety of situations. Until this is done, I can only make some tentative recommendations.

The selection index (forage ratio), Manly's α and the Rank Preference Index would appear to be the best indices of preference for most situations. The only exception would seem to be the variable prey case (cafeteria experiment) in which some prey types are eaten entirely; in these cases use Rodgers' index of preference or the methods of Manly *et al.* (1993, Chapter 6)¹.

Measures of resource preference are usually presented and discussed in the literature without any method of estimating standard errors of these measures or their confidence limits. General methods of estimating confidence limits can be applied to these measures, under the usual assumptions of approximate normality. Because of the complex nature of these measures, the best approach to estimating probable errors would seem to be resampling schemes such as the jackknife and bootstrap methods discussed in Chapter 15 (page 000).

Dietary preference is one component of diet selection models (Ellis *et al.*, 1976). There is now an elegant body of theory on optimal foraging in animals (Stephens and Krebs 1986) within which measures of preference also reside.

¹ Manly *et al.* (1993) provide a computer program RSF (*Resource Selection Functions*) for the more complex designs to estimate preferences.

Combining field measures of diet preference with theoretical insights from optimal foraging theory is a major challenge for ecologists.

Food preference is only one form of preference, and it is important to note that any resource axis can be analyzed by means of these same preference indices. For example, habitat preferences, temperature preferences, or nest site preferences could be analyzed using the same approaches I have just outlined.

14.5 ESTIMATION OF THE GRINNELLIAN NICHE

The Grinnellian niche is a spatial niche and is always associated initially with a map in geographical space. Given that we have a set of known locations for any particular species, we can generate a map like that in Figure 14.5, a starting point for describing the Grinnellian niche. The next step is to select a set of biotic and abiotic variables that could be used to describe the niche of the particular species. Biotic variables could be plant communities, particular food plants, or competing species. Abiotic variables could be soil type, temperature, rainfall, or sunlight. Peterson et al. (2011) split the variables that could affect a species niche as those that can be modified by the species and those that are not. Variables that are not dynamically affected by the species, such as rainfall, they call “scenopoetic” and they point out that these variables are the key to defining the Grinnellian niche.

The key heuristic device for understanding how spatial modelling can be used to generate predictions of potential geographic ranges is an oversimplified Venn diagram called the BAM Diagram (Soberón 2007{ #16364}, Peterson et al., 2011{ #16358}). Figure 14.6 gives a simple BAM diagram. In the BAM diagram the universe of concern for any particular species is described as three circles. One circle includes all the abiotic factors that affect a species, and this would include for example temperature, soil factors, and rainfall for terrestrial organisms. Only part of this abiotic space could be inhabited by the species of interest. A second circle includes the biotic interactions that affect all species – predators, parasites, competitors, and again we would expect that only a part of this universe could be inhabited by the species of interest. The third circle represents the movement potential of the species, or those regions that the species has colonized. Again not

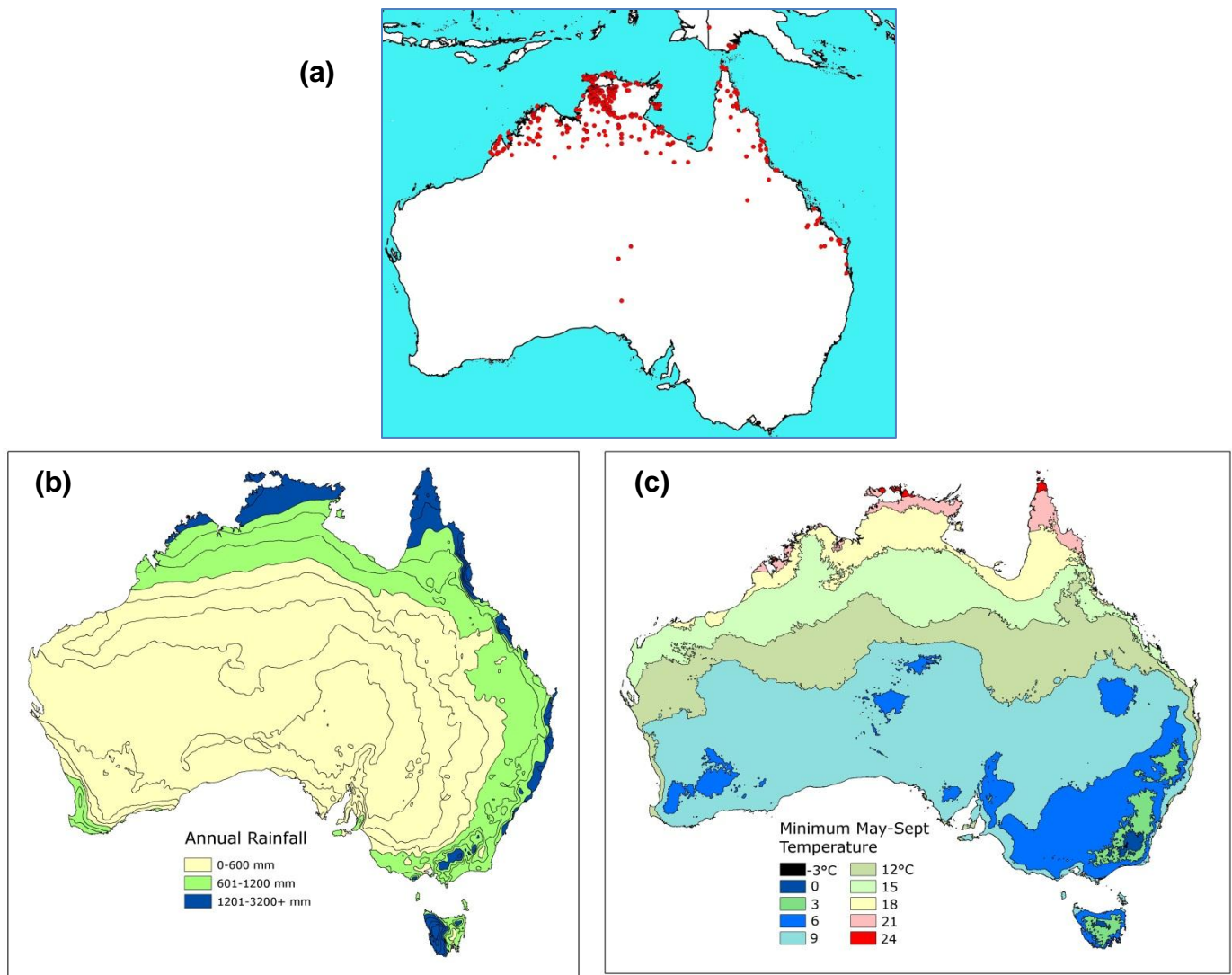


Figure 14.5 An example of the general approach of species distribution modelling to the definition of the Grinnellian niche. (a) A map of the geographical distribution of the frillneck lizard (*Chlamydosaurus kingie*) in northern Australia based on 1047 collected specimens for which exact geographic coordinates were available (red dots). (b) Two scenopoetic variables that might be part of the factors determining the Grinnellian niche, annual rainfall and minimum annual temperature. By overlaying a series of variables like these two in a GIS framework, one can extract the best predictors of the current geographical distribution of this lizard. By projecting the changes in rainfall and temperature with climate models, predictions can be made of the potential future changes in geographic range limits. The frillneck lizard is an arboreal species that feeds on insects and small vertebrates. It is a relatively large lizard up to 85 cm in length (Shine and Lambeck 1989{ #16398}).

the whole potential movement universe will be occupied, as for example when a species has not reached an island area.

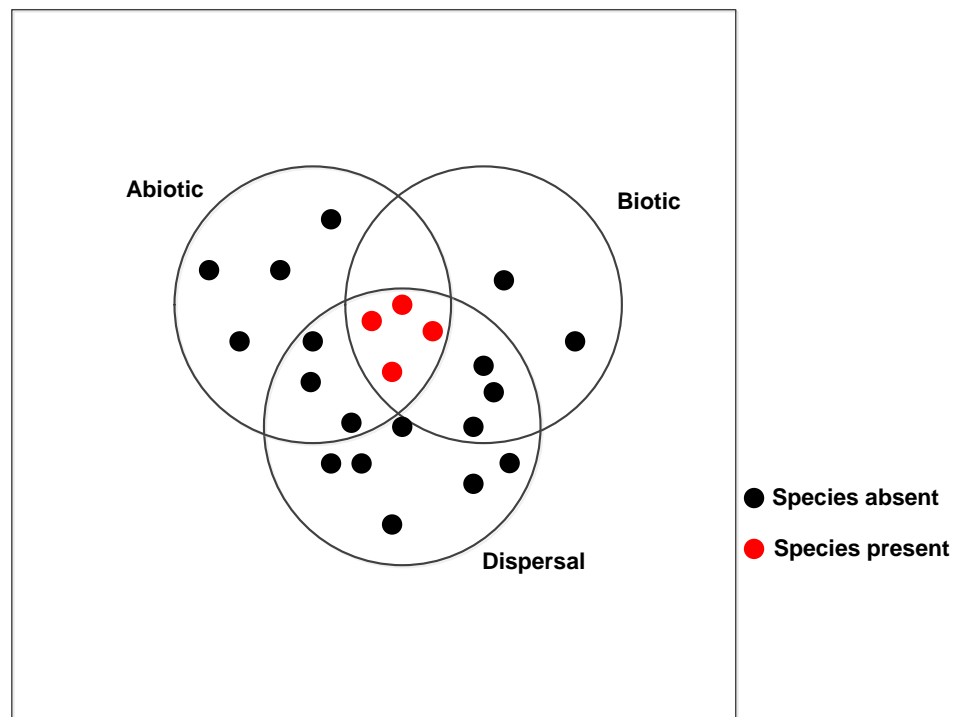


Figure 14.6 A BAM diagram to illustrate schematically how the Grinnellian niche can be operationally defined and estimated from data on three conceptual universes. The abiotic circle includes all the possible variations of abiotic data that exist and the part that the species of interest can exist within. The biotic circle does the same for the biotic interactions that the species can face. The dispersal circle describes the movement potential of the species. The intersection provides two areas, one the realized range of the species (red dots) and the other the potential range of the species or the invadable distributional area where it could exist. Modified from Soberon 2007.)

Where the three circles overlap in the BAM diagram is where the species currently exists as well as the area that it could potentially invade. Of course in the real world the species may occupy all of its potential geographic range, but in the current time when species are being accidentally moved between continents, we may not know the potential range.

The techniques of applying these simple ideas to the real world are explored in detail in Peterson et al. (2011) and are too complex to go into here. They rely heavily on GIS procedures that use remotely-sensed data and represent an important approach to our attempt to predict the effects of climate change on species

distributions. They assume that the current correlations of scenopoetic variables and species presence/absence are an accurate reflection of niche limitations. By combining detailed physiological data that define the Eltonian niche mechanistically and detailed spatial models of the Grinnellian niche we may be able to refine these predictions and make them more accurate (Kearney and Porter 2009{ #16363}).

14.6 SUMMARY

How organisms utilize their environment can be quantified by measuring the *niche*. On a local level to study competition and community organization, many methods have been proposed to measure and compare Eltonian niches.

Organisms may be *generalists* and utilize a wide spectrum of resources, or be *specialists* and use only a few resources. *Niche breadth* is usually measured by the same general formulae used to measure species diversity (heterogeneity measures). Levins' measure (= Simpson's diversity) and the Shannon-Wiener measure have both been used to estimate niche breadth, although neither of these measures takes account of possible differences in resource abundance. The choice of a measure of niche breadth depends upon whether you choose to emphasize resources used often or those used less frequently, and whether you wish to take resource availability into account.

Niche overlap is important in analyzing community organization, and several measures of overlap are in common use. Bias can be severe in two of the commonly-used indices of niche overlap (Percentage Overlap and Simplified Morisita Index). Only Morisita's original measure is free from bias over most of the range of possible overlap, and this overlap measure is recommended.

Resource selection by animals can occur for food, habitat, or other resources like nest sites. Several measures of preference are commonly used. The selection index (forage ratio), Manly's α and the Rank Preference Index appear to be the most easily understood measures of preference, and are recommended for most studies of preference. Habitat preference can be analyzed using the same methods as dietary preferences.

Grinnellian niches are distributional niches concerned with describing and comparing geographic range limits and the factors like temperature and rainfall that set these limits. These approaches to niche studies are GIS-based and computer intensive, and are oriented to trying to predict changes in distributions as climate changes.

Defining a *resource*, determining the resources that are limiting to plants and animals, and sampling the array of resources actually used by organisms are all problems of heroic proportion to which ecologists must address more attention.

SELECTED READINGS

- Arthur, S. M., Manly, B.F.J., McDonald, L.L., & Garner, G.W. 1996. Assessing habitat selection when availability changes. *Ecology* **77**: 215-227.
- Brito, A.F., Presley, S.J., and Santos, G.M.M. 2012. Temporal and trophic niche overlap in a guild of flower-visiting ants in a seasonal semi-arid tropical environment. *Journal of Arid Environments* **87**: 161-167. { #16377 }
- Broennimann, O., et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* **21**(4): 481-497. { #16379 }
- Cherry, S. 1996. A comparison of confidence interval methods for habitat use-availability studies. *Journal of Wildlife Management* **60**: 653-658.
- Colwell, R.K. & Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**: 567-576.
- Kearney, M., and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**(4): 334-350. { #16363 }
- Manly, B.F.J., McDonald, L.L., & Thomas, D.L. 1993. *Resource selection by animals: Statistical design and analysis for field studies*. Chapman and Hall, London.
- Mueller, L.D. & Altenberg, L. 1985. Statistical inference on measures of niche overlap. *Ecology* **66**: 1204-1210.
- Peterson, A.T., et al. 2011. *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton, New Jersey. 326 pp. { #16358 }
- Sinervo, B., et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**(5980): 894-899. { #15793 }

QUESTIONS AND PROBLEMS

14.1 Calculate dietary niche breadth for meadow voles from the data given in Table 14.2 (page 000). How does niche breadth change when you use a measure of niche breadth that allows for differences in abundance of the food resources, as given in Table 14.2?

14.2 Calculate the niche breadth for two hypothetical species utilizing four resources:

	Resource type			
	A	B	C	D
Relative availability of resource	0.40	0.40	0.10	0.10
Relative utilization				
Species 1	0.40	0.40	0.10	0.10
Species 2	0.25	0.25	0.25	0.25

Which of these two species is a "generalist" and which is a "specialist"?

Compare your evaluation with that of Petraitis (1979).

14.3 Calculate niche overlap for two separate species pairs from the following hypothetical data (percent utilization):

	Resource type				
	A	B	C	D	E
Community X					
Species 1	60	30	10	0	0
Species 2	0	0	10	30	60
Community Y					
Species 3	0	90	10	0	0
Species 4	0	0	10	90	0

Would you expect a measure of niche overlap to give equal overlap values for these two communities? Compare your answer with the comments in Hurlbert (1978, p. 68).

14.4 What measure of niche overlap would you recommend using for the data in Table 14.1 (page 000)? Review the recommendations in Linton *et al.* (1981) regarding sample size and discuss whether the data in Table 14.1 meet Linton's criteria for adequate sampling for all the species pairs.

14.5 Ivlev (1961, Table 18) gives data on the diet of carp during a depletion experiment over 5 days as follows:

Food type	Biomass of food remaining (grams)				
	Day 0	Day 1	Day 2	Day 3	Day 4
Chironomid larvae	10.0	6.92	4.21	1.64	0.32
Amphipods	10.0	7.63	5.59	3.72	2.26
Freshwater isopods	10.0	8.50	7.13	5.95	4.94
Mollusks	10.0	8.95	7.98	6.95	6.25

Calculate Manly's α for these four food types, and compare these values with those calculated using Rodgers' technique.

14.6 Arnett *et al.* (unpublished, 1989; data in Manly *et al.* 1993) reported on habitat selection in radio-collared bighorn sheep in Wyoming. Ten habitat types were mapped and the locations of individual sheep were obtained during autumn 1988 as follows:

Habitat	Available proportion	Habitat locations for bighorn sheep number						Total
		A	B	C	D	E	F	
Riparian	0.06	0	0	0	0	0	0	0
Conifer	0.13	0	2	1	1	0	2	6
Shrub type A	0.16	0	1	2	3	2	1	9
Aspen	0.15	2	2	1	7	2	4	18
Rock outcrop	0.06	0	2	0	5	5	2	14
Sagebrush	0.17	16	5	14	3	18	7	63
Ridges	0.12	5	10	9	6	10	6	46
Shrub type B	0.04	14	10	8	9	6	15	62
Burnt areas	0.09	28	35	40	31	25	19	178
Clearcuts	0.02	8	9	4	9	0	19	49
Total	1.00	73	76	79	74	68	75	445

- (a) What type of design is this study?
- (b) Calculate the selection indices for each of the 6 sheep. Which habitats are preferred and which are avoided?
- (c) What two methods could be used to obtain average selection ratios for these sheep? Which method is better? Manly *et al.* (1993, page 55) discusses this problem.
- (d) How would you test the hypothesis that these 6 sheep use habitats in the same manner? Do they? What assumptions must you make to do this test?

14.7 Calculate the selection index (forage ratio) for the preference data in Box 14.5 (page 000), and compare these values to those estimated in Box 14.5 using Johnson's (1980) rank preference index.