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# **Constructing Species Frequency Distributions - A Step Toward Systemic Management**

by  
C. W. Fowler and M. A. Perez

**U.S. DEPARTMENT OF COMMERCE**  
National Oceanic and Atmospheric Administration  
National Marine Fisheries Service  
Alaska Fisheries Science Center

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by

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November 1999

## **Abstract**

There is practical importance to understanding the process of constructing frequency distributions for the characteristics of species. Such distributions represent diversity and are needed to measure and observe the limits to variation among species so that such information can be used in management. Basically, the construction of species frequency distributions involves four steps: 1) data collection (measuring species); 2) finding the range of values within the data (maximum minus minimum); 3) subdivision of the range into categories or bins; 4) finding the portion of species that fall in each category established in step 3 (i.e., fraction of the sample of species measured); and 4) plotting the results in a histogram to produce a graphic representation of an underlying probability distribution. Various measures of species are possible and can be represented in such distributions to depict variation and its limits. Examples are chromosome count, population variation, geographic range size, carbon dioxide production, biomass consumption, and mean adult body mass. Management depends on such measures so that efforts can be made, where possible, to keep species within the normal range of natural variation in order to implement one of the primary principles of management.

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## ----- Introduction -----

There is a great deal of variation among species with regard to mean adult body size, biomass consumption, geographic range size, carbon dioxide production, population size and other characteristics that can be measured or estimated. This diversity exhibits limits, however, and both variation and its limits are of practical importance. To derive useful information from the measure of species, data must be collected, analyzed and displayed.

This document presents the basic processes underlying the graphic and quantitative presentation of variation among species. We begin by describing the general process of building the probability distributions that represent various collections of species - what we call simple species frequency distributions. Then we proceed to generate more complex distributions using both observed and derived data. Finally, we briefly discuss the use of species frequency distributions in management.

In general, variability can be shown in histograms (bar graphs), whether it is for body temperature, rain fall, or seed numbers (e.g., see Schmid 1983). Similar displays can be constructed for measures that apply to species (e.g., mean adult body size, population size, population variation, or rate of increase in population numbers). Thus, histograms show variation among species as a graphic presentation of what statisticians call dispersion. However, it is important to recognize that variability is constrained and that frequency distributions also demonstrate these limits as well as the resulting central tendencies or aggregations. In this paper, we present part of the analytic mechanics

needed to make such information available for use in management. Management based on information about the limits to variation among species (Fowler 1999, Fowler et al. 1999, Fowler unpub. manuscript) would replace present approaches (e.g., single-species approaches) to include applications for ecosystems and the biosphere. This form of management is discussed at the end of this document where we indicate that it would make direct use of such information to ensure that human influences within ecosystems and the biosphere would fall within the normal ranges of observed natural variation among species. In the next section, we describe the construction of species frequency distributions as observed probability distributions of species-level traits (e.g., Fowler 1999, Fowler et al. 1999, Fowler unpub. manuscript). They are often shown graphically in histograms (bar graphs) to visually demonstrate the central tendencies, limits, and other statistical properties of variation among species. Such distributions are an integration of the factors that influence the measurements of species by reflecting all of the influential elements that determine where each species falls within the distribution.

We have concentrated on the production of graphic presentations using both observed and derived data. Mathematical models of frequency distributions (normal distributions, log normal distributions, etc.; Christensen 1984) can also be fit to such data to provide quantitative descriptions as probability distributions. Such analytic treatment, however, is beyond the scope of this paper.

## ----- Frequency Distributions -----

In this section, we describe the general process of presenting frequency distributions as they apply to species. After describing frequency distributions themselves, we demonstrate this process using raw data for the body size of marine mammals. We then repeat the process after applying a transformation to the data. We also provide a second example that makes use of data for the body size of terrestrial mammals, again proceeding from raw to transformed data.

Statistically, a frequency distribution presents the distribution of a variable in a way that illustrates both its limits (constraints on its dispersion) and its central

tendencies (location in the spectrum of real numbers toward which variation is constrained). It represents measurements from a probability distribution characteristic of natural systems being measured, including measurement error.

The general concept of frequency distributions and their construction is described in most elementary statistical texts (e.g., Dixon and Massey 1957, Huntsberger 1961, Alder and Roessler 1964) and books on graphic presentation of data (e.g., Schmid 1983). One product of the process of constructing frequency distributions is a histogram (bar graph) as a

graphic presentation commonly found in elementary texts for such things as rainfall (Alder and Roessler 1964), grain production (Huntsberger 1961), age (referred to as an age distribution within a population, Schmid 1983), or the height of individual humans (Dixon and Massey 1957). In the following paragraphs, we review the general process by way of example, then we proceed to a consideration of types of measurements that apply to species and conclude with other examples of species frequency distributions.

### Basic steps - raw data

The first step in constructing a frequency distribution is the collection of data, either from original research or from published literature. For example, columns E and H of Appendix Table 1 are lists of values resulting from the measurement of a variable: in this case the mean adult body mass (kg) of 103 species of marine mammals. At the species level, these values exemplify raw data or original measurements. In this particular case the data were collected from the published literature (Appendix Table 1, Column B), which, of course, is based on field research conducted over a long history of studies by many researchers and measurements of individual organisms.

The second step in producing a frequency distribution is the analytic step of finding the range of the data: the difference between the maximum and the minimum of observed measurements. In this case, the difference is about 150,000 kg: Maximum (Max) = 150,000 kg, Minimum (Min) = 27.2 kg (Max-Min = range = 149,972.8 kg, Appendix Table 1).

The third step is that of dividing this range of observed values into convenient increments, or categories, often called bins. For graphic presentation, it is often useful to pick between 5 and 50 (usually 10-20) bins. Here, we choose to use 20. If needed (e.g., for comparison or observing change), empty bins can be added above or below the range covered by the data. The size range of each individual bin is first approximated by dividing the range by the number of bins. For our example (using the rounded range size), the bin size would be  $150,000/20$  or 7,500 kg. For convenience, this value can also be rounded and we use 10,000 kg for this example where 10,000 kg is now the increment from each bin's lower bound to its upper bound. The lower bound of the first bin must be less than the minimum of the data. Here, we selected 0.0 kg, which is smaller than the minimum of 27.2 kg, the adult body mass of sea otters (*Enhydra lutris*).

Next, the values of the raw data (i.e., those of columns E and H, Appendix Table 1) are assigned to each bin as counts. Thus, for our example, we count 93

species for which measured body size falls in the first bin (i.e., between a body size larger than 0.0 kg and less than, or equal to, 10,000 kg, as arranged from the top of column H in Appendix Table 1, in order by size). Two were species assigned to the second bin (species numbered 15 and 16 near the end of column H in Appendix Table 1), and so forth, for the complete range of data. These counts are summarized in Table 1a (third column of the left section of Table 1). To compare between samples of different sizes (i.e., different from the 103 species in this sample), the data can be expressed in terms of the fraction (alternatively, percent) of the overall sample. Thus, the 93 species from the first bin comprise 0.903 (93/103 or 90.3%) of the total of 103 species. Table 1a (fourth column) presents these portions where, for example, the 2 species in the second bin were 1.9% of the total ( $2/103 = 0.019$ ), and so forth, through the entire series of bins.

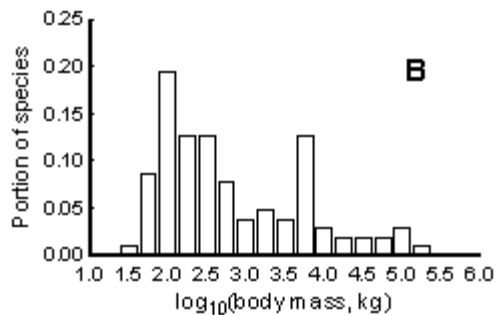
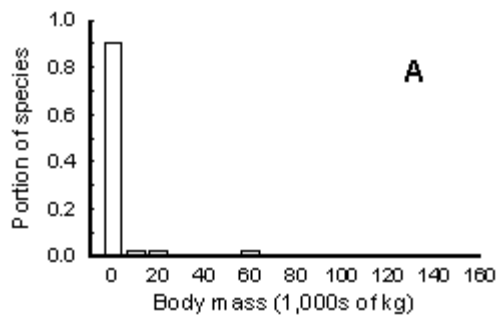
The final graphic presentation of the resulting frequency distribution is accomplished by drawing a histogram (Fig. 1A) with data from the first and fourth columns of Table 1a. The first column (alternatively the second column or, better, a midpoint between the upper and lower limits of the bins) provides the measure used for the abscissa (x-axis). The fourth column provides the data to be plotted as the height of the bars corresponding to values shown on the ordinate (y-axis). Additional bins can be added to the left (lower) and right (upper) portions of the abscissa to meet the needs of individual applications (e.g., for comparison with other data, as we will do below, or for aesthetic purposes).

### Transformed data

As can be seen from Figure 1A, the raw data of our example are not normally distributed: there is an extreme right skew to the data. In a normal distribution, half the species would have had mean body sizes above the mean of the distribution and half below. Data such as those displayed in Figure 1A need to be transformed to achieve a distribution that is closer to normal. Here (as is often the case with species-level measurements), a distribution that is normal (or more nearly normal) can be achieved by using a log transform - that is, by taking the logarithm (using base 10, but any logarithmic base could be used) of each value in columns E and H of Appendix Table 1. These values are presented in columns F and I, respectively, of Appendix Table 1. Other transformations are useful and appropriate for other kinds of data (e.g., arcsine for portions, Dixon and Massey 1957, Huntsberger 1961, Alder and Roessler 1964).

**Table 1.** Data regarding body mass of 103 species of marine mammals from Appendix Table 1 consolidated into frequency distributions, both for the raw data (Table 1a) and  $\log_{10}$  transformed data (Table 1b).

Table 1a Raw data (kg)				Table 1b Transformed data ( $\log_{10}$ (kg))			
Bin size		Number of species	Portion of species	Bin size		Number of species	Portion of species
from	to (and including)			from	to (and including)		
0	10,000	93	0.903	0.75	1.00	0	0.000
10,000	20,000	2	0.019	1.00	1.25	0	0.000
20,000	30,000	2	0.019	1.25	1.50	1	0.010
30,000	40,000	1	0.010	1.50	1.75	9	0.087
40,000	50,000	0	0.000	1.75	2.00	20	0.194
50,000	60,000	1	0.010	2.00	2.25	13	0.126
60,000	70,000	2	0.019	2.25	2.50	13	0.126
70,000	80,000	1	0.010	2.50	2.75	8	0.078
80,000	90,000	0	0.000	2.75	3.00	4	0.039
90,000	100,000	0	0.000	3.00	3.25	5	0.049
100,000	110,000	0	0.000	3.25	3.50	4	0.039
110,000	120,000	0	0.000	3.50	3.75	13	0.126
120,000	130,000	0	0.000	3.75	4.00	3	0.029
130,000	140,000	0	0.000	4.00	4.25	2	0.019
140,000	150,000	1	0.010	4.25	4.50	2	0.019
150,000	160,000	0	0.000	4.50	4.75	2	0.019
160,000	170,000	0	0.000	4.75	5.00	3	0.029
170,000	180,000	0	0.000	5.00	5.25	1	0.010
180,000	190,000	0	0.000	5.25	5.50	0	0.000
190,000	200,000	0	0.000	5.50	5.75	0	0.000



**Figure 1.**

The frequency distribution of the adult body mass of 103 species of marine mammals (data from Table 1): **Panel A** shows the distribution of the raw data and **Panel B** shows the distribution after  $\log_{10}$  transformation of the same data.



The process described above can now be repeated to achieve a graph using the transformed values. In other words, the range is determined; this range is subdivided into segments or bins (first and second columns of Table 1b). Then the count of values (i.e., next to last column of Table 1b) is determined for each bin and the portion of the sample in each bin is calculated using the same procedures that were used for the raw data (i.e., the last column of Table 1b was determined by dividing the values in the next to last column by the total number of species, 103). Finally, a corresponding graph is drawn (Fig. 1B). Note the continued presence of a right-handed skew, but one that is much less extreme than that observed before the transformation.

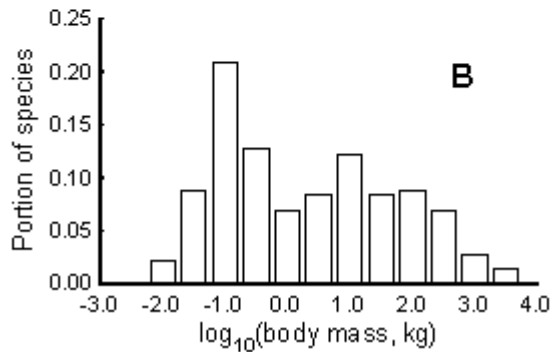
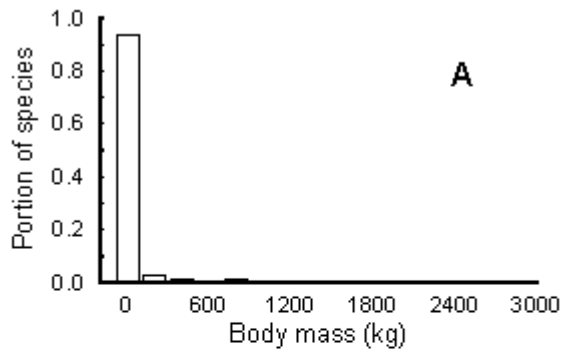
#### Terrestrial mammal example

Here, we repeat the steps described above using the body mass (kg) of 368 species of terrestrial

mammals, starting with the information found in Appendix Table 2 (Damuth 1987). Table 2 summarizes the data for the frequency distribution for both the original measurements and after  $\log_{10}$  transformation. As in the previous example, the values presented in Table 2 resulted from finding the range of data (both raw and transformed) and dividing it into increments, then finding the count and portion of species in each bin. Note that the bin sizes are different from the previous example. The raw data for marine mammals above were divided into 10,000 kg increments, whereas the terrestrial data were divided into 200 kg increments. For the  $\log_{10}$  transformed data, the increments corresponding to the bin size were 0.25 for marine mammals and 0.5 for terrestrial mammals. The results for the sample of terrestrial mammals are shown in Figure 2 based on the numerical information in Table 2.

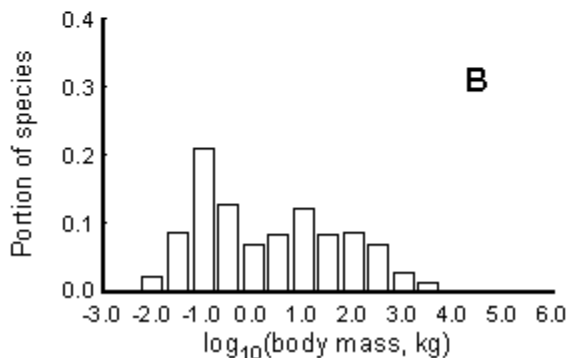
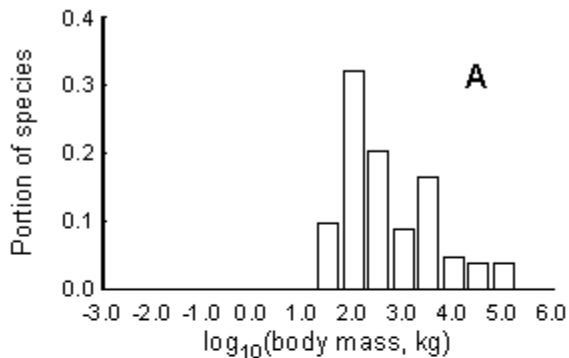
**Table 2.** Data regarding body mass of 368 species of terrestrial mammalian primary consumers from Appendix Table 2 consolidated into frequency distributions, both for the raw data (Table 2a) and  $\log_{10}$  transformed data (Table 2b).

Table 2a				Table 2b			
Raw data (kg)				Transformed data ( $\log_{10}(\text{kg})$ )			
Bin size		Number of species	Portion of species	Bin size		Number of species	Portion of species
from	to (and including)			from	to (and including)		
0	200	343	0.932	-3.5	-3.00	0	0.000
200	400	11	0.030	-3.0	-2.50	0	0.000
400	600	5	0.014	-2.5	-2.00	8	0.022
600	800	0	0.000	-2.0	-1.50	32	0.087
800	1,000	4	0.011	-1.5	-1.00	77	0.209
1,000	1,200	1	0.003	-1.0	-0.50	47	0.128
1,200	1,400	1	0.003	-0.5	0.00	25	0.068
1,400	1,600	0	0.000	0.0	0.50	31	0.084
1,600	1,800	0	0.000	0.5	1.00	45	0.122
1,800	2,000	1	0.003	1.0	1.50	31	0.084
2,000	2,200	0	0.000	1.5	2.00	32	0.087
2,200	2,400	1	0.003	2.0	2.50	25	0.068
2,400	2,600	0	0.000	2.5	3.00	10	0.027
2,600	2,800	0	0.000	3.0	3.50	5	0.014
2,800	3,000	1	0.003	3.5	4.00	0	0.000
3,000	3,200	0	0.000	4.0	4.50	0	0.000



**Figure 2.**

The frequency distribution of the adult body mass of the 368 species of terrestrial mammalian primary consumers from Table 2: **Panel A** shows the distribution of the raw data and **Panel B** shows the distribution after  $\log_{10}$  transformation.



**Figure 3.**

A comparison of body mass among marine (**Panel A**) and terrestrial (**Panel B**) mammals based on the  $\log_{10}$  transformed data from Figures 1 and 2.

Figure 3 shows a comparison of the distribution of the adult body size of marine and terrestrial mammals as a composite of Figures 1B and 2B. Several features of these graphs are of note, each of which is necessary

to accomplish the comparison. First, bins containing zeros have been added to the range of values for marine mammals at the low end of the scale (in converting Fig. 1B to Fig. 3A). Other bins have been

added to the high end of the range used for terrestrial species (converting Fig. 2B to Fig. 3B). Second, the scales on both the x and y axes were made the same. In part, this was accomplished by adding bins, as just mentioned, but it also involved using the same bin size. It is important that identical ranges and scales be used to accommodate the comparison between the two groups. The bin size used in this comparison was the same as that chosen for the terrestrial species in Figure 2B (i.e., 0.5 for the log transformation). And third, each number among the labels used for the abscissa represents the lower end of the range for the

corresponding bin that is depicted by the bar directly above it. These numbers could have been either the upper bound or the midpoint of the range of each bin and remained equally as useful. For quantitative analysis, however, the use of midpoints to define bins is imperative (because midpoints are used as surrogates for the raw data, multiplied by corresponding counts, such that either the upper or lower range limits would result in bias of one-half the range size of each bin; Dixon and Massey 1957, Huntsberger 1961, Alder and Roessler 1964).

## ----- Measures of Species -----

The examples described above, and examples provided in the general texts referred to above, demonstrate the general procedure for producing frequency distributions. The data used in these examples were representative of species-level measurements. That is, the mean adult body masses represent species-specific measurements. Note that measurements of individuals were necessary to calculate these means as species-level measurements. Frequency distributions among individuals within a species can be produced by the same process, and these could be presented as individual-level frequency distributions (one per species). The species-level measurements used in the examples for marine and terrestrial mammals were the means of such distributions among individuals from each species, respectively.

Measurements can be made of many other species-level characteristics and the data for producing the relevant distributions can be derived through two processes. The first process involves direct measurement, such as measuring body weight or mass in the examples above, measures of total biomass, or population variation. The second process involves indirect measures to result in estimates of such characteristics as carbon dioxide production or total annual energy consumption. These indirect measures are derived by the quantitative combination of separate sets of related information. Other measures of species include the numbers of species consumed as prey (number of resource species) and the number of consumer species for which a species serves as a resource. Each measure can be portrayed in a species frequency distribution such as those shown in Figures 1-3. Further demonstration of such measures will be presented in the examples below.

### Simple or direct measures

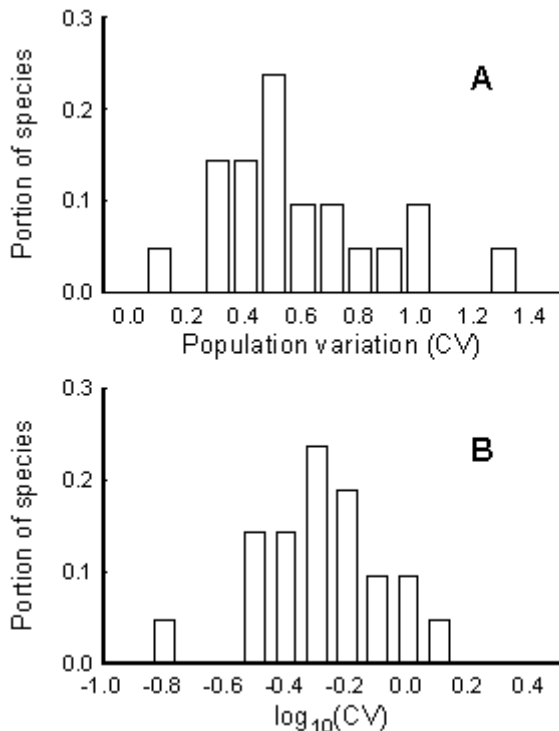
Calling measures of species "simple" minimizes the difficulty of making measurements in field research. The important concept here is that the measurements are achieved less by inference than by direct observation in field or laboratory research. Comparing the set of examples in this section (as well as those described above) with those of the following section will illustrate the point.

*Population Variation-* Appendix Table 3 presents measures of population variability for 21 species of marine fish (from Spencer and Collie 1997). Table 3 summarizes the data from Appendix Table 3. The range of these measures of variation from Appendix Table 3 (from a minimum of 0.17 to a maximum of 1.32) was divided into 15 categories with bins corresponding to increments of 0.1, measured in units of coefficient of variation. The number of species in each category (bin) as well as the portion of species per bin (the total number of species is 21) are presented in Table 3. The values for this portion were then plotted in Figure 4A, the graphic presentation of the resulting species frequency distribution. In other words, the same process discussed previously was repeated: data collection, range subdivision, finding the portion of species in each category, and plotting the results.

As above, the log transformation achieves a frequency distribution that is closer to a normal distribution (Fig. 4B). The data for the intermediate steps in proceeding from Appendix Table 3 to Figure 4B are found in Table 3b.

**Table 3.** Data regarding population variation of 21 marine fish species from Appendix Table 3 consolidated into frequency distributions, both for the raw data (Table 3a) and  $\log_{10}$  transformed data (Table 3b).

Table 3a				Table 3b			
Raw data (CV)				Transformed data ( $\log_{10}(CV)$ )			
Bin size		Number of species	Portion of species	Bin size		Number of species	Portion of species
from	to (and including)			from	to (and including)		
0.0	0.1	0	0.000	-1.0	-0.9	0	0.000
0.1	0.2	1	0.048	-0.9	-0.8	0	0.000
0.2	0.3	0	0.000	-0.8	-0.7	1	0.048
0.3	0.4	3	0.143	-0.7	-0.6	0	0.000
0.4	0.5	3	0.143	-0.6	-0.5	0	0.000
0.5	0.6	5	0.238	-0.5	-0.4	3	0.143
0.6	0.7	2	0.095	-0.4	-0.3	3	0.143
0.7	0.8	2	0.095	-0.3	-0.2	5	0.238
0.8	0.9	1	0.048	-0.2	-0.1	4	0.190
0.9	1.0	1	0.048	-0.1	0.0	2	0.095
1.0	1.1	2	0.095	0.0	0.1	2	0.095
1.1	1.2	0	0.000	0.1	0.2	1	0.048
1.2	1.3	0	0.000	0.2	0.3	0	0.000
1.3	1.4	1	0.048	0.3	0.4	0	0.000
1.4	1.5	0	0.000	0.4	0.5	0	0.000



**Figure 4.**

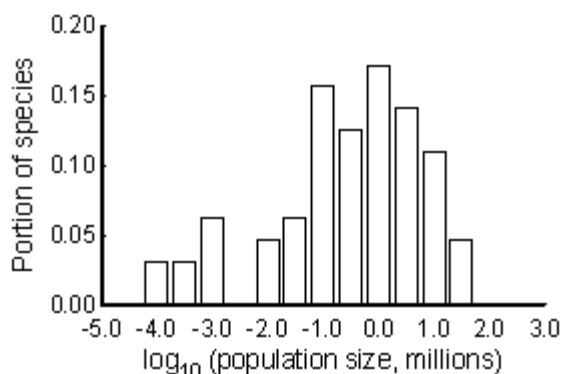
The frequency distribution of the population variability (coefficient of variation) for the 21 species of marine fish from Table 3: **Panel A** shows the distribution of the raw data and **Panel B** shows the distribution after  $\log_{10}$  transformation.

Variation in population abundance is a good example of a species-level characteristic that reflects the influence of a variety of factors. These can include the effects of the environment, genetics, and even mean population size itself. Environmental factors clearly play a role in eliciting population fluctuation. The genetically determined nature of the species, however, involves adaptations that result in varying degrees of both resistance and response to environmental influence, a set of characteristics that vary from species to species. Body size may also be correlated with population variation. These, as well as other factors, influence population variability to result in the observed distribution. The degree of influence will vary from case to case, and from influential factor to influential factor. The resulting distribution is an integration of the combined set of influential elements (Fowler 1999, Fowler unpub. manuscript, Fowler et al. 1999).

*Population Size-* Appendix Table 4 contains data for the estimated total population size of 63 species of marine and terrestrial mammals within a specified range of body size. In general, body size ranges from that of bacteria (or viruses) to that of blue whales (or redwood trees). The species of this sample were chosen to correspond to the same 0.1% of that range occupied by humans. Thus, the species in this sample are mammals of roughly the same body mass as humans (data from Ridgway and Harrison 1981-99, Kowak 1991). Table 4 presents the steps between obtaining the raw data and the graphic depiction of the frequency distribution as outlined for each of the examples above. Although these data exhibit a very strong right skew before transformation (Appendix Table 4), there is a left skew after  $\log_{10}$  transformation, as can be seen in Figure 5. The latter skew may reflect cumulative effects of anthropogenic influence (e.g., factors that have resulted in species with population size sufficiently small to be afforded protected status such as provided by the U.S. Endangered Species Act).

**Table 4.** Data regarding population size of 63 species of mammals from Appendix Table 4 consolidated into a frequency distribution for the  $\log_{10}$  transformed data.

Bin size $\log_{10}$ (millions)		Number of species	Portion of species
from	to (and including)		
-5.5	-5.0	0	0.000
-5.0	-4.5	0	0.000
-4.5	-4.0	2	0.031
-4.0	-3.5	2	0.031
-3.5	-3.0	4	0.063
-3.0	-2.5	0	0.000
-2.5	-2.0	3	0.047
-2.0	-1.5	4	0.063
-1.5	-1.0	10	0.156
-1.0	-0.5	8	0.125
-0.5	0.0	11	0.172
0.0	0.5	9	0.141
0.5	1.0	7	0.109
1.0	1.5	3	0.047
1.5	2.0	0	0.000
2.0	2.5	0	0.000



**Figure 5.**  
The frequency distribution of population size ( $\log_{10}$  numbers) for the 63 species of mammals from Appendix Table 4 and Table 4.

**Table 5.** Data regarding geographic range for 523 species of mammals from Appendix Table 5 consolidated into a frequency distribution for the  $\log_{10}$  transformed data.

Bin size $\log_{10}(\text{km}^2)$			Number of species	Portion of species
from	to (and including)	Midpoint		
1.25	1.75	1.5	0	0.000
1.75	2.25	2.0	2	0.004
2.25	2.75	2.5	5	0.010
2.75	3.25	3.0	13	0.025
3.25	3.75	3.5	21	0.040
3.75	4.25	4.0	45	0.086
4.25	4.75	4.5	64	0.122
4.75	5.25	5.0	73	0.140
5.25	5.75	5.5	100	0.191
5.75	6.25	6.0	76	0.145
6.25	6.75	6.5	76	0.145
6.75	7.25	7.0	46	0.088
7.25	7.75	7.5	2	0.004
7.75	8.25	8.0	0	0.000
8.25	8.75	8.5	0	0.000

Population size is another example of a species-level characteristic that integrates the influence of a variety of factors. The effects of the environment (often seen as the environmental components of carrying capacity) are among such factors. The balance between the positive influence of food supplies and habitat and the negative influence of parasites, diseases and predation are included. Other factors included are the genetic characteristics of individual species and their contribution to varying levels of observed population size. Population size is a good example of a species-level measurement that is influenced by body size (within any particular habitat, small-bodied species such as bacteria show huge

population densities compared to those of large-bodied species; Damuth, 1987). Another component of the variation in observed population levels among species is the short-term population variation demonstrated above in Figure 4.

*Geographic Range-* Appendix Table 5 presents the measured geographic ranges for 523 species of terrestrial mammals found in North America (Pagel et al. 1991). Table 5 contains the breakdown of these data prior to plotting them in a frequency distribution. In this example, the bars of the histogram are plotted for the midpoints of the bins chosen for breaking the  $\log_{10}$  transformed data into a frequency distribution

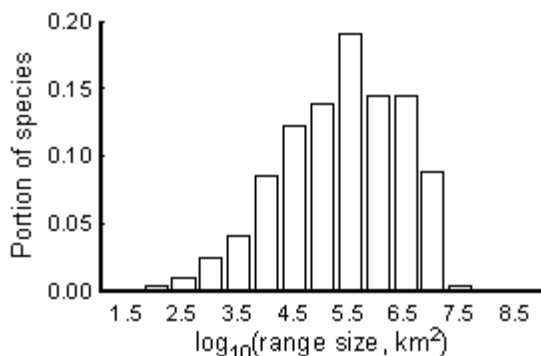
(Table 5). Otherwise, all steps from collecting and examining the raw data to the drawing of the graph (Fig. 6) are the same as in our previous examples. These steps can be followed in the columns of Appendix Table 5 and Table 5. Note that there are several empty bins (categories with no species) included in both Table 5 and Figure 6. The decision to include these bins was made to better illustrate the limits of variation, the concept of natural variation, and the central tendencies regarding geographic range for this set of species.

Geographic range can be measured for an entire species, as shown for the species included in Figure 6. Alternatively, species within a particular ecosystem have geographic ranges within that ecosystem. Any particular ecosystem will be unlikely to contain the entire ranges of all the species represented in it. Nevertheless, the portion of any ecosystem occupied by each species can be determined (even though making such measurements will usually involve very difficult logistic challenges and expensive research). With such data, a table similar to Table 5 could be constructed. It would apply to any individual ecosystem (rather than a continent or the biosphere). Such a table could also apply to any other category of species (such as birds, primary consumers, invertebrates, or plants) or it could include all species represented in any particular ecosystem.

*Chromosome Count-* Our final example of the direct measure of a species-level trait is based on the number of chromosomes per nucleus for angiosperm plants. Appendix Table 6 shows the frequency distribution of 19,747 species of flowering plants according to their diploid chromosome count. Owing to both the large

number of species involved and the range of chromosome count covered, Appendix Table 6 is not a complete list of the species, and is restricted to those species with 120 chromosomes or less (Masterson 1994). However, the  $\log_{10}$  transformed data include all 19,838 species (i.e., including the 91 species with more than 120 chromosomes, Table 6). Figure 7 shows the distribution of the complete sample across the range of chromosome number using the  $\log_{10}$  transformation and illustrates a histogram wherein the bars are labeled according to the range of each bin (note that the log of most whole numbers is not a whole number). We have also broken the rule of uniform bin size to facilitate a meaningful view of the data. This figure includes one bin (the last on the right) that is of a different range than the remainder. The count of species in this bin is, therefore, not strictly comparable to counts in the other bins, but helps illustrate the shape of the distribution by avoiding a compression of the largest part of the distribution on the left (i.e., where the greatest number of species occur).

Other simple, or direct, measures of species that can also be presented in frequency distributions include trophic level (Fig. 8), number of species consumed, metabolic rates, intrinsic rates of increase, and number of consuming species (e.g., count of predators, parasites and diseases), each of which would be the complex result of many influential factors. The number and types of such measures (or dimensions) is reflective of the complexity of nature and, specifically, those over which species exhibit natural variation. What we have (or can have) to work with is limited by our ability to make direct measurements.

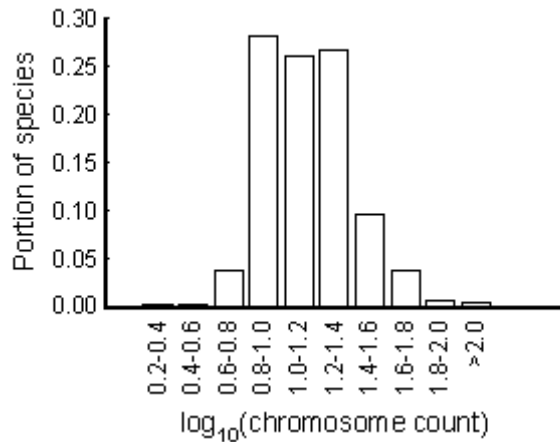


**Figure 6.**

The frequency distribution of geographic range size ( $\log_{10}$  km<sup>2</sup>) for the 523 species of terrestrial mammals from Table 5.

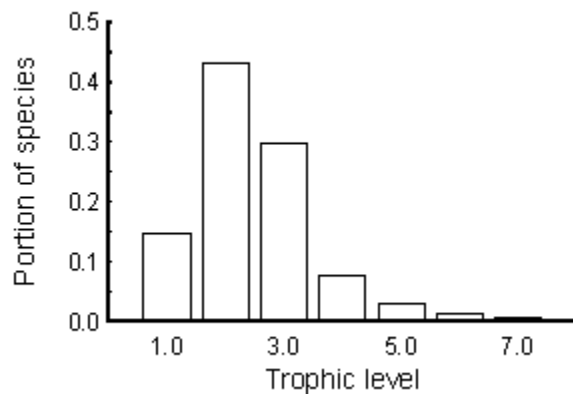
**Table 6.** Data regarding the chromosome count of 19,838 species of angiosperm plants, including the 19,747 species from Appendix Table 6, consolidated into a frequency distribution for the  $\log_{10}$  transformed data (from Masterson 1994).

Bin size		Number of species	Portion of species
$\log_{10}$ (chromosome count)			
from	to (and including)		
0.0	0.2	0	0.000
0.2	0.4	26	0.001
0.4	0.6	29	0.001
0.6	0.8	761	0.038
0.8	1.0	5,588	0.282
1.0	1.2	5,205	0.262
1.2	1.4	5,314	0.268
1.4	1.6	1,932	0.097
1.6	1.8	748	0.038
1.8	2.0	132	0.007
More than 2.0		103	0.005



**Figure 7.**

The frequency distribution of diploid chromosome number ( $\log_{10}$  chromosome numbers) for the 19,838 species of angiosperm plants from Table 6.



**Figure 8.**

The frequency distribution of trophic level for insect species from 95 insect-dominated food webs (from Schoenly et al. 1991).



### Derived species-level measures

Although most measures of species are conceptually possible as direct measures (e.g., those presented above), there are other measures that are more conveniently determined through estimation processes. Such estimates are based on a combination of two or more different measures of species, at least one of which is correlated with a third characteristic, such as body size. For example, if there is a known correlative relationship between resource consumption rate (by individual animals) and body mass, it is possible to calculate a species-level consumption rate. This is carried out multiplying two values: the mass-specific consumption rate expected for the corresponding body size, and total population size at any given time.

Clearly, this introduces another source of variation into the resulting species frequency distribution. Each variable has its own variance and the multiplication of one by the other introduces variation through the process of calculation that may not be consistent with the actual natural variation of the variable being estimated. However, it is variation that can be evaluated (e.g., through techniques such as the delta method; Seber 1973). The misrepresentation of variation is one potential problem with such procedures and must be taken into account in the use of the resulting frequency distributions.

*Carbon Dioxide Production-* In this example, we consider a derived species frequency distribution for carbon dioxide production. Based on the relationship between respiration rate and body size (Peters 1983), a first approximation of expected rate of carbon dioxide production (in metric tons per year) for each individual animal of body mass  $W$  (kg) can be obtained from the equation:

$$CO_2 = 0.0103 \cdot W^{0.751}. \quad (1)$$

This assumes that there are about 3 kcal of energy metabolized per gram of  $CO_2$  produced (Moen 1973).

Thus, the average adult pronghorn antelope (*Antilocapra americana*) from Appendix Table 4 would be estimated to produce 0.206 metric tons (t) of carbon dioxide each year (adult body mass of 54 kg). Equation 1 can be used to calculate  $CO_2$  for each individual species listed in Appendix Table 4. The next step is to estimate  $CO_2$  production for all individuals within a species (i.e., for the species as an aggregate). A species-by-species approximation of the carbon dioxide production for each species can thus be calculated by multiplying the estimated population size for each species (Appendix Table 7) by the  $CO_2$  produced per individual (using Equation 1) to obtain

the estimates of total  $CO_2$  production (Appendix Table 7). There are other assumptions involved in these calculations, one of which is that every individual (regardless of age or size) is assumed to produce the same amount of carbon dioxide as an adult (because we used mean adult body size in Equation 1). A more realistic estimate would account for age (and size) structure within the total population of each species along with the corresponding metabolic rates.

With the completion of the series of steps involved in getting at the indirect measure of a species (e.g.,  $CO_2$  production), we now have another set of data to be used for graphic presentation in a frequency distribution. The next steps are exactly the same as those used for directly measured data and, in this case, result in the distribution shown in Figure 9 (complete with log transformed data, listed in Appendix Table 7, and summarized by distribution in Table 7).

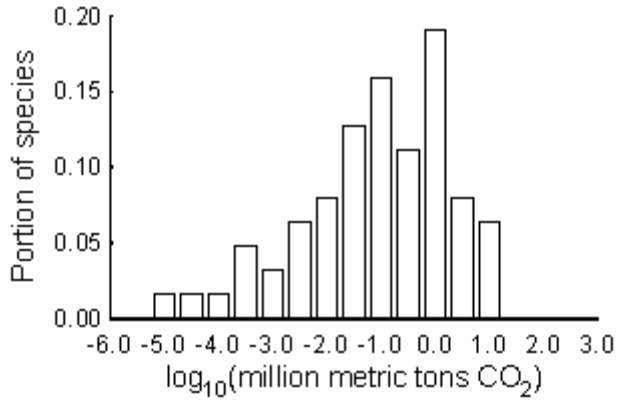
Again, problems that cannot be ignored in this approach include any variance and bias introduced by the estimation process. The estimation process introduces a component of variation resulting from the combination of variation inherent in measures of body size, respiration rates, carbon dioxide production, metabolic rates, diet type, and population size. Bias is inherent in assuming that all individuals produce carbon dioxide at the same rate as adults (we applied adult body size to the entire population). Because of these problems, comparisons among different groups of species, with distributions all produced in the same manner, would be subject to misinterpretation. It is important to take such factors into account. However, for the purposes of management, such distributions, which otherwise must be considered as first approximations, nevertheless serve as useful guiding information, as will be seen below.

*Energy Consumption-* Inherent in the relationship above, for carbon dioxide production, is the relationship between metabolic rate and body size (Peters 1983). Thus, to provide metabolic needs, ingestion of energy is also related to body size and the relationship can be used to estimate energy consumption per unit area for species for which there are estimates of density.

The relationship between ingestion rates ( $I$ ) in watts (1 watt = 1 joule per second), and body size (mass,  $W$ , in kg), for endotherms may be approximated by:

$$I = 10.7 \cdot W^{0.70}, \quad (2)$$

as based on observations from a variety of historical studies (see Peters 1983, and the references therein).



**Figure 9.**

The frequency distribution of annual CO<sub>2</sub> production (log<sub>10</sub> million metric tons) estimated for the 63 species of mammals from Table 7.

**Table 7.** Data regarding CO<sub>2</sub> production for 63 species of mammals from Appendix Table 7 consolidated into a frequency distribution for the log<sub>10</sub> transformed data.

Bin size		Number of species	Portion of species
log <sub>10</sub> (million tons CO <sub>2</sub> )			
from	to (and including)		
-6.5	-6.0	0	0.000
-6.0	-5.5	0	0.000
-5.5	-5.0	1	0.016
-5.0	-4.5	1	0.016
-4.5	-4.0	1	0.016
-4.0	-3.5	3	0.048
-3.5	-3.0	2	0.032
-3.0	-2.5	4	0.063
-2.5	-2.0	5	0.079
-2.0	-1.5	8	0.127
-1.5	-1.0	10	0.159
-1.0	-0.5	7	0.111
-0.5	0.0	12	0.190
0.0	0.5	5	0.079
0.5	1.0	4	0.063
1.0	1.5	0	0.000
1.5	2.0	0	0.000

The combination of estimated ingestion rates from this equation with information regarding density allows for an estimate of the consumption of energy ( $I$ , ingested joules per day) per unit area (km<sup>2</sup>) with the equation:

$$I = 9.245 \cdot 10^5 \cdot W^{0.7} \cdot D, \quad (3)$$

where  $D$  is density in individuals per square kilometer.

Appendix Table 8 lists the 368 species of mammals from Damuth (1987) with corresponding measured or estimated body sizes and densities and the estimated energy consumption per unit area (J/10<sup>6</sup>km<sup>2</sup>day) for each of these species based on Equation 3. Appendix Table 8 also presents the log<sub>10</sub> transformed value for estimated daily energy consumption per unit area following the pattern for tables in previous examples. These transformed data

are shown in Figure 10A as a frequency distribution (20 bins with each bin spanning an increment of 0.25, including the data from the 16 non-zero bins shown summarized in Table 8). Here, the bins are represented on the abscissa by numbers corresponding to their upper bounds.

Again the problems of confounding sources of variance and potential bias must be recognized. To help see some of the effects of estimation, one further graph of a species frequency distribution is useful. Instead of using the estimates of density directly from field observations (Appendix Table 8), it would be possible to use estimates of density from the relationship between density and body size (Peters 1983):

$$D = 103 \cdot W^{-0.93}. \quad (4)$$

Thus, the resulting estimate of daily energy consumption per unit area is based only on body size. Figure 10B shows the resulting frequency distribution (not included in tabular form). Note the change in variance (reduced) and the altered non-normal shape of the distribution. But it is also important to note the relatively small change in the mean. Bias in central tendencies may outweigh other problems only if there is bias in the underlying formulae. The main point being demonstrated here is that estimation processes as outlined above can have significant effects on the resulting frequency distributions - effects that must be

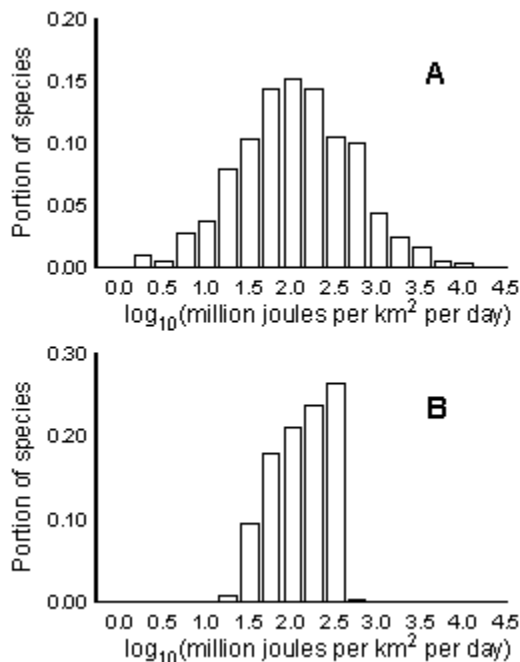
recognized in both the construction of species frequency distributions and in their use.

*Consumption of Biomass from Ecosystems-* Another example of derived species-level measures is that of estimated food consumption in a given ecosystem. In particular, Perez and McAlister (1993) presented estimates of total annual food consumption in the eastern Bering Sea ecosystem for 20 species of marine mammals.

Total food consumption ( $F$ ) for marine mammal species in the eastern Bering Sea ecosystem was based on the following expression:

$$F = (E \cdot N \cdot T) / K, \quad (5)$$

where  $E$  is the estimated daily energy requirements (kcal/day) per average body mass (kg) of an individual,  $N$  is the estimated number of individuals in the population,  $T$  is the time period in days (in this case, two semiannual periods of 182 days were used), and  $K$  is the estimated energy value (kcal/g) of the diet. Individual daily energy requirements for active marine mammals were calculated using known relationships between body mass and energy consumption (see Perez and McAlister 1993 and references therein). The estimated percentage of fish in the average annual diet of each marine mammal species was used to determine the portion of total food consumption represented by fish species.



**Figure 10.**

The frequency distribution of estimated energy consumption per unit area (joules per km<sup>2</sup> per day) for the 368 species of terrestrial mammals from Appendix Table 8 and Table 8: **Panel A**) shows the estimates based on observed population density, and **Panel B**) shows estimates wherein density is also estimated.

**Table 8.** Data regarding energy consumption per unit area for 368 species of terrestrial mammalian primary consumers from Appendix Table 8 consolidated into a frequency distribution for the  $\log_{10}$  transformed data (million joules per square kilometer per day).

Bin size $\log_{10}(J/10^6\text{km}^2\text{day})$		Number of species	Portion of species
from	to (and including)		
0.00	0.25	3	0.008
0.25	0.50	2	0.005
0.50	0.75	10	0.027
0.75	1.00	14	0.038
1.00	1.25	29	0.079
1.25	1.50	38	0.103
1.50	1.75	53	0.144
1.75	2.00	56	0.152
2.00	2.25	53	0.144
2.25	2.50	39	0.106
2.50	2.75	37	0.101
2.75	3.00	16	0.044
3.00	3.25	9	0.025
3.25	3.50	6	0.016
3.50	3.75	2	0.005
3.75	4.00	1	0.003

Appendix Table 9 shows the data for the 20 species of marine mammals from Perez and McAlister (1993) modified for inclusion in Appendix Table 9 by averaging data for seasonal abundance to obtain single annual values. Average annual values of body mass, population numbers, daily individual energy

requirements, energy value of the diet, and estimated total annual food consumption (biomass in  $10^3$  t) are all listed in Appendix Table 9. This table also presents the  $\log_{10}$  transformation of total annual food consumption values. Table 9 allocates these data into appropriate bins representing the frequency

**Table 9.** Data regarding estimates of  $\log_{10}$  transformed values of total annual food consumption ( $10^3$  t) for 20 species of marine mammals in the eastern Bering Sea ecosystem from Appendix Table 9 consolidated into a frequency distribution.

Bin size ( $\log_{10}$ annual food consumption, $10^3$ t)		Number of species	Portion of species
from	to (and including)		
-1.50	-1.00	0	0.000
-1.00	-0.50	0	0.000
-0.50	0.00	1	0.050
0.00	0.50	0	0.000
0.50	1.00	2	0.100
1.00	1.50	3	0.150
1.50	2.00	5	0.250
2.00	2.50	7	0.350
2.50	3.00	2	0.100
3.00	3.50	0	0.000

distribution of the  $\log_{10}$  transformed data illustrated in Figure 11A.

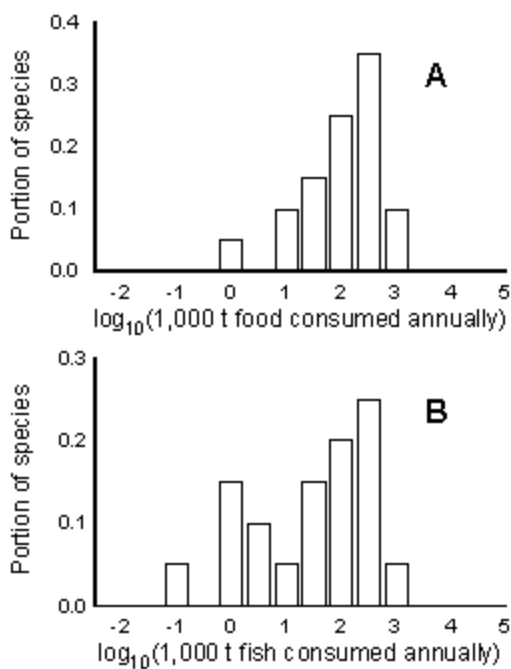
Appendix Table 10 presents the average annual fish consumption estimates for the 20 species of marine mammals discussed above. The table presents the total average annual food consumption values (from Appendix Table 9), the estimated percentage of fish in the diet, the estimates of the average annual fish consumption ( $10^3$  t), and the  $\log_{10}$  transformation of the estimates of annual fish consumption. Figure 11B illustrates the frequency distribution derived from these data as estimated average annual fish consumption by marine mammal species in the eastern Bering Sea ecosystem.

As stated previously, variation among data sources will bias the data and affect the usefulness of comparability among species. The quantity and quality of data available on distribution, diet, abundance, and biomass of marine mammals in the Bering Sea vary widely. Population values are available for most pinniped species, but not for many cetaceans. Estimated energy values of the average diet of each marine mammal species do not take into account intra-annual changes in the energy content of prey species. Also, the relative importance of each prey species to the diet of marine mammals in the Bering Sea is generally not known on a seasonal basis. Thus, the width and amplitude of the frequency distribution, and the component allocation of species in the distribution, will likely change as additional data become available in the future. However, the

illustrations in Figure 11 serve as a first approximation for use in management (Panel A for total biomass consumption within the ecosystem, and Panel B for consumption from finfish), and also serves as another example of a frequency distribution at the species level as based on a set of derived data.

#### *Consumption of Biomass from Individual Prey Species-*

The previous examples typify indirect or derived measures of species and their influence on or within ecosystems. The example shown in Figure 11B illustrates the influence of 20 species of marine mammals on a specific taxonomic category (fish). The field sampling and data analysis for species-level measures can be quite complicated. In all cases, there is a great deal of field work behind the data used. The extent of field work required to measure species is exemplified by the effort necessary to produce estimates of the rates at which predators consume from a particular (single) prey resource (Overholtz et al. 1991, Livingston 1993, Crawford et al. 1991). Appendix Table 11 lists estimates of consumption rates by 20 predators that feed on walleye pollock (*Theragra chalcogramma*) of the eastern Bering Sea as produced by Livingston (1993; where much of the procedure and effort to derive such estimates are documented). Some of these estimated consumption rates are the means of measurements made over several years, and represent only the period for which the estimates were made. Table 10 and Figure 12 present these data in the format of frequency distributions.

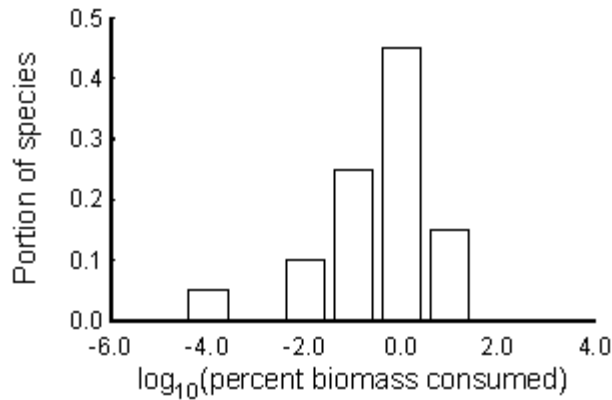


**Figure 11.**

The frequency distribution of consumption rates by 20 species of marine mammals in the Bering Sea ecosystem from Appendix Tables 9 and 10 for the total biomass consumed (**Panel A**) and for the consumption of fish only (**Panel B**) (from Perez and McAlister 1993).

**Table 10.** Data regarding consumption of walleye pollock by 20 species of predators in the eastern Bering Sea from Appendix Table 10 consolidated into a frequency distribution for the  $\log_{10}$  transformed data regarding annual rates expressed as the percent of the pollock standing stock biomass.

Bin size		Number of species	Portion of species
$\log_{10}$ (percent pollock biomass consumed)			
from	to (and including)		
-7	-6	0	0.000
-6	-5	0	0.000
-5	-4	1	0.050
-4	-3	0	0.000
-3	-2	2	0.100
-2	-1	5	0.250
-1	0	9	0.450
0	1	3	0.150
1	2	0	0.000
2	3	0	0.000
3	4	0	0.000



**Figure 12.** The frequency distribution of consumption rates ( $\log_{10}$  portion of standing stock biomass consumed) on walleye pollock (*Theragra chalcogramma*) by vertebrate predators for the 20 species of birds, mammals and fish from Table 10.

----- **Bivariate Space** -----

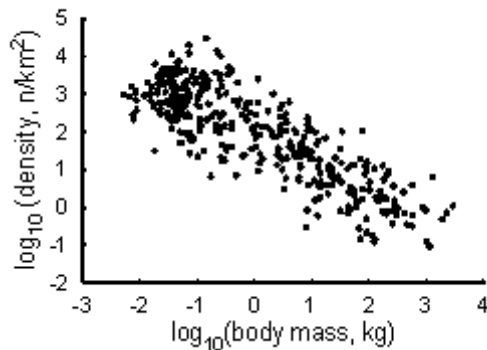
The frequency distributions presented so far are for species in their distributions across a single dimension -- each example being only one of many ways of measuring species. As mentioned earlier, measures of species are often correlated. This is clear from Equations 1-5 used in the indirect estimation processes above. Species are thus distributed in a frequency of occurrence that involves more than one

dimension. The process for deriving the numerical information for the resulting frequency distributions rapidly becomes more complicated than the examples above would indicate.

To illustrate the process, it is helpful to examine an example of a species frequency distribution in two dimensions. Appendix Table 8 presents information regarding body mass and population density for 368

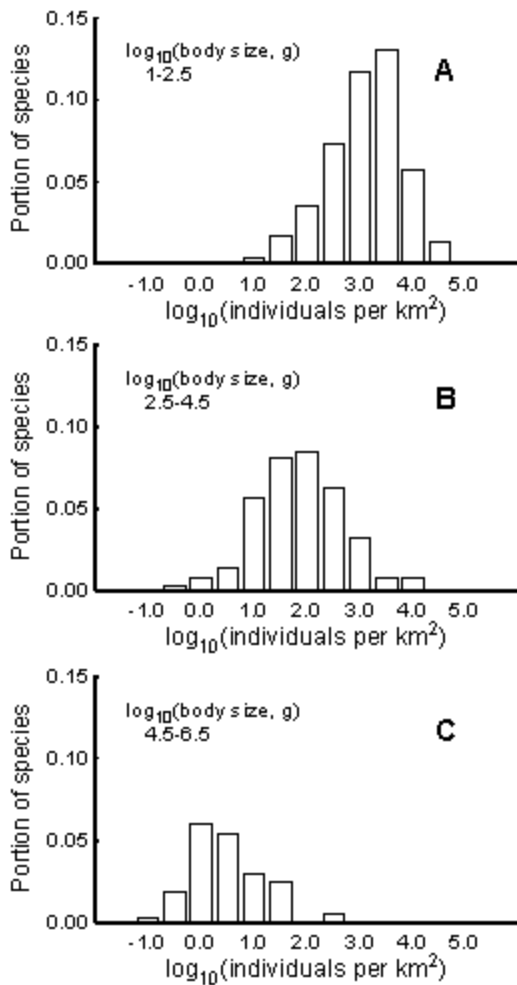


A variety of graphic presentations are possible for two-dimensional information. One is shown in Figure 13, which is simply a plot of the raw data in a scatterplot. The density of points and their distribution is obvious, as is the correlation between mass and density in the log scale (mentioned above in relation to estimating density; Peters 1983, Damuth 1987).



**Figure 13.**

Population density of 368 terrestrial mammalian herbivore species in relation to adult body mass (Damuth 1987) from Appendix Table 2 to show the density of species represented by density of plotted points.



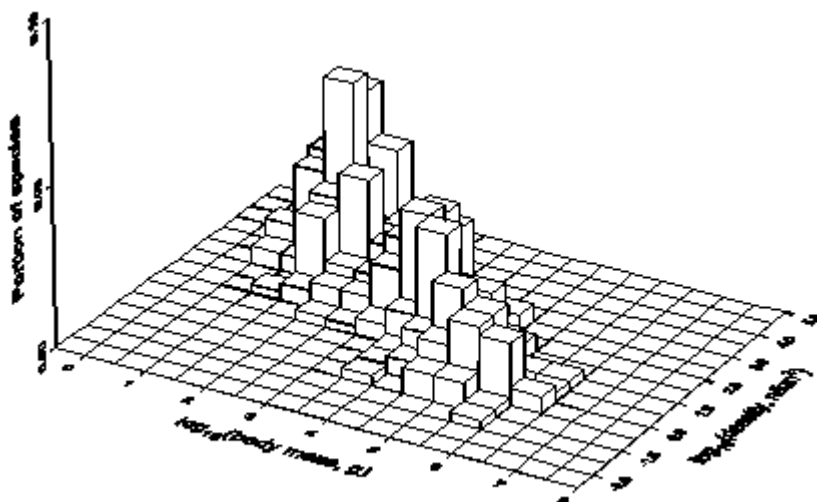
**Figure 14.**

The frequency distribution of population density ( $\log_{10}$  numbers per  $\text{km}^2$ ) for 368 species of terrestrial mammalian herbivores in three different size categories from Appendix Tables 8: **Panel A** is for species with log body mass ( $\log_{10}$  grams) between 1 and 2.5; **Panel B** is for log body mass between 2.5 to 4.5, and **Panel C** is for log body mass between 4.5 to 6.5.



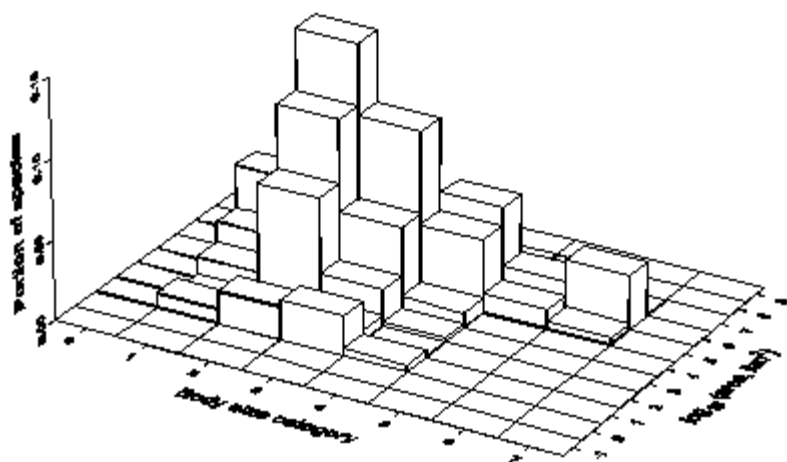
A third option is that of a three-dimensional bar graph (Fig. 15). This graph, as a whole, represents a two-dimensional frequency distribution. Within this graph there are essentially one-dimensional frequency distributions along any cross-section. For example, a cross-section parallel to the y-axis (the body size increment held constant) would look similar to one of the graphs of Figure 14.

Any pairwise combination of measures can be used to construct a species frequency distribution such as those presented in Figures 13-15. Another example of this type of information is shown in Figure 16 which illustrates the relationship between body size and geographic range (from Brown and Nicoletto 1991).



**Figure 15.**

A three-dimensional bar graph showing the frequency distribution of population density ( $\log_{10}$  numbers per  $\text{km}^2$ ) for 368 species of terrestrial mammalian herbivores in 14 different size categories from Table 11.



**Figure 16.**

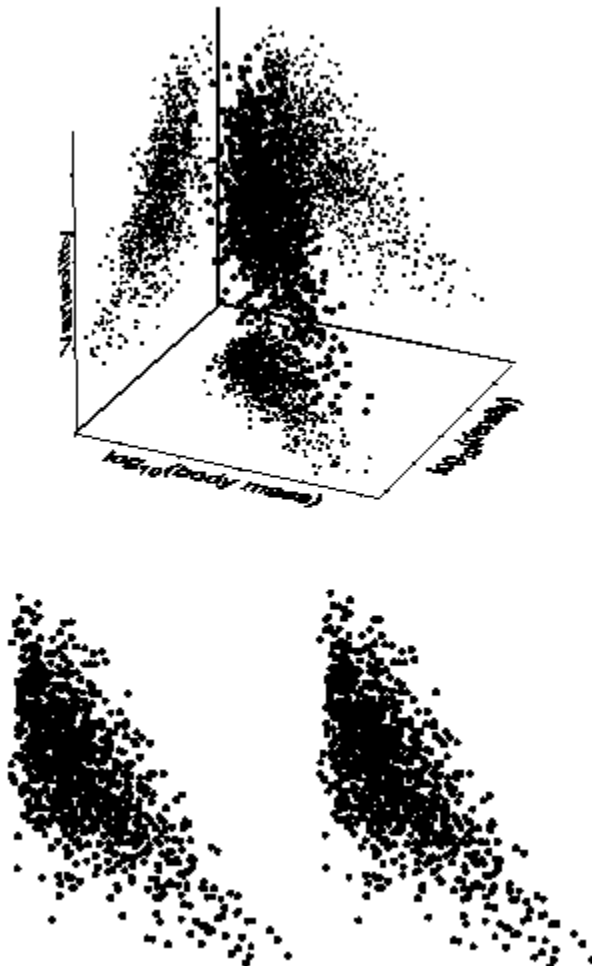
A three-dimensional bar graph showing the frequency distribution of geographic range size ( $\log_{10}$   $\text{km}^2$ ) for terrestrial mammals of various body masses from Brown and Nicoletto (1991). Category 1 contains species of less than 16 g body mass, category 2 is from 16 to 128 g, with an eight-fold increase in each higher category, and category 6 is species larger than 65,536 g.

## ----- More Complex Correlations -----

In progressing from two to three dimensions, we encounter even more constraints when presenting data in tables and graphs. To take this step in tabular form, we could extrapolate from the process outlined above for cases with two dimensions. To add the third dimension, we could produce a multi-paged table; each page would be similar in design to that of Table 11. Each page of the three-dimensional table would represent a different bin for one of the three variables. Each individual three-dimensional bin is now like a cube and is represented by a single element on one of the pages (as a sub-table of the entire multi-paged table). Counts of species would occupy these cubes in the page/category-specific tables like the top panel of Table 11. The portions of species found in each bin would also occur in such tables with information like that of the bottom panel of Table 11. In many cases, the size of such a table would rapidly become

voluminous and impractical, but, up to a point, could be stored on computers for analysis.

Graphically depicting frequency distributions for species in three-dimensional space is impossible with printed histograms or bar graphs. The remaining option is that of showing the data plotted in three-dimensional space as demonstrated in Figure 17 (with hypothetical data showing the interrelationships among population density, population variation and body size). Here the density of points in space is representative of the frequency of species in the cubes of space defined by the bins for all three measures of a species. The three-dimensional visualization possible in the stereogram (bottom section of Figure 17 for the same data as presented in the larger dots of the top section) is comparable to similar presentations in two-dimensional space (e.g., Fig. 13).



**Figure 17.**

A cluster of hypothetical species (heavy points in the top panel) distributed in three-dimensional space (shown projected in each two-dimensional combination on the walls and floor of the top section, and as a stereogram in the bottom section) much as might be expected for population variability, body size, and population density (the latter two variables shown after  $\log_{10}$  transformation).

All species occur in multidimensional space, of course, and the task of defining their frequency in the more complex n-dimensional compartments (a cube for three-dimensional cases) is an extension of the process begun above in progressing from one dimension, then to two, and finally to three dimensions. Printed graphic

presentation becomes impossible beyond three dimensions without resorting to multiple graphs. With computer technology, however, data can be analyzed and through the repetitive video display of multiple graphs it is possible to include other dimensions (e.g., time).

### ————— Use of Species Frequency Distributions —————

In our introductory remarks, we mentioned an alternative form of management that makes use of species frequency distributions. In this management, the central tendencies of such distributions provide standards of comparison and specific measurable goals or objectives for management (e.g., control of human influence on individual species, ecosystems, or the biosphere). Species frequency distributions provide guidance for management because they are based on empirical examples of sustainability represented by species that have survived the risks associated with being elements of complex systems (e.g., ecosystems) as well as through being complex systems themselves.

Figures 18, 19, and 20 illustrate where humans are located on a variety of such frequency distributions. In some cases, humans are located in the tails of the distributions, and in many cases are clear outliers. Successful management would result in humans (and hopefully other outlying species, through their responses to human action) falling within the normal range of natural variation, optimally in more central locations within such distributions (as humans do for trophic level, Fig. 18A). Maximal sustainability for humans would be achieved close to the central tendencies when such central tendencies are: 1) from collections of species unaffected by abnormal influence, and 2) representative of species otherwise similar to humans (e.g., similar body size as shown in Figs. 13 and 16). Human interactions and influences on other systems (e.g., species, ecosystems) are the only things over which we have much control. Sustainability for our species is of special importance, but depends on the capacity of other systems to sustain us, thus emphasizing the need to change in order to achieve systemic sustainability.

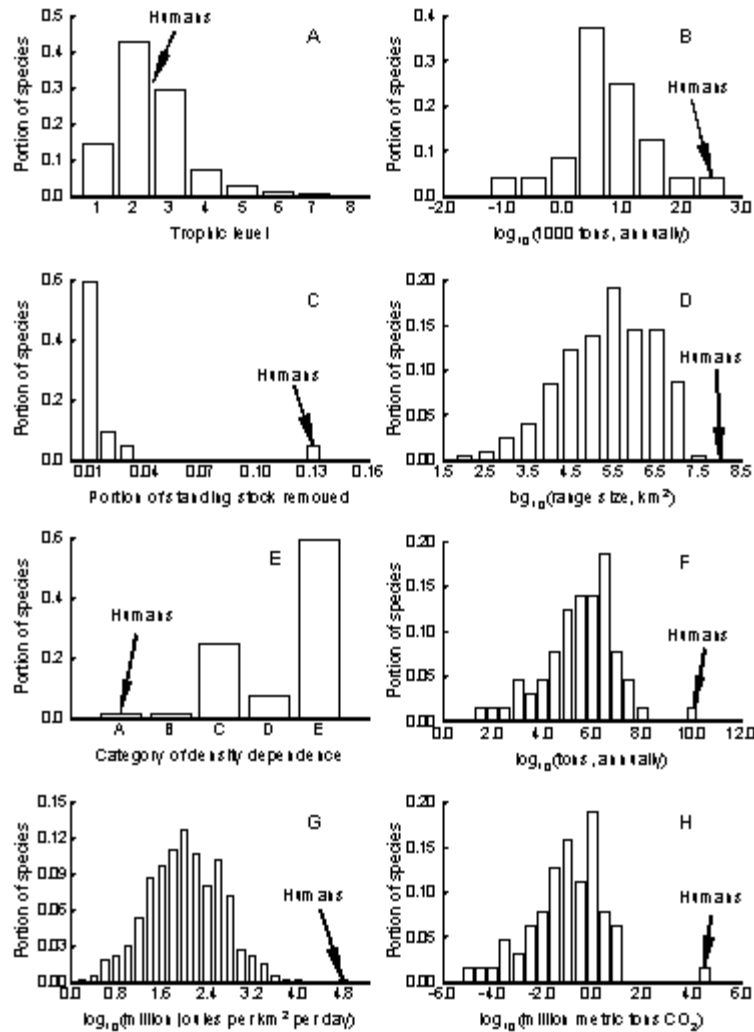
Now we can see that the bias of estimation procedures would have to be extreme to be misleading regarding the magnitude, but especially the direction, of change required for effective management. Even so, measures of the extent of change required of humans through effective management may be substantively affected by bias. Such bias can come both from procedural effects (e.g., error in estimation), as well as the effects of influence by outlying species, especially

humans, on existing distributions.

Management based on empirical examples addresses a number of problems and issues that have frustrated past attempts to achieve maximal sustainability. It is simultaneously applicable with regard to ecosystems (Fig. 18B), taxonomic groups of species (Fig. 11B), single species resources (Fig. 18C), and the biosphere (Fig. 18F; also Fowler 1999, Fowler et al. 1999, Fowler unpub. manuscript) as shown in Figure 20. It applies in a variety of ways (Figs. 18, 19 and 20). Control, in this form of management, involves changes in human activities where control is an option (e.g., promoting or limiting commercial fishing operations rather than controlling fish populations or their ecosystems; Campbell 1974, Bateson 1979, Allen and Starr 1982, Salthe 1985, O'Neill et al. 1986, Wilber 1995, Holling and Meffe 1996, Mangel et al. 1996). Such change and action would be an application of a core principle of management: maintaining elements of biological organization within their normal ranges of natural variation (Christensen et al. 1996, Mangel et al. 1996) as direct recognition of the limits to variation (Pickett et al. 1992).

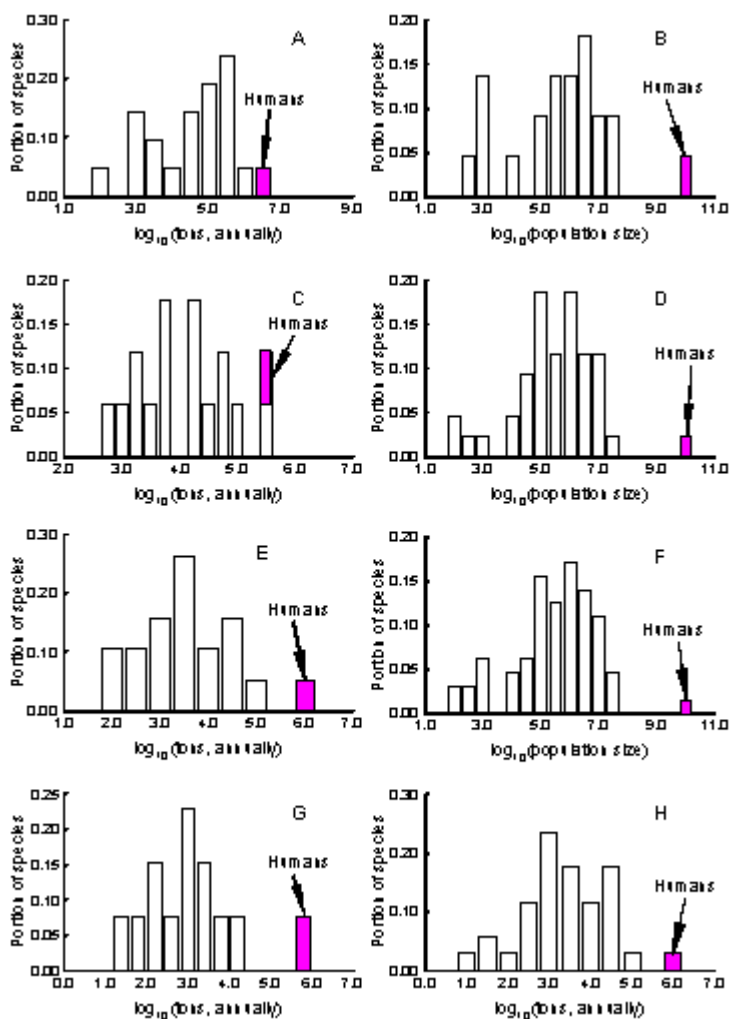
Species frequency distributions are increasingly recognized as phenomena of importance in ecological studies, especially in what has been called "macroecology" (the study of large-scale ecological patterns, exemplified and defined in Brown 1995; see also Rosenzweig 1995). As such, the management that we are describing brings the science of macroecology into practical application.

Among the forces contributing to the formation of species frequency distributions are the dynamics of selective extinction and speciation (Slatkin 1981, Arnold and Fristrup 1982, Fowler and MacMahon 1982, Levinton 1988, Cristoffer 1990). Extinction is one of the forces that contributes to preventing the accumulation of certain types of species (e.g., those in and beyond the tails of species frequency distributions). Management based on this approach thus accounts for the risk of extinction along with the other factors that contribute to the limits of variation and the positions of individual species within species frequency distributions.



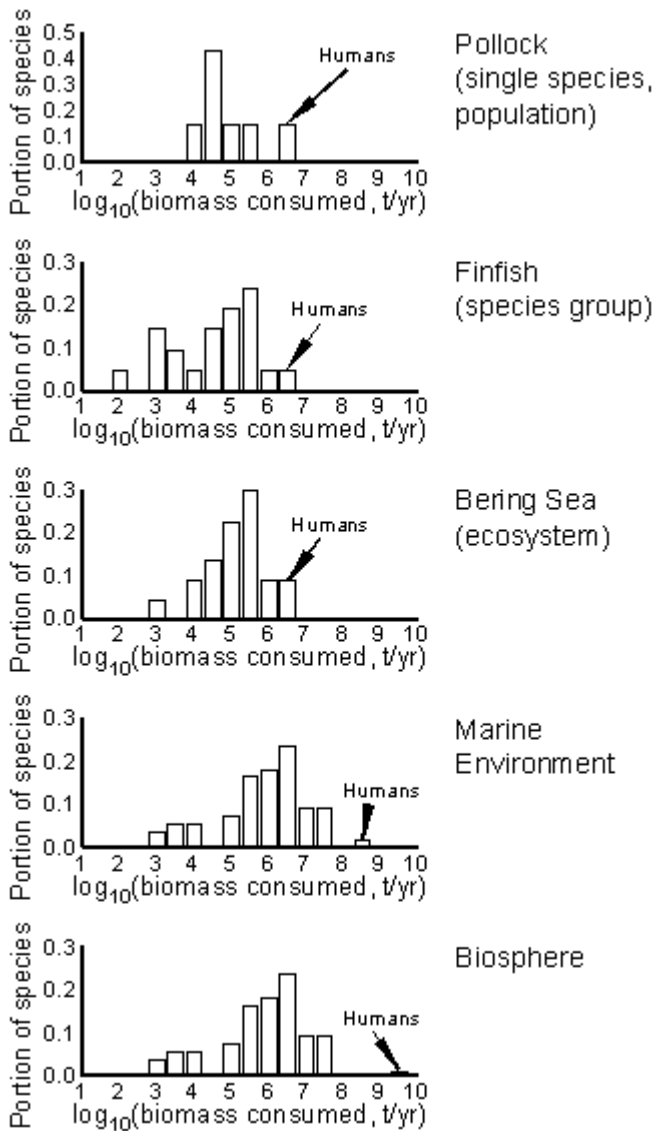
**Figure 18.**

Frequency distributions among species showing the change needed by humans as management to achieve a position near central tendencies (e.g., means of the distributions): A) trophic level based on species from 95 insect-dominated food webs (from Schoenly et al. 1991, an example of little if any change needed by humans); B) a frequency distribution representing consumption of biomass from the Georges Bank ecosystem by 24 species of marine mammals, sea birds and humans (from Backus and Bourne 1986); C) consumption rate of walleye pollock (*Theragra chalcogramma*) by vertebrate predators (Fig. 12; human consumption is about 60-fold the mean consumption rate); D) range size (Fig. 6) showing humans at 70% of the Earth's non-Antarctic terrestrial surface (about 71.4 million km<sup>2</sup>, although 95% might be more realistic, Pimentel et al. 1992); E) density dependence for 64 species of invertebrates, fish, birds and mammals in five statistical categories (from A: positive and significant to E: negative and significant at the 0.05 probability level; Tanner 1966, Pimm 1982); F) Total biomass ingested (i.e., not including biomass used for combustion, construction or other purposes) for humans and the 63 species of mammals from Figure 5 based on relationships from Peters (1983); G) energy consumption per unit area based on the 386 species of mammalian primary consumers of Damuth (1987) and size-specific energetic estimates based on relationships from Peters (1983); H) carbon dioxide production (Fig. 9) showing humans at 25 billion tons annually (Ehrlich and Ehrlich 1996).



**Figure 19.**

Frequency distributions among species showing the change needed by humans as management to achieve a position near central tendencies (e.g., means of the distributions): A) Human consumption (harvest) of finfish in the Bering Sea compared to that of various species of marine mammals from Figure 11; B) The total populations of marine mammals from the collection depicted in Figure 5 in comparison to the total population of humans; C) The consumption of mackerel, herring, sand eel, and hake by consumers in the northwest Atlantic compared to consumption (harvest) of the same species by humans (corresponding to the consumption of these species by dogfish, Overholtz et al. 1991); D) The total populations of terrestrial mammals from the collection depicted in Figure 5 in comparison to the total population of humans; E) The consumption of lantern fish, lightfish, anchovy and hake by consumers (33 species of marine birds) in the ecosystem off the southwest coast of Africa compared to consumption (harvest) of the same species by humans (from Crawford et al. 1991); F) The combination of B and D above (also the distribution of Fig. 5 expanded) to show the human population (5.7 billion) several orders of magnitude larger than the mean; G) The consumption of anchovy by consumers (33 species of marine birds) in the ecosystem(s) off the southwest coast of Africa compared to consumption (harvest) by humans (from Crawford et al. 1991); H) The consumption of biomass by consumers (33 species of marine birds) in the ecosystem(s) off the southwest coast of Africa compared to consumption (harvest) by humans (from Crawford et al. 1991).

**Figure 20.**

The frequency distribution of consumption rates for marine mammals showing consumption rates at a variety of levels of biological organization in comparison to the rate at which humans harvest biomass. The top panel shows the natural variation in consumption of pollock as observed for 6 species of marine mammals in the Bering Sea in comparison to recent takes of pollock by commercial fisheries (compare to Fig. 19C). The second panel shows consumption of finfish in the Bering Sea by 20 species of marine mammals compared to fisheries takes (see Fig. 11). Total biomass consumption is shown for 20 species of marine mammals in the Bering Sea in the third panel, again compared to the commercial take which is predominantly pollock (see Fig. 11). Total biomass consumption for the entire marine environment is shown in the fourth panel for 55 species of marine mammals, here compared to the take of about 110 million metric tons estimated as the harvest of biomass for human use in the late 1990s (Committee on Ecosystem Management for Sustainable Marine Fisheries 1999). World-wide consumption of biomass by humans is compared to that of the same 55 species of marine mammals in the bottom panel. The last two panels are based on population and body size data from the marine mammal series by Ridgway and Harrison (1981-99) and equations representing ingestion rates as a function of body size in Peters (1983).

Keeping ecosystems themselves within their normal ranges of natural variation has been suggested as a goal for management (Rapport et al. 1981, Rapport et al. 1985), but action to control ecosystems is not considered an option (Campbell 1974, Bateson 1979, Allen and Starr 1982, Salthe 1985, O'Neill et al. 1986, Wilber 1995, Holling and Meffe 1996, Mangel et al. 1996). The remaining alternative is that of management defined to include human species-level change, constraint, and action. Such changes, constraints and action are within our species purview. They are changes where control is an option (Holling and Meffe 1996, Fowler unpub. manuscript), difficult as any such changes may be. Applied at the level of ecosystems and the biosphere, our influence on

ecosystems and the biosphere would be controlled. Human influence would be constrained to fall within the normal ranges of natural variation exhibited among species. Thus, it is important to know how to construct species frequency distributions to provide the needed information concerning such variation and its limits.

The data chosen for any particular distribution must be specific to the management question being addressed. Thus, to address the question of what is the most sustainable level of biomass consumption from a particular ecosystem, data such as shown in Figure 11A and Figures 18, 19 and 20 would be used. If the question is related to most sustainable harvest rate from the finfish of the Bering Sea, data like that of Figure 11B (see also Fig. 19A and second panel of Fig. 20)

would be used. Finding the most sustainable trophic level would be guided by data such as those shown in Figure 8. The process is more complicated than can be readily described here, involving among other things, the need to take into account the factors contributing to the variation observed in species frequency distributions (Fowler 1999, Fowler et al. 1999, Fowler unpub. manuscript), and data for species otherwise similar to humans.

Although fairly straight-forward in concept, such management would face serious challenges in implementation. For example, reducing commercial takes of fish by one or two orders of magnitude (Figs. 18B, 18C, 19A, 19C, 19E, 19G, 19H and 20) represents major change. The management implications obviated by the information such as that shown in Figures 18, 19 and 20 are not trivial.

Adding to such challenges are complicating factors such as the need to ensure that the sample of species chosen for guidance are species that are similar to humans in regard to features other than those for which guidance is sought. This is because certain measures of species are related to others. Such relationships are exemplified by population density (Fig. 15) and distribution (Fig. 16) in relationship to body mass. But body size is not the only factor for such consideration. Because of the complexity of nature, other factors such

as similarity of trophic level, for example, must also be considered when selecting species to construct informative frequency distributions to guide management. Such issues, however, are beyond the scope of this paper. They emphasize the importance of adequate data and clear graphic presentation of species frequency distributions. Here we have focused on the process of the analysis and display of such information to usefully depict the distributions represented.

It should be noted that the preceding discussion also applies to the assessment of any aberrant species. That is, species frequency distributions can be applied to the measure of species other than humans. Although complete control of other species and their relationships with other biological systems is not an option, species frequency distributions can still serve among the important tools at our disposal. It is important to successful management to identify problems that emerge from the collective influence of the variety of ways humans are found outside the normal ranges of natural variation. This is not only important in assessing individual species (e.g., the status of endangered species) but also is important at the ecosystem level in addressing the position and shapes of such distributions that characterize such systems.

## ----- Summary -----

Species frequency distributions can be constructed using any of a very large variety of measures that describe the natural variation of species. There are several critical steps. First, measurements are collected for a sample of species. Second, the measurements are ordered and subdivided into groups corresponding to uniform categories, increments, or bins, often after transformation of the data (e.g., frequently a  $\log_{10}$  transform). Third, the number of species in each category are counted and the count is converted to either a portion, or a percent, of the total sample. Finally, these portions (or percents) are plotted in histograms to graphically present the distribution for visual perception of the underlying probability distribution to see variability and its limits. The basic steps are laid out in many elementary statistical texts as applied to any form of measurement, here exemplified by measures of species shown in a variety of tables and graphs. After the data are collected, the remaining steps can be achieved with relative ease in many of the software applications available for data analysis today.

Measurements of species can include a wide variety of variables. Examples are: population size, population variation, mean adult body size, total metabolic rates, geographic range size, portion of a prey species' biomass consumed, chromosome count, carbon dioxide produced, energy consumed, or intrinsic rates of increase. Others would include consumption rates for nitrogen (or any other element), mobility, mortality rates, total biomass, and suppressing effects on resource species. It is not clear that there is a limit to such a list. As has been demonstrated in a variety of scientific publications, there are relationships between and among many such measures, some of which form consistent higher-level patterns (e.g., Charnov 1993). Frequency distributions in two-dimensional space can show such relationships and the distribution of species within them. Three-dimensional relationships can be depicted in stereograms, but not in ordinary frequency distributions. Graphic demonstration of frequency distributions in more than three dimensions is not

simple. However, it is possible to take advantage of sophisticated graphic software and modern computers to make useful presentations of data.

The utility of species frequency distributions stems from their demonstration of the limits and central tendencies in the variation among species. We need

such information to find the proper place for aberrant species (including humans) as sustainable components of ecosystems or the biosphere by falling within the normal range of natural variation. Data chosen for guidance must always be specific to the management question being addressed.

### ————— **Acknowledgments** —————

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species frequency distributions. These people are too numerous to name but are cited with our tables and figures (our citations often open a trail of references to establish their identity). It takes much time and effort to produce data of the kind that can be used in producing species frequency distributions and we want to acknowledge the people involved.



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-----**Appendix**-----

Appendix Tables 1 through 11

**Appendix Table 1.** List of 103 species of marine mammals with measures of their adult body mass. Columns A and G are species number, B indicates the primary source of information (see footnotes), C indicates the type of data (see footnotes), D is the species name, E and H are the body mass in kilograms, F and I are the  $\log_{10}$  of body mass. Columns A, B, C, D, E, and F are in order by scientific name and columns G, H, and I are in order by body mass.

A	B	C	D	E	F	G	H	I
1	1	2	<i>Arctocephalus australis</i>	104.0	2.017	27	27.2	1.434
2	1	1	<i>Arctocephalus forsteri</i>	103.8	2.016	70	37.5	1.574
3	1	2	<i>Arctocephalus galapagoensis</i>	45.5	1.658	21	40.0	1.602
4	1	2	<i>Arctocephalus gazella</i>	83.5	1.922	22	40.0	1.602
5	1	2	<i>Arctocephalus philippii</i>	90.0	1.954	88	42.5	1.628
6	1	2	<i>Arctocephalus pusillus</i>	411.0	2.614	20	45.0	1.653
7	1	2	<i>Arctocephalus tropicalis</i>	110.0	2.041	3	45.5	1.658
8	1	3	<i>Balaena glacialis</i>	53,000.0	4.724	19	50.0	1.699
9	1	3	<i>Balaena mysticetus</i>	70,000.0	4.845	77	55.0	1.740
10	1	5	<i>Balaenoptera acutorostrata</i>	10,000.0	4.000	89	55.0	1.740
11	1	5	<i>Balaenoptera borealis</i>	30,000.0	4.477	87	59.5	1.775
12	1	5	<i>Balaenoptera edeni</i>	26,000.0	4.415	49	60.0	1.778
13	1	5	<i>Balaenoptera musculus</i>	150,000.0	5.176	48	70.0	1.845
14	1	5	<i>Balaenoptera physalus</i>	80,000.0	4.903	80	71.3	1.853
15	1	3	<i>Berardius arnuxi</i>	10,200.0	4.009	82	72.0	1.857
16	1	2	<i>Berardius bairdii</i>	14,250.0	4.154	86	72.0	1.857
17	1	1	<i>Callorhinus ursinus</i>	135.8	2.133	95	75.0	1.875
18	1	3	<i>Caperea marginata</i>	3,250.0	3.512	25	80.0	1.903
19	1	5	<i>Cephalorhynchus commersoni</i>	50.0	1.699	4	83.5	1.922
20	1	5	<i>Cephalorhynchus eutropia</i>	45.0	1.653	81	85.0	1.929
21	1	5	<i>Cephalorhynchus heavisidii</i>	40.0	1.602	92	85.0	1.929
22	1	5	<i>Cephalorhynchus hectori</i>	40.0	1.602	5	90.0	1.954
23	1	2	<i>Cystophora cristata</i>	360.0	2.556	40	90.0	1.954
24	1	3	<i>Delphinapterus leucas</i>	1,000.0	3.000	45	90.0	1.954
25	1	2	<i>Delphinus delphis</i>	80.0	1.903	78	95.0	1.978
26	1	3	<i>Dugong dugon</i>	565.0	2.752	44	100.0	2.000
27	2	1	<i>Enhydra lutris</i>	27.2	1.434	73	100.0	2.000
28	1	5	<i>Erignathus barbatus</i>	190.0	2.279	83	100.0	2.000
29	1	2	<i>Eumetopias jubatus</i>	636.5	2.804	93	100.0	2.000
30	1	2	<i>Feresa attenuata</i>	160.0	2.204	94	100.0	2.000
31	1	5	<i>Globicephala macrorhynchus</i>	1,900.0	3.279	2	103.8	2.016
32	1	5	<i>Globicephala melaena</i>	2,650.0	3.423	1	104.0	2.017
33	1	2	<i>Grampus griseus</i>	375.0	2.574	7	110.0	2.041
34	1	1	<i>Halichoerus grypus</i>	227.5	2.357	96	110.0	2.041
35	1	2	<i>Hydrurga leptonyx</i>	347.5	2.541	43	115.0	2.061
36	1	4	<i>Hyperoodon ampullatus</i>	10,000.0	4.000	46	115.0	2.061
37	1	2	<i>Hyperoodon planifrons</i>	7,050.0	3.848	79	130.0	2.114
38	1	5	<i>Kogia breviceps</i>	500.0	2.699	97	130.0	2.114
39	1	5	<i>Kogia simus</i>	350.0	2.544	17	135.8	2.133
40	1	5	<i>Lagenodelphis hosei</i>	90.0	1.954	85	147.5	2.169
41	1	2	<i>Lagenorhynchus acutus</i>	190.0	2.279	30	160.0	2.204
42	1	5	<i>Lagenorhynchus albirostris</i>	190.0	2.279	76	160.0	2.204
43	1	5	<i>Lagenorhynchus australis</i>	115.0	2.061	101	175.0	2.243
44	1	5	<i>Lagenorhynchus cruciger</i>	100.0	2.000	72	179.5	2.254
45	1	5	<i>Lagenorhynchus obliquidens</i>	90.0	1.954	102	183.0	2.262

Appendix Table 1. (Continued)

A	B	C	D	E	F	G	H	I
46	1	5	<i>Lagenorhynchus obscurus</i>	115.0	2.061	69	188.6	2.275
47	1	2	<i>Leptonychotes weddelli</i>	420.0	2.623	28	190.0	2.279
48	1	5	<i>Lissodelphis borealis</i>	70.0	1.845	41	190.0	2.279
49	1	5	<i>Lissodelphis peronii</i>	60.0	1.778	42	190.0	2.279
50	1	5	<i>Lobodon carcinophagus</i>	220.0	2.342	67	200.0	2.301
51	1	5	<i>Megaptera novaeangliae</i>	65,000.0	4.813	66	210.0	2.322
52	1	5	<i>Mesoplodon bidens</i>	3,400.0	3.531	50	220.0	2.342
53	1	5	<i>Mesoplodon bowdoini</i>	2,600.0	3.415	34	227.5	2.357
54	1	5	<i>Mesoplodon carlhubbsi</i>	3,400.0	3.531	75	232.0	2.365
55	1	5	<i>Mesoplodon densirostris</i>	3,600.0	3.556	65	280.0	2.447
56	1	5	<i>Mesoplodon europaeus</i>	5,600.0	3.748	84	315.0	2.498
57	1	5	<i>Mesoplodon ginkgodens</i>	3,600.0	3.556	35	347.5	2.541
58	1	5	<i>Mesoplodon grayi</i>	4,800.0	3.681	39	350.0	2.544
59	1	5	<i>Mesoplodon hectori</i>	2,000.0	3.301	23	360.0	2.556
60	1	5	<i>Mesoplodon layardii</i>	3,400.0	3.531	33	375.0	2.574
61	1	5	<i>Mesoplodon mirus</i>	3,200.0	3.505	6	411.0	2.614
62	1	5	<i>Mesoplodon stejnegeri</i>	4,800.0	3.681	47	420.0	2.623
63	1	2	<i>Mirounga angustirostris</i>	1,600.0	3.204	99	425.0	2.628
64	1	2	<i>Mirounga leonina</i>	1,540.0	3.188	38	500.0	2.699
65	1	2	<i>Monachus monachus</i>	280.0	2.447	26	565.0	2.752
66	1	2	<i>Monachus schauinslandi</i>	210.0	2.322	29	636.5	2.804
67	1	5	<i>Monachus tropicalis</i>	200.0	2.301	71	850.0	2.929
68	1	3	<i>Monodon monoceros</i>	1,200.0	3.079	24	1,000.0	3.000
69	1,2	2	<i>Neophoca cinerea</i>	188.6	2.275	68	1,200.0	3.079
70	1	3	<i>Neophocoena phocoenoides</i>	37.5	1.574	64	1,540.0	3.188
71	1	1	<i>Odobenus rosmarus</i>	850.0	2.929	63	1,600.0	3.204
72	2	2	<i>Ommatophoca rossi</i>	179.5	2.254	91	1,600.0	3.204
73	1	5	<i>Orcaella brevirostris</i>	100.0	2.000	100	1,600.0	3.204
74	1	1	<i>Orcinus orca</i>	3,500.0	3.544	31	1,900.0	3.279
75	1	1	<i>Otaria flavescens</i>	232.0	2.365	59	2,000.0	3.301
76	1	5	<i>Peponocephala electra</i>	160.0	2.204	53	2,600.0	3.415
77	1	5	<i>Phoca caspica</i>	55.0	1.740	32	2,650.0	3.423
78	1	5	<i>Phoca fasciata</i>	95.0	1.978	61	3,200.0	3.505
79	1	5	<i>Phoca groenlandica</i>	130.0	2.114	18	3,250.0	3.512
80	1	1	<i>Phoca hispida</i>	71.3	1.853	52	3,400.0	3.531
81	1	2	<i>Phoca larga</i>	85.0	1.929	54	3,400.0	3.531
82	1	5	<i>Phoca siberica</i>	72.0	1.857	60	3,400.0	3.531
83	1	1	<i>Phoca vitulina</i>	100.0	2.000	74	3,500.0	3.544
84	1	2	<i>Phocarcotos hookeri</i>	315.0	2.498	55	3,600.0	3.556
85	1	3	<i>Phocoena dalli</i>	147.5	2.169	57	3,600.0	3.556
86	1	3	<i>Phocoena dioptrica</i>	72.0	1.857	58	4,800.0	3.681
87	1	3	<i>Phocoena phocoena</i>	59.5	1.775	62	4,800.0	3.681
88	1	3	<i>Phocoena sinus</i>	42.5	1.628	56	5,600.0	3.748
89	1	3	<i>Phocoena spinipinnis</i>	55.0	1.740	98	5,600.0	3.748
90	1	1	<i>Physeter macrocephalus</i>	37,500.0	4.574	103	5,600.0	3.748
91	1	2	<i>Pseudorca crassidens</i>	1,600.0	3.204	37	7,050.0	3.848
92	1	5	<i>Sousa chinensis</i>	85.0	1.929	10	10,000.0	4.000
93	1	5	<i>Stenella attenuata</i>	100.0	2.000	36	10,000.0	4.000
94	1	5	<i>Stenella coeruleoalba</i>	100.0	2.000	15	10,200.0	4.009

Appendix Table 1. (Continued)

A	B	C	D	E	F	G	H	I
95	1	5	<i>Stenella longirostris</i>	75.0	1.875	16	14,250.0	4.154
96	1	5	<i>Stenella plagiodon</i>	110.0	2.041	12	26,000.0	4.415
97	1	2	<i>Steno bredanensis</i>	130.0	2.114	11	30,000.0	4.477
98	1	5	<i>Tasmacetus spepherdi</i>	5,600.0	3.748	90	37,500.0	4.574
99	1	3	<i>Trichechus inunguis</i>	425.0	2.628	8	53,000.0	4.724
100	1	5	<i>Trichechus manatus</i>	1,600.0	3.204	51	65,000.0	4.813
101	1	3	<i>Tursiops truncatus</i>	175.0	2.243	9	70,000.0	4.845
102	1	2	<i>Zalophus californianus</i>	183.0	2.262	14	80,000.0	4.903
103	1	5	<i>Ziphius cavirostris</i>	5,600.0	3.748	13	150,000.0	5.176

Source (column B):

- 1: Macdonald (1984)
- 2: Ridgway and Harrison (1981-99)

Data type (column C):

- 1: Mean of the midpoints of ranges reported for both sexes
- 2: Mean of weights reported for each sex
- 3: Midpoint of range of weights reported for species (both sexes)
- 4: Weight reported for males only
- 5: Single weight reported for species

**Appendix Table 2.** List of 368 species of terrestrial mammalian primary consumers arrayed in order by their mean adult body mass measured in kilograms and in  $\log_{10}(\text{kg})$ . The species number is the sequence number of the species as found with its specific name in Damuth (1987).

Species number	Mass		Species number	Mass		Species number	Mass	
	(kg)	$\log_{10}(\text{kg})$		(kg)	$\log_{10}(\text{kg})$		(kg)	$\log_{10}(\text{kg})$
209	0.005	-2.301	224	0.035	-1.456	231	0.065	-1.187
258	0.006	-2.194	248	0.036	-1.444	238	0.065	-1.187
185	0.007	-2.155	179	0.036	-1.444	219	0.065	-1.187
287	0.007	-2.131	305	0.038	-1.420	272	0.065	-1.187
289	0.008	-2.125	218	0.039	-1.415	202	0.069	-1.163
211	0.008	-2.086	226	0.039	-1.409	230	0.069	-1.161
259	0.009	-2.071	301	0.039	-1.409	229	0.069	-1.161
257	0.009	-2.066	240	0.039	-1.409	308	0.070	-1.155
260	0.012	-1.928	276	0.040	-1.398	181	0.070	-1.155
210	0.014	-1.870	190	0.040	-1.398	250	0.071	-1.149
291	0.015	-1.824	191	0.040	-1.398	336	0.071	-1.149
298	0.015	-1.824	192	0.040	-1.398	184	0.071	-1.149
319	0.016	-1.796	282	0.040	-1.398	217	0.072	-1.143
288	0.017	-1.770	280	0.040	-1.398	309	0.072	-1.143
263	0.018	-1.750	274	0.042	-1.377	278	0.077	-1.116
349	0.018	-1.745	293	0.042	-1.377	236	0.081	-1.092
290	0.020	-1.699	174	0.042	-1.377	317	0.085	-1.071
297	0.020	-1.699	345	0.042	-1.377	271	0.086	-1.066
178	0.020	-1.699	253	0.043	-1.367	206	0.088	-1.056
296	0.021	-1.678	239	0.044	-1.357	347	0.093	-1.032
318	0.021	-1.678	302	0.044	-1.357	227	0.097	-1.013
269	0.021	-1.678	320	0.044	-1.357	340	0.097	-1.013
172	0.022	-1.658	234	0.045	-1.352	337	0.100	-1.000
186	0.023	-1.648	322	0.045	-1.347	342	0.101	-0.996
197	0.023	-1.638	251	0.047	-1.328	182	0.103	-0.987
294	0.023	-1.638	273	0.049	-1.310	333	0.107	-0.971
299	0.024	-1.620	255	0.049	-1.310	215	0.108	-0.967
279	0.024	-1.618	256	0.049	-1.310	261	0.108	-0.967
228	0.026	-1.585	304	0.050	-1.301	286	0.112	-0.951
249	0.027	-1.569	283	0.050	-1.301	314	0.112	-0.951
196	0.027	-1.569	329	0.050	-1.301	321	0.115	-0.939
338	0.027	-1.569	343	0.051	-1.292	246	0.116	-0.936
292	0.028	-1.553	300	0.052	-1.284	327	0.120	-0.921
199	0.028	-1.553	220	0.053	-1.276	285	0.121	-0.917
350	0.029	-1.538	303	0.053	-1.276	313	0.122	-0.914
176	0.029	-1.536	316	0.054	-1.268	311	0.125	-0.903
235	0.030	-1.523	237	0.054	-1.268	177	0.127	-0.896
277	0.030	-1.523	212	0.055	-1.260	328	0.129	-0.889
201	0.031	-1.516	213	0.056	-1.252	267	0.130	-0.886
198	0.031	-1.509	351	0.056	-1.252	284	0.136	-0.866
180	0.033	-1.481	281	0.059	-1.229	183	0.143	-0.845
348	0.034	-1.469	214	0.060	-1.222	216	0.145	-0.839
262	0.034	-1.469	344	0.062	-1.208	221	0.145	-0.839
295	0.035	-1.456	310	0.062	-1.208	173	0.146	-0.836
254	0.035	-1.456	232	0.063	-1.201	166	0.154	-0.812
252	0.035	-1.456	242	0.064	-1.194	346	0.154	-0.812
275	0.035	-1.456	245	0.065	-1.187	188	0.170	-0.770

Appendix Table 2. (Continued)

Species number	Mass		Species number	Mass		Species number	Mass	
	(kg)	$\log_{10}(\text{kg})$		(kg)	$\log_{10}(\text{kg})$		(kg)	$\log_{10}(\text{kg})$
24	0.177	-0.752	57	1.024	0.010	6	6.000	0.778
339	0.200	-0.699	7	1.070	0.029	5	6.000	0.778
334	0.200	-0.699	205	1.130	0.053	35	6.100	0.785
341	0.207	-0.684	170	1.130	0.053	59	6.250	0.796
189	0.210	-0.678	55	1.150	0.061	63	6.300	0.799
270	0.218	-0.662	9	1.200	0.079	65	6.300	0.799
195	0.222	-0.654	47	1.250	0.097	2	6.550	0.816
203	0.241	-0.618	363	1.250	0.097	3	7.250	0.860
10	0.241	-0.618	361	1.360	0.134	1	7.250	0.860
266	0.248	-0.606	160	1.360	0.134	28	7.800	0.892
247	0.250	-0.602	167	1.640	0.215	42	7.850	0.895
265	0.250	-0.602	40	1.700	0.230	14	8.000	0.903
315	0.251	-0.600	208	2.000	0.301	62	8.150	0.911
264	0.254	-0.595	366	2.080	0.318	25	8.150	0.911
187	0.257	-0.590	39	2.100	0.322	66	8.150	0.911
30	0.260	-0.585	161	2.420	0.384	175	8.200	0.914
268	0.260	-0.585	159	2.430	0.386	130	8.210	0.914
324	0.275	-0.561	11	2.520	0.401	61	8.350	0.922
326	0.275	-0.561	13	2.600	0.415	64	8.350	0.922
29	0.300	-0.523	12	2.600	0.415	225	8.620	0.936
355	0.300	-0.523	207	2.700	0.431	43	9.100	0.959
68	0.315	-0.502	23	2.700	0.431	27	9.500	0.978
306	0.316	-0.500	353	2.700	0.431	26	9.850	0.993
312	0.321	-0.493	38	2.700	0.431	368	10.00	1.000
330	0.350	-0.456	163	2.710	0.433	72	10.70	1.029
332	0.351	-0.455	365	2.800	0.447	360	11.00	1.041
45	0.385	-0.415	364	3.000	0.477	136	11.30	1.053
241	0.400	-0.398	164	3.020	0.480	357	12.00	1.079
223	0.400	-0.398	162	3.030	0.481	129	12.30	1.090
204	0.400	-0.398	145	3.200	0.505	95	12.50	1.097
56	0.425	-0.372	243	3.400	0.531	36	12.50	1.097
222	0.475	-0.323	165	3.400	0.531	60	12.80	1.107
193	0.487	-0.312	354	3.500	0.544	108	13.30	1.124
331	0.500	-0.301	19	3.500	0.544	122	13.60	1.134
323	0.530	-0.276	17	3.550	0.550	52	13.90	1.143
37	0.600	-0.222	18	3.600	0.556	94	14.00	1.146
69	0.600	-0.222	67	3.600	0.556	117	14.20	1.152
71	0.665	-0.177	244	3.950	0.597	120	14.30	1.155
70	0.665	-0.177	200	4.000	0.602	73	17.10	1.233
325	0.680	-0.167	16	4.050	0.607	51	17.50	1.243
8	0.680	-0.167	21	4.350	0.638	54	18.60	1.270
169	0.692	-0.160	20	4.500	0.653	53	19.50	1.290
46	0.725	-0.140	115	4.940	0.694	50	19.50	1.290
335	0.800	-0.097	22	4.950	0.695	116	20.00	1.301
307	0.800	-0.097	41	5.000	0.699	104	21.00	1.322
168	0.854	-0.069	44	5.150	0.712	93	21.70	1.336
362	0.872	-0.059	34	5.800	0.763	139	21.70	1.336
4	0.960	-0.018	33	5.800	0.763	367	22.50	1.352
194	1.020	0.009	32	5.900	0.771	48	22.70	1.356
171	1.020	0.009	15	6.000	0.778	125	24.00	1.380



**Appendix Table 2.** (Continued)

Species number	Mass		Species number	Mass		Species number	Mass	
	(kg)	$\log_{10}(\text{kg})$		(kg)	$\log_{10}(\text{kg})$		(kg)	$\log_{10}(\text{kg})$
356	25.00	1.398	143	74.80	1.874	100	203.0	2.307
132	28.00	1.447	91	75.00	1.875	109	211.0	2.324
81	29.80	1.474	124	75.90	1.880	106	225.0	2.352
83	31.00	1.491	74	83.40	1.921	123	250.0	2.398
78	31.00	1.491	119	85.10	1.930	150	259.0	2.413
79	31.80	1.502	113	89.00	1.949	87	263.0	2.420
358	31.90	1.504	118	89.30	1.951	152	270.0	2.431
233	32.80	1.516	111	90.60	1.957	90	274.0	2.438
142	40.80	1.611	140	90.60	1.957	155	300.0	2.477
359	41.40	1.617	92	100.0	2.000	96	310.0	2.491
114	42.00	1.623	128	100.0	2.000	151	390.0	2.591
134	42.50	1.628	141	110.0	2.041	77	403.0	2.605
133	43.50	1.638	352	118.0	2.072	138	453.0	2.656
49	45.00	1.653	102	122.0	2.086	137	544.0	2.736
80	46.50	1.667	86	125.0	2.097	84	551.0	2.741
146	47.50	1.677	31	127.0	2.104	88	568.0	2.754
82	48.10	1.682	99	138.0	2.140	85	850.0	2.929
75	52.40	1.719	89	149.0	2.173	105	912.0	2.960
58	53.00	1.724	76	158.0	2.199	148	952.0	2.979
135	55.30	1.743	121	167.0	2.223	154	997.0	2.999
103	58.80	1.769	98	170.0	2.230	149	1120	3.049
131	59.40	1.774	144	171.0	2.233	153	1255	3.099
126	60.90	1.785	97	175.0	2.243	157	1810	3.258
127	65.70	1.818	156	175.0	2.243	147	2220	3.346
112	69.30	1.841	110	194.0	2.288	158	2860	3.456
101	70.00	1.845	107	197.0	2.294			

**Appendix Table 3.** List of 21 species of marine fish with estimates of their population variability (coefficient of variation and its  $\log_{10}$  transformation) as found in Spencer and Collie (1997).

Species name	Species number in source document *	Variability	
		CV	$\log_{10}(\text{CV})$
<i>Clupea harengus</i>	12, 13, 15	0.58	-0.234
<i>Clupea pallasii</i>	14	1.01	0.004
<i>Cololabis saira</i>	16	0.44	-0.357
<i>Engraulis capensis</i>	11	0.43	-0.367
<i>Engraulis japonicus</i>	9	0.60	-0.222
<i>Engraulis mordax</i>	10	0.65	-0.187
<i>Gadus macrocephalus</i>	22	0.32	-0.495
<i>Hippoglossus stenolepis</i>	30	0.44	-0.357
<i>Lepidopsetta bilineata</i>	24	0.36	-0.444
<i>Melanogrammus aeglefinus</i>	21	0.68	-0.168
<i>Merluccius productus</i>	23	0.17	-0.770
<i>Pleuronectes aspera</i>	25	0.76	-0.119
<i>Pleuronectes ferrugineus</i>	26, 27	0.59	-0.233
<i>Sardinops caeruleus</i>	7	0.92	-0.036
<i>Sardinops melanostictus</i>	6	1.32	0.121
<i>Sardinops ocellatus</i>	8	0.88	-0.056
<i>Sardinops sagax</i>	5	1.10	0.041
<i>Scomber japonicus</i>	19, 20	0.77	-0.116
<i>Scomber scombrus</i>	17	0.60	-0.222
<i>Sebastes alutus</i>	28, 29	0.40	-0.403
<i>Trachinus japonicus</i>	18	0.58	-0.237

\*For cases with more than one number, there were a corresponding number of measures that were averaged for this table.

**Appendix Table 4.** List of 63 species of mammals of very roughly the same adult body mass as humans, showing their adult body mass (kg), estimated population size (millions) and the  $\log_{10}$  of estimated population size in millions as based on information from Kowak (1991) and Ridgway and Harrison (1981-99).

Species name	Body mass (kg)	Population size	
		(millions)	$\log_{10}$ (millions)
<i>Acinonyx jubatus</i>	54	0.01500	-1.824
<i>Ailuropoda melanoleuca</i>	115	0.00100	-3.000
<i>Antidorcas marsupialis</i>	39	0.60000	-0.222
<i>Antilocapra americana</i>	54	0.87500	-0.058
<i>Antilope cervicapra</i>	38	4.00000	0.602
<i>Arctocephalus australis</i>	159	0.32200	-0.492
<i>Arctocephalus forsteri</i>	160	0.03900	-1.409
<i>Arctocephalus galapagoensis</i>	150	0.00500	-2.301
<i>Arctocephalus gazella</i>	140	0.37000	-0.432
<i>Arctocephalus philippi</i>	140	0.00100	-3.000
<i>Arctocephalus townsendi</i>	150	0.00050	-3.301
<i>Arctocephalus tropicalis</i>	165	0.11300	-0.947
<i>Bahyrousa babyrussa</i>	80	0.00400	-2.398
<i>Callorhinus ursinus</i>	125	2.00000	0.301
<i>Canis lupus</i>	40	0.21000	-0.678
<i>Canis rufus</i>	30	0.00010	-4.000
<i>Capra ibex</i>	62	0.01000	-2.000
<i>Capra pirenaica</i>	58	0.02800	-1.553
<i>Capra walie</i>	100	0.00020	-3.699
<i>Cervus elephus</i>	200	1.00000	0.000
<i>Connochaetes taurinus</i>	195	3.10000	0.491
<i>Damaliscus dorcus</i>	110	0.15000	-0.824
<i>Delphinus delphis</i>	68	9.00000	0.954
<i>Enhydra lutris</i>	25	0.15000	-0.824
<i>Felis concolor</i>	50	0.03200	-1.495
<i>Gorilla gorilla</i>	135	0.05000	-1.301
<i>Hemitragus jemlahicus</i>	75	0.02500	-1.602
<i>Kobus kob</i>	125	1.00000	0.000
<i>Kobus leche</i>	125	0.10000	-1.000
<i>Kobus megercerus</i>	125	0.03500	-1.456
<i>Lama guanicoe</i>	110	0.57500	-0.240
<i>Lama pacos</i>	60	3.50000	0.544
<i>Lasiornhinus krefftis</i>	25	0.00004	-4.398
<i>Lipototes vexillifer</i>	160	0.00030	-3.523
<i>Litorcranius walleri</i>	40	0.07000	-1.155
<i>Macropus fuliginosus</i>	55	1.77000	0.248
<i>Macropus giganteus</i>	55	8.90000	0.949
<i>Macropus rufus</i>	55	8.30000	0.919

Appendix Table 4. (Continued)

Species name	Body mass (kg)	Population size	
		(millions)	$\log_{10}$ (millions)
<i>Odocoileus virginianus</i>	96	28.00000	1.447
<i>Oedocoileus hemionus</i>	60	5.50000	0.740
<i>Oreamnoa americanus</i>	95	0.10000	-1.000
<i>Ovis canadensis</i>	56	1.70000	0.230
<i>Ovis dalli</i>	90	0.11000	-0.959
<i>Pan troglodytes</i>	45	0.20000	-0.699
<i>Panthera leo</i>	175	0.40000	-0.398
<i>Panthera tigris</i>	175	0.10000	-1.000
<i>Phoca caspica</i>	100	0.56000	-0.252
<i>Phoca groenlandica</i>	125	2.00000	0.301
<i>Phoca hispida</i>	100	1.20000	0.079
<i>Phoca siberica</i>	100	0.04000	-1.398
<i>Phoca vitulina</i>	90	0.30000	-0.523
<i>Phocoenoides dalli</i>	100	2.15000	0.332
<i>Platanista indi</i>	100	0.00050	-3.301
<i>Pongo pygmaeus</i>	50	0.04300	-1.367
<i>Rangifer tarandus</i>	95	2.00000	0.301
<i>Rupicapra pyrenaica</i>	37	0.03100	-1.509
<i>Rupicapra rupicapra</i>	37	0.52300	-0.281
<i>Saiga tatarica</i>	47	2.00000	0.301
<i>Stenella attenuata</i>	110	22.00000	1.342
<i>Stenella coeruleoalba</i>	110	23.00000	1.362
<i>Stenella longirostris</i>	110	9.00000	0.954
<i>Ursus americans</i>	180	0.45000	-0.347
<i>Vicugna vicugna</i>	50	0.12500	-0.903

**Appendix Table 5.** List of 523 species of North American mammals with estimates of their geographic range measured in 1,000s of square kilometers and in  $\log_{10}$ (square km) from Pagelet al. 1991 (with original data provided by M. Pagel, University of Oxford, Oxford, England).

Species number	Range		Species number	Range		Species number	Range	
	(10 <sup>3</sup> km <sup>2</sup> )	$\log_{10}$ (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	$\log_{10}$ (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	$\log_{10}$ (km <sup>2</sup> )
1	9,670.778	6.985	47	2,333.192	6.368	93	94.876	4.977
2	1,571.410	6.196	48	216.464	5.335	94	3,642.413	6.561
3	2,187.916	6.340	49	1,099.084	6.041	95	125.845	5.100
4	3,193.138	6.504	50	734.515	5.866	96	349.296	5.543
5	1,714.437	6.234	51	592.093	5.772	97	2,327.579	6.367
6	8,076.901	6.907	52	114.524	5.059	98	10,436.650	7.019
7	4,886.909	6.689	53	1,131.389	6.054	99	4,112.251	6.614
8	7,714.576	6.887	54	408.377	5.611	100	5,223.393	6.718
9	1,327.660	6.123	55	107.330	5.031	101	27.721	4.443
10	19,332.696	7.286	56	207.220	5.316	102	3,507.620	6.545
11	10,160.661	7.007	57	1,789.655	6.253	103	13,133.046	7.118
12	5,750.426	6.760	58	263.119	5.420	104	509.266	5.707
13	13,982.183	7.146	59	76.530	4.884	105	1,579.293	6.198
14	17,984.416	7.255	60	2.595	3.414	106	834.870	5.922
15	2,054.723	6.313	61	4.309	3.634	107	724.066	5.860
16	8,409.801	6.925	62	12.436	4.095	108	18.258	4.261
17	14,500.110	7.161	63	353.162	5.548	109	2,395.183	6.379
18	3,553.487	6.551	64	42.726	4.631	110	4,882.245	6.689
19	11,915.631	7.076	65	597.553	5.776	111	690.746	5.839
20	12,706.118	7.104	66	193.942	5.288	112	766.714	5.885
21	10,267.445	7.011	67	391.390	5.593	113	19.162	4.282
22	166.599	5.222	68	745.708	5.873	114	3,200.227	6.505
23	2,332.388	6.368	69	2,031.511	6.308	115	5,306.882	6.725
24	11,008.500	7.042	70	61.626	4.790	116	930.876	5.969
25	12,135.639	7.084	71	142.143	5.153	117	3,963.142	6.598
26	1,306.068	6.116	72	101.260	5.005	118	140.443	5.148
27	9,524.647	6.979	73	126.288	5.101	119	14,804.126	7.170
28	6,482.713	6.812	74	0.699	2.844	120	1,980.779	6.297
29	11,581.971	7.064	75	349.009	5.543	121	104.094	5.017
30	1,718.494	6.235	76	997.555	5.999	122	94.335	4.975
31	13,335.867	7.125	77	1,082.909	6.035	123	1,002.139	6.001
32	11,088.732	7.045	78	1,166.147	6.067	124	125.071	5.097
33	9,737.300	6.988	79	609.494	5.785	125	3,065.501	6.487
34	2,162.633	6.335	80	1,800.301	6.255	126	2,786.063	6.445
35	15,072.308	7.178	81	209.817	5.322	127	4,130.542	6.616
36	7,382.603	6.868	82	215.817	5.334	128	1,456.825	6.163
37	97.140	4.987	83	25.769	4.411	129	1,465.123	6.166
38	7,529.020	6.877	84	93.512	4.971	130	599.336	5.778
39	1.621	3.210	85	10.964	4.040	131	4,829.205	6.684
40	4.052	3.608	86	16.030	4.205	132	487.293	5.688
41	3,913.670	6.593	87	118.271	5.073	133	282.013	5.450
42	674.202	5.829	88	128.410	5.109	134	4.509	3.654
43	10,029.454	7.001	89	90.369	4.956	135	264.089	5.422
44	15,067.531	7.178	90	9.304	3.969	136	92.483	4.966
45	928.815	5.968	91	23.624	4.373	137	58.302	4.766
46	196.534	5.293	92	306.866	5.487	138	4,654.624	6.668

Appendix Table 5. (Continued)

Species number	Range		Species number	Range		Species number	Range	
	(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )
139	0.950	2.978	188	1.617	3.209	237	39.565	4.597
140	115.509	5.063	189	6,896.771	6.839	238	1,805.627	6.257
141	43.174	4.635	190	553.512	5.743	239	1.394	3.144
142	149.256	5.174	191	404.282	5.607	240	3,086.579	6.489
143	4,339.389	6.637	192	361.098	5.558	241	332.793	5.522
144	10.584	4.025	193	956.530	5.981	242	128.583	5.109
145	53.857	4.731	194	2,278.309	6.358	243	428.609	5.632
146	8,440.765	6.926	195	36.649	4.564	244	7.286	3.862
147	2,820.147	6.450	196	3,422.040	6.534	245	7.501	3.875
148	197.017	5.295	197	345.716	5.539	246	15.216	4.182
149	104.827	5.020	198	878.163	5.944	247	75.007	4.875
150	5,416.801	6.734	199	1,105.274	6.043	248	648.271	5.812
151	198.682	5.298	200	11,239.258	7.051	249	0.429	2.632
152	8.350	3.922	201	938.035	5.972	250	1.929	3.285
153	64.822	4.812	202	501.638	5.700	251	15.430	4.188
154	984.299	5.993	203	184.000	5.265	252	1.714	3.234
155	91.911	4.963	204	26.946	4.430	253	387.885	5.589
156	77.389	4.889	205	3,953.100	6.597	254	161.619	5.208
157	231.715	5.365	206	245.499	5.390	255	161.919	5.209
158	817.889	5.913	207	8.324	3.920	256	60.775	4.784
159	5,811.235	6.764	208	16.880	4.227	257	1,418.094	6.152
160	340.259	5.532	209	238.373	5.377	258	0.405	2.607
161	44.088	4.644	210	25.892	4.413	259	24.310	4.386
162	375.022	5.574	211	112.021	5.049	260	292.067	5.465
163	4,285.374	6.632	212	14,483.560	7.161	261	18.485	4.267
164	528.169	5.723	213	7.595	3.881	262	25.879	4.413
165	356.870	5.553	214	76.197	4.882	263	12.939	4.112
166	7,929.817	6.899	215	504.873	5.703	264	2.958	3.471
167	12,498.145	7.097	216	13,689.319	7.136	265	2.218	3.346
168	49.804	4.697	217	2,013.211	6.304	266	514.331	5.711
169	448.832	5.652	218	42.415	4.628	267	448.776	5.652
170	401.007	5.603	219	33.537	4.526	268	6.697	3.826
171	1,253.922	6.098	220	0.233	2.367	269	184.124	5.265
172	3,956.219	6.597	221	243.421	5.386	270	24.760	4.394
173	234.308	5.370	222	136.644	5.136	271	197.333	5.295
174	788.013	5.897	223	406.769	5.609	272	13.639	4.135
175	3,189.549	6.504	224	0.149	2.173	273	277.136	5.443
176	176.278	5.246	225	1.016	3.007	274	714.539	5.854
177	107.030	5.030	226	0.618	2.791	275	863.462	5.936
178	305.589	5.485	227	0.740	2.869	276	5.602	3.748
179	10,870.202	7.036	228	35.803	4.554	277	4.749	3.677
180	625.067	5.796	229	30.733	4.488	278	2,503.359	6.399
181	4,016.231	6.604	230	13.318	4.124	279	187.820	5.274
182	3,125.474	6.495	231	107.565	5.032	280	92.199	4.965
183	4,361.341	6.640	232	30.098	4.479	281	48.980	4.690
184	528.470	5.723	233	15.344	4.186	282	392.074	5.593
185	10.838	4.035	234	29.153	4.465	283	311.023	5.493
186	230.456	5.363	235	565.780	5.753	284	2,753.152	6.440
187	375.935	5.575	236	44.217	4.646	285	885.106	5.947

Appendix Table 5. (Continued)

Species number	Range		Species number	Range		Species number	Range	
	(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )
286	75.969	4.881	335	23.329	4.368	384	11.410	4.057
287	24.790	4.394	336	8.973	3.953	385	414.894	5.618
288	431.731	5.635	337	1,615.070	6.208	386	36.303	4.560
289	86.346	4.936	338	303.930	5.483	387	24.509	4.389
290	6.908	3.839	339	3,687.043	6.567	388	22.770	4.357
291	590.528	5.771	340	111.762	5.048	389	57.148	4.757
292	76.197	4.882	341	46.656	4.669	390	13.335	4.125
293	15.620	4.194	342	42.685	4.630	391	7.620	3.882
294	0.376	2.575	343	610.002	5.785	392	7.363	3.867
295	90.388	4.956	344	1,472.616	6.168	393	8.323	3.920
296	109.486	5.039	345	13,970.908	7.145	394	48.020	4.681
297	122.766	5.089	346	3,634.371	6.560	395	11.107	4.046
298	510.638	5.708	347	1,452.128	6.162	396	33.320	4.523
299	1,034.361	6.015	348	2,665.587	6.426	397	34.523	4.538
300	3,915.678	6.593	349	0.987	2.994	398	66.900	4.825
301	7,408.815	6.870	350	2.218	3.346	399	1,503.989	6.177
302	213.840	5.330	351	518.617	5.715	400	160.771	5.206
303	2,827.290	6.451	352	4.965	3.696	401	5,722.671	6.758
304	403.899	5.606	353	0.511	2.708	402	73.954	4.869
305	1,477.021	6.169	354	924.245	5.966	403	0.828	2.918
306	3,704.408	6.569	355	94.540	4.976	404	116.170	5.065
307	11,219.063	7.050	356	101.667	5.007	405	1,867.021	6.271
308	1,530.641	6.185	357	466.755	5.669	406	1,317.123	6.120
309	26.651	4.426	358	72.606	4.861	407	4,619.523	6.665
310	26.460	4.423	359	207.447	5.317	408	2.330	3.367
311	2.117	3.326	360	352.934	5.548	409	52.920	4.724
312	1.455	3.163	361	9,199.065	6.964	410	392.799	5.594
313	300.026	5.477	362	522.766	5.718	411	2,519.913	6.401
314	73.851	4.868	363	5,571.919	6.746	412	8.081	3.907
315	2,276.508	6.357	364	1,088.213	6.037	413	2,987.234	6.475
316	3,646.526	6.562	365	1,037.234	6.016	414	376.850	5.576
317	174.320	5.241	366	871.115	5.940	415	8.103	3.909
318	1,316.687	6.119	367	0.157	2.196	416	20.258	4.307
319	1,999.190	6.301	368	3.779	3.577	417	118.512	5.074
320	989.600	5.995	369	72.606	4.861	418	6.381	3.805
321	881.649	5.945	370	21.728	4.337	419	22.252	4.347
322	2,390.334	6.378	371	91.390	4.961	420	27.277	4.436
323	76.197	4.882	372	207.447	5.317	421	14.521	4.162
324	1,195.167	6.077	373	82.979	4.919	422	8.298	3.919
325	705.868	5.849	374	2.593	3.414	423	15.559	4.192
326	26.851	4.429	375	1,784.009	6.251	424	7.779	3.891
327	95.350	4.979	376	6.690	3.825	425	5.518	3.742
328	1,866.304	6.271	377	3.122	3.494	426	226.266	5.355
329	897.261	5.953	378	972.002	5.988	427	4,030.675	6.605
330	11.305	4.053	379	59.363	4.774	428	265.532	5.424
331	1,776.577	6.250	380	489.511	5.690	429	331.915	5.521
332	921.986	5.965	381	25.931	4.414	430	507.343	5.705
333	228.592	5.359	382	129.654	5.113	431	264.701	5.423
334	138.298	5.141	383	207.447	5.317	432	198.525	5.298

**Appendix Table 5.** (Continued)

Species number	Range		Species number	Range		Species number	Range	
	(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )		(10 <sup>3</sup> km <sup>2</sup> )	log <sub>10</sub> (km <sup>2</sup> )
433	507.092	5.705	464	76.761	4.885	495	1,383.109	6.141
434	2,966.944	6.472	465	28.623	4.457	496	193.737	5.287
435	5,927.052	6.773	466	53.332	4.727	497	322.358	5.508
436	5.543	3.744	467	36.037	4.557	498	531.080	5.725
437	91.437	4.961	468	300.530	5.478	499	3,912.196	6.592
438	457.183	5.660	469	1.855	3.268	500	3,467.540	6.540
439	26.852	4.429	470	29.891	4.476	501	5,545.246	6.744
440	41.650	4.620	471	3,969.246	6.599	502	1,715.500	6.234
441	286.469	5.457	472	7,771.747	6.891	503	6.653	3.823
442	863.318	5.936	473	7,950.383	6.900	504	1,229.200	6.090
443	346.643	5.540	474	1,747.351	6.242	505	35.520	4.550
444	22.440	4.351	475	2,605.028	6.416	506	2,438.916	6.387
445	1,694.204	6.229	476	28.747	4.459	507	458.805	5.662
446	3.746	3.574	477	4,018.504	6.604	508	50.864	4.706
447	235.299	5.372	478	679.751	5.832	509	21.183	4.326
448	33.298	4.522	479	93.006	4.969	510	12.501	4.097
449	376.061	5.575	480	222.861	5.348	511	329.685	5.518
450	9.185	3.963	481	363.812	5.561	512	1,891.591	6.277
451	5,159.040	6.713	482	681.316	5.833	513	56.176	4.750
452	1,103.715	6.043	483	3,915.084	6.593	514	80.305	4.905
453	193.118	5.286	484	49.607	4.696	515	6.142	3.788
454	127.194	5.104	485	242.351	5.384	516	5.016	3.700
455	1.184	3.073	486	96.675	4.985	517	4,010.100	6.603
456	28.884	4.461	487	53.527	4.729	518	10,446.774	7.019
457	43.289	4.636	488	310.484	5.492	519	512.831	5.710
458	102.074	5.009	489	7.512	3.876	520	1,059.952	6.025
459	18.671	4.271	490	327.023	5.515	521	7,938.016	6.900
460	615.184	5.789	491	13.349	4.125	522	2,963.526	6.472
461	370.178	5.568	492	551.580	5.742	523	184.680	5.266
462	137.037	5.137	493	15.289	4.184			
463	18.036	4.256	494	6.963	3.843			



**Appendix Table 6.** Frequency distribution of 19,747 species of angiosperm plants according to counts of their chromosome number (from Masterson 1994, original data provided by J. Masterson, University of Chicago, Chicago, IL).

Count	Number of species	Portion of species	Count	Number of species	Portion of species	Count	Number of species	Portion of species
1	0	0.0000	41	23	0.0012	81	1	0.0001
2	26	0.0013	42	76	0.0038	82	3	0.0002
3	29	0.0015	43	20	0.0010	83	1	0.0001
4	111	0.0056	44	33	0.0017	84	4	0.0002
5	265	0.0134	45	60	0.0030	85	7	0.0004
6	385	0.0194	46	25	0.0013	86	1	0.0001
7	1,157	0.0583	47	7	0.0004	87	2	0.0001
8	1,736	0.0875	48	79	0.0040	88	3	0.0002
9	1,722	0.0868	49	19	0.0010	89	0	0.0000
10	973	0.0491	50	33	0.0017	90	4	0.0002
11	1,541	0.0777	51	18	0.0009	91	2	0.0001
12	1,318	0.0664	52	24	0.0012	92	1	0.0001
13	601	0.0303	53	4	0.0002	93	1	0.0001
14	1,214	0.0612	54	48	0.0024	94	1	0.0001
15	531	0.0268	55	16	0.0008	95	2	0.0001
16	846	0.0427	56	31	0.0016	96	1	0.0001
17	548	0.0276	57	24	0.0012	97	0	0.0000
18	956	0.0482	58	17	0.0009	98	1	0.0001
19	460	0.0232	59	3	0.0002	99	1	0.0001
20	801	0.0404	60	46	0.0023	100	3	0.0002
21	429	0.0216	61	2	0.0001	101	0	0.0000
22	381	0.0192	62	9	0.0005	102	0	0.0000
23	183	0.0092	63	9	0.0005	103	1	0.0001
24	530	0.0267	64	13	0.0007	104	2	0.0001
25	180	0.0091	65	5	0.0003	105	0	0.0000
26	206	0.0104	66	7	0.0004	106	0	0.0000
27	226	0.0114	67	1	0.0001	107	0	0.0000
28	281	0.0142	68	4	0.0002	108	2	0.0001
29	90	0.0045	69	2	0.0001	109	0	0.0000
30	303	0.0153	70	12	0.0006	110	1	0.0001
31	46	0.0023	71	2	0.0001	111	0	0.0000
32	177	0.0089	72	21	0.0011	112	3	0.0002
33	81	0.0041	73	2	0.0001	113	0	0.0000
34	130	0.0066	74	4	0.0002	114	0	0.0000
35	66	0.0033	75	4	0.0002	115	0	0.0000
36	191	0.0096	76	3	0.0002	116	0	0.0000
37	19	0.0010	77	3	0.0002	117	1	0.0001
38	72	0.0036	78	4	0.0002	118	0	0.0000
39	44	0.0022	79	0	0.0000	119	0	0.0000
40	122	0.0062	80	6	0.0003	120	2	0.0001

**Appendix Table 7.** List of 63 species of mammals of very roughly the same adult body mass as humans, showing their adult body size (kg), estimated population size (millions), estimated total carbon dioxide production (million metric tons per year) and the  $\log_{10}$  of total  $\text{CO}_2$  production (based on Appendix Table 4 and equations for estimating  $\text{CO}_2$  production as presented in the text).

Species name	Body mass (kg)	Population size ( $10^6$ )	$\text{CO}_2$ production	
			$10^6$ metric tons	$\log_{10}(10^6$ metric tons)
<i>Acinonyx jubatus</i>	54	0.01500	0.003	-2.510
<i>Ailuropoda melanoleuca</i>	115	0.00100	0.000	-3.440
<i>Antidorcas marsupialis</i>	39	0.60000	0.097	-1.014
<i>Antilocapra americana</i>	54	0.87500	0.180	-0.744
<i>Antilope cervicapra</i>	38	4.00000	0.633	-0.199
<i>Arctocephalus galapagoensis</i>	150	0.00500	0.002	-2.654
<i>Arctocephalus australis</i>	159	0.32200	0.149	-0.826
<i>Arctocephalus forsteri</i>	160	0.03900	0.018	-1.741
<i>Arctocephalus gazella</i>	140	0.37000	0.156	-0.807
<i>Arctocephalus philippi</i>	140	0.00100	0.000	-3.375
<i>Arctocephalus townsendi</i>	150	0.00050	0.000	-3.654
<i>Arctocephalus tropicalis</i>	165	0.11300	0.054	-1.269
<i>Bahyrusa babyrussa</i>	80	0.00400	0.001	-2.956
<i>Callorhinus ursinus</i>	125	2.00000	0.774	-0.111
<i>Canis lupus</i>	40	0.21000	0.035	-1.462
<i>Canis rufus</i>	30	0.00010	0.000	-4.878
<i>Capra ibex</i>	62	0.01000	0.002	-2.641
<i>Capra pirenaica</i>	58	0.02800	0.006	-2.216
<i>Capra walie</i>	100	0.00020	0.000	-4.184
<i>Cervus elephus</i>	200	1.00000	0.551	-0.259
<i>Connochaetes taurinus</i>	195	3.10000	1.675	0.224
<i>Damaliscus dorcus</i>	110	0.15000	0.053	-1.278
<i>Delphinus delphis</i>	68	9.00000	2.205	0.343
<i>Enhydra lutris</i>	25	0.15000	0.017	-1.761
<i>Felis concolor</i>	50	0.03200	0.006	-2.206
<i>Hemitragus jemlahicus</i>	75	0.02500	0.007	-2.181
<i>Kobus kob</i>	125	1.00000	0.387	-0.412
<i>Kobus leche</i>	125	0.10000	0.039	-1.412
<i>Kobus megecerus</i>	125	0.03500	0.014	-1.868
<i>Lama guanicoe</i>	110	0.57500	0.202	-0.694
<i>Lama pacos</i>	60	3.50000	0.780	-0.108
<i>Lasiorhinus krefftis</i>	25	0.00004	0.000	-5.335
<i>Lipotes vexillifer</i>	160	0.00030	0.000	-3.855
<i>Litorcranius walleri</i>	40	0.07000	0.012	-1.939
<i>Macropus fuliginosus</i>	55	1.77000	0.370	-0.432
<i>Macropus giganteus</i>	55	8.90000	1.859	0.269
<i>Macropus rufus</i>	55	8.30000	1.734	0.239

Appendix Table 7. (Continued)

Species name	Body mass (kg)	Population size (10 <sup>6</sup> )	CO <sub>2</sub> production	
			10 <sup>6</sup> metric tons	log <sub>10</sub> (10 <sup>6</sup> metric tons)
<i>Odocoileus virginianus</i>	96	28.00000	8.886	0.949
<i>Oedocoileus hemionus</i>	60	5.50000	1.226	0.089
<i>Oreamnoa americanus</i>	95	0.10000	0.031	-1.502
<i>Ovis canadensis</i>	56	1.70000	0.360	-0.444
<i>Ovis dalli</i>	90	0.11000	0.033	-1.478
<i>Pan troglodytes</i>	45	0.20000	0.036	-1.445
<i>Panthera leo</i>	175	0.40000	0.199	-0.701
<i>Panthera tigris</i>	175	0.10000	0.050	-1.303
<i>Phoca caspica</i>	100	0.56000	0.183	-0.737
<i>Phoca groenlandica</i>	125	2.00000	0.774	-0.111
<i>Phoca hispida</i>	100	1.20000	0.393	-0.406
<i>Phoca siberica</i>	100	0.04000	0.013	-1.883
<i>Phoca vitulina</i>	90	0.30000	0.091	-1.042
<i>Phocoenoides dalli</i>	100	2.15000	0.704	-0.153
<i>Platanista indi</i>	100	0.00050	0.000	-3.786
<i>Pongo pygmaeus</i>	50	0.04300	0.008	-2.078
<i>Rangifer tarandus</i>	95	2.00000	0.630	-0.201
<i>Rupicapra pyrenaica</i>	37	0.03100	0.005	-2.318
<i>Rupicapra rupicapra</i>	37	0.52300	0.081	-1.091
<i>Saiga tatarica</i>	47	2.00000	0.371	-0.430
<i>Stenella attenuata</i>	110	22.00000	7.733	0.888
<i>Stenella coeruleoalba</i>	110	23.00000	8.085	0.908
<i>Stenella longirostris</i>	110	9.00000	3.164	0.500
<i>Ursus americans</i>	180	0.45000	0.229	-0.640
<i>Vicugna vicugna</i>	50	0.12500	0.024	-1.614

**Appendix Table 8.** List of 368 species of terrestrial mammalian primary consumers with measures, or estimates, of their mean adult body mass (g), density (individuals [n] per square kilometer), energy consumption per unit area (million joules per square kilometer per day), and  $\log_{10}(J/10^6\text{km}^2\text{day})$  arranged by species number (as found with specific names in Damuth 1987).

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	$\log_{10}(J/10^6\text{km}^2\text{day})$
1	7,250.0	25.000	92.49	1.966
2	6,550.0	51.000	175.73	2.245
3	7,250.0	74.000	273.76	2.437
4	960.0	100.000	89.85	1.953
5	6,000.0	13.500	43.75	1.641
6	6,000.0	45.000	145.82	2.164
7	1,070.0	150.000	145.40	2.163
8	680.0	255.000	179.97	2.255
9	1,200.0	15.000	15.76	1.197
10	241.0	900.000	307.30	2.488
11	2,520.0	37.000	65.33	1.815
12	2,600.0	80.000	144.37	2.159
13	2,600.0	35.000	63.16	1.800
14	8,000.0	33.000	130.79	2.117
15	6,000.0	45.000	145.82	2.164
16	4,050.0	53.000	130.44	2.115
17	3,550.0	108.000	242.38	2.384
18	3,600.0	20.000	45.33	1.656
19	3,500.0	20.000	44.44	1.648
20	4,500.0	42.000	111.28	2.046
21	4,350.0	34.000	87.97	1.944
22	4,950.0	22.500	63.73	1.804
23	2,700.0	22.500	41.69	1.620
24	177.0	250.000	68.77	1.837
25	8,150.0	230.000	923.52	2.965
26	9,850.0	112.000	513.49	2.711
27	9,500.0	30.000	134.10	2.127
28	7,800.0	0.300	1.17	0.067
29	300.0	17.500	6.97	0.843
30	260.0	17.500	6.30	0.799
31	127,000.0	1.800	49.41	1.694
32	5,900.0	5.100	16.33	1.213
33	5,800.0	30.000	94.94	1.977
34	5,800.0	6.200	19.62	1.293
35	6,100.0	22.000	72.12	1.858
36	12,500.0	12.000	65.00	1.813
37	600.0	288.000	186.21	2.270
38	2,700.0	250.000	463.24	2.666
39	2,100.0	1,030.000	1,600.65	3.204
40	1,700.0	350.000	469.13	2.671
41	5,000.0	25.000	71.31	1.853
42	7,850.0	35.000	136.89	2.136
43	9,100.0	20.000	86.75	1.938
44	5,150.0	100.000	291.19	2.464
45	385.0	121.000	57.35	1.759
46	725.0	215.000	158.70	2.201

Appendix Table 8. (Continued)

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	log <sub>10</sub> (J/10 <sup>6</sup> km <sup>2</sup> day)
47	1,250.0	26.200	28.32	1.452
48	22,700.0	4.000	32.90	1.517
49	45,000.0	2.500	33.20	1.521
50	19,500.0	10.300	76.17	1.882
51	17,500.0	4.000	27.42	1.438
52	13,900.0	1.800	10.50	1.021
53	19,500.0	12.500	92.44	1.966
54	18,600.0	2.300	16.45	1.216
55	1,150.0	9.000	9.18	0.963
56	425.0	675.000	342.83	2.535
57	1,024.0	40.000	37.60	1.575
58	53,000.0	2.000	29.78	1.474
59	6,250.0	29.000	96.70	1.985
60	12,800.0	57.000	313.93	2.497
61	8,350.0	150.000	612.60	2.787
62	8,150.0	107.000	429.64	2.633
63	6,300.0	42.000	140.83	2.149
64	8,350.0	33.000	134.77	2.130
65	6,300.0	11.400	38.23	1.582
66	8,150.0	154.000	618.36	2.791
67	3,600.0	175.000	396.60	2.598
68	315.0	33.000	13.59	1.133
69	600.0	23.000	14.87	1.172
70	665.0	25.000	17.37	1.240
71	665.0	25.000	17.37	1.240
72	10,700.0	5.200	25.26	1.402
73	17,100.0	69.500	468.80	2.671
74	83,400.0	7.760	158.70	2.201
75	52,400.0	13.100	193.51	2.287
76	158,000.0	2.060	65.89	1.819
77	403,000.0	0.720	44.36	1.647
78	31,000.0	0.830	8.49	0.929
79	31,800.0	4.650	48.42	1.685
80	46,500.0	0.930	12.64	1.102
81	29,800.0	4.800	47.76	1.679
82	48,100.0	13.000	180.86	2.257
83	31,000.0	35.000	358.04	2.554
84	551,000.0	0.320	24.54	1.390
85	850,000.0	1.000	103.87	2.017
86	125,000.0	0.146	3.96	0.598
87	263,000.0	0.850	38.84	1.589
88	568,000.0	0.610	47.78	1.679
89	149,000.0	2.700	82.89	1.919
90	274,000.0	1.200	56.43	1.752
91	75,000.0	3.100	58.86	1.770
92	100,000.0	4.600	106.82	2.029
93	21,700.0	8.600	68.54	1.836
94	14,000.0	8.000	46.91	1.671
95	12,500.0	4.000	21.67	1.336
96	310,000.0	0.930	47.68	1.678

Appendix Table 8. (Continued)

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	log <sub>10</sub> (J/10 <sup>6</sup> km <sup>2</sup> day)
97	175,000.0	5.480	188.28	2.275
98	170,000.0	12.700	427.59	2.631
99	138,000.0	1.420	41.32	1.616
100	203,000.0	7.590	289.33	2.461
101	70,000.0	18.800	340.12	2.532
102	122,000.0	11.000	293.60	2.468
103	58,800.0	1.060	16.97	1.230
104	21,000.0	6.640	51.72	1.714
105	912,000.0	0.937	102.25	2.010
106	225,000.0	0.774	31.71	1.501
107	197,000.0	0.660	24.64	1.392
108	13,300.0	17.900	101.26	2.005
109	211,000.0	9.110	356.80	2.552
110	194,000.0	1.690	62.41	1.795
111	90,600.0	15.500	335.91	2.526
112	69,300.0	0.150	2.69	0.431
113	89,000.0	0.510	10.92	1.038
114	42,000.0	1.030	13.03	1.115
115	4,940.0	111.000	313.93	2.497
116	20,000.0	10.000	75.27	1.877
117	14,200.0	3.530	20.91	1.320
118	89,300.0	10.000	214.54	2.332
119	85,100.0	12.600	261.35	2.417
120	14,300.0	4.600	27.38	1.437
121	167,000.0	0.750	24.94	1.397
122	13,600.0	1.900	10.92	1.038
123	250,000.0	0.360	15.88	1.201
124	75,900.0	1.680	32.17	1.507
125	24,000.0	5.710	48.83	1.689
126	60,900.0	1.300	21.33	1.329
127	65,700.0	0.270	4.67	0.670
128	100,000.0	2.880	66.88	1.825
129	12,300.0	0.600	3.21	0.507
130	8,210.0	0.850	3.43	0.535
131	59,400.0	1.460	23.55	1.372
132	28,000.0	6.690	63.73	1.804
133	43,500.0	0.810	10.50	1.021
134	42,500.0	0.800	10.21	1.009
135	55,300.0	2.840	43.56	1.639
136	11,300.0	1.530	7.72	0.888
137	544,000.0	3.810	289.57	2.462
138	453,000.0	0.345	23.07	1.363
139	21,700.0	7.460	59.45	1.774
140	90,600.0	0.209	4.53	0.656
141	110,000.0	0.182	4.52	0.655
142	40,800.0	10.300	127.70	2.106
143	74,800.0	110.000	2,084.64	3.319
144	171,000.0	1.790	60.51	1.782
145	3,200.0	3.100	6.47	0.811

Appendix Table 8. (Continued)

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	log <sub>10</sub> (J/10 <sup>6</sup> km <sup>2</sup> day)
146	47,500.0	3.500	48.27	1.684
147	2,220,000.0	0.740	150.52	2.178
148	952,000.0	0.840	94.46	1.975
149	1,120,000.0	0.093	11.72	1.069
150	259,000.0	3.740	169.08	2.228
151	390,000.0	2.570	154.73	2.190
152	270,000.0	1.500	69.82	1.844
153	1,255,000.0	6.270	855.51	2.932
154	997,000.0	0.120	13.94	1.144
155	300,000.0	0.630	31.57	1.499
156	175,000.0	0.800	27.49	1.439
157	1,810,000.0	0.490	86.39	1.936
158	2,860,000.0	1.090	264.72	2.423
159	2,430.0	25.600	44.06	1.644
160	1,360.0	141.000	161.66	2.209
161	2,420.0	13.000	22.31	1.349
162	3,030.0	9.970	20.03	1.302
163	2,710.0	101.000	187.63	2.273
164	3,020.0	18.600	37.28	1.571
165	3,400.0	5.840	12.72	1.104
166	154.0	558.000	139.25	2.144
167	1,640.0	131.000	171.23	2.234
168	854.0	35.400	29.30	1.467
169	692.0	544.000	388.67	2.590
170	1,130.0	588.000	592.16	2.772
171	1,020.0	68.800	64.49	1.810
172	22.0	3,450.000	220.51	2.343
173	146.0	1,590.000	382.25	2.582
174	42.0	3,300.000	331.66	2.521
175	8,200.0	25.000	100.81	2.004
176	29.1	3,626.000	281.88	2.450
177	127.0	32.000	6.98	0.844
178	20.0	1,240.000	74.14	1.870
179	36.0	949.000	85.62	1.933
180	33.0	2,550.000	216.47	2.335
181	70.0	12,400.000	1,781.96	3.251
182	103.0	862.000	162.33	2.210
183	143.0	30,900.000	7,321.51	3.865
184	71.0	257.000	37.30	1.572
185	7.0	1,550.000	44.44	1.648
186	22.5	400.000	25.97	1.414
187	257.0	21.000	7.50	0.875
188	170.0	6.500	1.74	0.240
189	210.0	111.000	34.42	1.537
190	40.0	400.000	38.85	1.589
191	40.0	1,350.000	131.12	2.118
192	40.0	286.000	27.78	1.444
193	487.0	2,040.000	1,139.74	3.057
194	1,020.0	278.000	260.60	2.416

**Appendix Table 8.** (Continued)

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	log <sub>10</sub> (J/10 <sup>6</sup> km <sup>2</sup> day)
195	222.0	1,250.000	402.96	2.605
196	27.0	1,160.000	85.57	1.932
197	23.0	1,890.000	124.62	2.096
198	31.0	556.000	45.18	1.655
199	28.0	4,600.000	348.08	2.542
200	4,000.0	40.300	98.32	1.993
201	30.5	250.000	20.08	1.303
202	68.7	741.000	105.10	2.022
203	241.0	247.000	84.34	1.926
204	400.0	4,200.000	2,044.55	3.311
205	1,130.0	2,470.000	2,487.48	3.396
206	88.0	1,940.000	327.23	2.515
207	2,700.0	90.000	166.76	2.222
208	2,000.0	100.000	150.19	2.177
209	5.0	985.000	22.32	1.349
210	13.5	1,980.000	89.91	1.954
211	8.2	1,170.000	37.48	1.574
212	55.0	1,429.000	173.46	2.239
213	56.0	585.000	71.91	1.857
214	60.0	504.000	65.02	1.813
215	108.0	469.000	91.30	1.960
216	145.0	1,450.000	346.92	2.540
217	72.0	950.000	139.24	2.144
218	38.5	1,209.000	114.33	2.058
219	65.0	1,310.000	178.74	2.252
220	53.0	449.000	53.11	1.725
221	145.0	205.000	49.05	1.691
222	475.0	7.000	3.84	0.585
223	400.0	40.000	19.47	1.289
224	35.0	1,610.000	142.42	2.154
225	8,620.0	3.900	16.29	1.212
226	39.0	1,700.000	162.22	2.210
227	97.0	531.000	95.88	1.982
228	26.0	1,950.000	140.10	2.146
229	69.0	293.000	41.68	1.620
230	69.0	1,090.000	155.07	2.191
231	65.0	695.000	94.83	1.977
232	63.0	91.000	12.15	1.084
233	32,800.0	104.000	1,106.76	3.044
234	44.5	325.000	34.01	1.532
235	30.0	666.000	52.89	1.723
236	81.0	2,900.000	461.58	2.664
237	54.0	387.000	46.38	1.666
238	65.0	777.000	106.01	2.025
239	44.0	1,380.000	143.29	2.156
240	39.0	620.000	59.16	1.772
241	400.0	175.000	85.19	1.930
242	64.0	256.000	34.55	1.538
243	3,400.0	296.000	644.52	2.809



Appendix Table 8. (Continued)

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	log <sub>10</sub> (J/10 <sup>6</sup> km <sup>2</sup> day)
244	3,950.0	616.000	1,489.72	3.173
245	65.0	667.000	91.01	1.959
246	116.0	150.000	30.70	1.487
247	250.0	2,390.000	837.26	2.923
248	36.0	2,200.000	198.49	2.298
249	27.0	3,770.000	278.10	2.444
250	71.0	19,900.000	2,888.29	3.461
251	47.0	7,500.000	815.52	2.911
252	35.0	3,000.000	265.38	2.424
253	43.0	6,750.000	689.67	2.839
254	35.0	12,000.000	1,061.54	3.026
255	49.0	4,500.000	503.80	2.702
256	49.0	4,040.000	452.30	2.655
257	8.6	380.000	12.58	1.100
258	6.4	868.000	23.38	1.369
259	8.5	699.000	22.96	1.361
260	11.8	919.000	37.98	1.580
261	108.0	189.000	36.79	1.566
262	34.0	3,170.000	274.79	2.439
263	17.8	31.000	1.71	0.233
264	254.0	9,880.000	3,499.83	3.544
265	250.0	140.000	49.04	1.691
266	248.0	93.000	32.40	1.511
267	130.0	1,610.000	356.86	2.552
268	260.0	1,600.000	576.11	2.761
269	21.0	351.000	21.72	1.337
270	218.0	14,000.000	4,456.10	3.649
271	86.0	4,220.000	700.44	2.845
272	65.0	2,300.000	313.82	2.497
273	49.0	50.200	5.62	0.750
274	42.0	532.000	53.47	1.728
275	35.0	129.000	11.41	1.057
276	40.0	1,050.000	101.99	2.009
277	30.0	620.000	49.24	1.692
278	76.5	58.800	8.99	0.954
279	24.1	2,455.000	167.25	2.223
280	40.0	200.000	19.43	1.288
281	59.0	1,900.000	242.25	2.384
282	40.0	1,700.000	165.12	2.218
283	50.0	100.000	11.35	1.055
284	136.0	2,970.000	679.42	2.832
285	121.0	2,700.000	569.14	2.755
286	112.0	1,110.000	221.66	2.346
287	7.4	294.000	8.76	0.943
288	17.0	480.000	25.61	1.408
289	7.5	214.000	6.44	0.809
290	20.0	2,970.000	177.58	2.249
291	15.0	701.000	34.27	1.535
292	28.0	585.000	44.27	1.646

**Appendix Table 8.** (Continued)

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	log <sub>10</sub> (J/10 <sup>6</sup> km <sup>2</sup> day)
293	42.0	4,790.000	481.41	2.683
294	23.0	293.000	19.32	1.286
295	35.0	4,650.000	411.35	2.614
296	21.0	1,890.000	116.93	2.068
297	20.0	1,060.000	63.38	1.802
298	15.0	1,040.000	50.84	1.706
299	24.0	4,450.000	302.28	2.480
300	52.0	4,090.000	477.35	2.679
301	39.0	434.000	41.41	1.617
302	44.0	263.000	27.31	1.436
303	53.0	876.000	103.61	2.015
304	50.0	777.000	88.23	1.946
305	38.0	1,900.000	178.04	2.251
306	316.0	1,060.000	437.52	2.641
307	800.0	583.000	461.04	2.664
308	70.0	79.000	11.35	1.055
309	72.0	27.000	3.96	0.597
310	62.0	4,480.000	591.37	2.772
311	125.0	1,770.000	381.70	2.582
312	321.0	38.000	15.86	1.200
313	122.0	3,650.000	773.84	2.889
314	112.0	227.000	45.33	1.656
315	251.0	3,350.000	1,176.86	3.071
316	54.0	50.000	5.99	0.778
317	85.0	69.000	11.36	1.055
318	21.0	598.000	37.00	1.568
319	16.0	1,530.000	78.25	1.893
320	44.0	224.000	23.26	1.367
321	115.0	144.000	29.29	1.467
322	45.0	870.000	91.76	1.963
323	530.0	701.000	415.54	2.619
324	275.0	45.000	16.85	1.227
325	680.0	431.000	304.19	2.483
326	275.0	300.000	112.35	2.051
327	120.0	1,460.000	305.98	2.486
328	129.0	2,220.000	489.41	2.690
329	50.0	50.000	5.68	0.754
330	350.0	5,130.000	2,274.43	3.357
331	500.0	500.000	284.55	2.454
332	351.0	3,280.000	1,457.12	3.163
333	107.0	105.000	20.31	1.308
334	200.0	318.000	95.29	1.979
335	800.0	330.000	260.97	2.417
336	71.0	94.000	13.64	1.135
337	100.0	23.000	4.24	0.628
338	27.0	1,850.000	136.47	2.135
339	200.0	3,822.000	1,145.30	3.059
340	97.0	2,060.000	371.98	2.571
341	207.0	148.000	45.43	1.657

**Appendix Table 8.** (Continued)

Species number	Mass (g)	Density (n/km <sup>2</sup> )	Energy consumed	
			(J/10 <sup>6</sup> km <sup>2</sup> day)	log <sub>10</sub> (J/10 <sup>6</sup> km <sup>2</sup> day)
342	101.0	725.000	134.67	2.129
343	51.0	528.000	60.79	1.784
344	62.0	550.000	72.60	1.861
345	42.0	343.000	34.47	1.537
346	154.0	2,200.000	549.03	2.740
347	93.0	2,480.000	434.81	2.638
348	34.0	214.000	18.55	1.268
349	18.0	6,430.000	357.12	2.553
350	29.0	330.000	25.59	1.408
351	56.0	279.000	34.30	1.535
352	118,000.0	0.121	3.16	0.499
353	2,700.0	407.000	754.15	2.877
354	3,500.0	190.000	422.19	2.626
355	300.0	150.000	59.70	1.776
356	25,000.0	20.800	183.03	2.263
357	12,000.0	47.000	247.42	2.393
358	31,900.0	15.000	156.55	2.195
359	41,400.0	0.700	8.77	0.943
360	11,000.0	100.000	495.32	2.695
361	1,360.0	19.600	22.47	1.352
362	872.0	125.000	105.00	2.021
363	1,250.0	83.000	89.71	1.953
364	3,000.0	511.000	1,019.33	3.008
365	2,800.0	150.000	285.11	2.455
366	2,080.0	75.000	115.77	2.064
367	22,500.0	11.000	89.91	1.954
368	10,000.0	20.000	92.67	1.967

**Appendix Table 9.** List of 20 species of marine mammals in the eastern Bering Sea ecosystem with estimates of their total annual food consumption ( $10^3$  metric tons(t)) and in  $\log_{10}$  ( $10^3$  t) from Perez and McAlister (1993).

Species	Body mass (kg)	Population size	Daily energy requirements ( $10^3$ kcal)	Diet energy value (kcal/g)	Consumption ( $10^3$ t)	$\log_{10}(10^3\text{t})$
<i>Balaena mysticetus</i>	46,000	148	603.1	1.80	18.1	1.257
<i>Balaenoptera acutorostrata</i>	6,000	1,900	130.9	1.72	52.6	1.721
<i>Balaenoptera physalus</i>	49,000	500	632.3	2.00	57.5	1.760
<i>Berardius bairdii</i>	8,000	209	268.1	1.20	17.0	1.230
<i>Callorhinus ursinus</i>	43	219,750	7.1	1.31	432.4	2.636
<i>Delphinapterus leucas</i>	800	10,750	47.7	1.30	143.5	2.157
<i>Enhydra lutris</i>	20	79,000	4.9	0.90	157.1	2.196
<i>Erignathus barbatus</i>	241	77,500	12.2	1.30	265.1	2.423
<i>Eschrichtius robustus</i>	18,000	2,500	298.4	1.00	271.5	2.434
<i>Eumetopias jubatus</i>	212	32,000	20.7	1.30	185.2	2.268
<i>Megaptera novaeangliae</i>	30,000	63	437.7	1.80	5.5	0.744
<i>Mesoplodon stejnegeri</i>	2,000	200	94.8	1.20	5.8	0.760
<i>Orcinus orca</i>	4,000	500	159.4	1.80	16.1	1.207
<i>Phoca fasciata</i>	46	66,000	3.5	1.20	70.7	1.850
<i>Phoca hispida</i>	34	300,500	2.8	1.20	256.7	2.409
<i>Phoca largha</i>	62	77,000	4.4	1.39	89.1	1.950
<i>Phoca vitulina</i>	49	45,000	3.7	1.40	43.3	1.637
<i>Phocoena phocoena</i>	50	750	6.0	1.63	1.0	-0.001
<i>Phocoenoides dalli</i>	95	64,100	9.6	1.33	169.0	2.228
<i>Physeter macrocephalus</i>	36,000	3,791	828.5	1.20	952.8	2.979

**Appendix Table 10.** List of 20 species of marine mammals in the eastern Bering Sea ecosystem with estimates of their total annual food and fish consumption ( $10^3$  t), and in  $\log_{10}(10^3$  t) transformed values of fish consumption from Perez and McAlister (1993).

Species	Food consumption ( $10^3$ t)	Percent fish diet	Fish consumption	
			( $10^3$ t)	$\log_{10}(10^3$ t)
<i>Balaena mysticetus</i>	18.1	<0.01	0.04	-1.444
<i>Balaenoptera acutorostrata</i>	52.6	60.00	31.6	1.499
<i>Balaenoptera physalus</i>	57.5	16.00	9.2	0.964
<i>Berardius bairdii</i>	17.0	10.00	1.7	0.230
<i>Callorhinus ursinus</i>	432.4	67.00	289.7	2.462
<i>Delphinapterus leucas</i>	143.5	93.00	133.5	2.125
<i>Enhydra lutris</i>	157.1	18.00	28.3	1.452
<i>Erignathus barbatus</i>	265.1	23.00	61.0	1.785
<i>Eschrichtius robustus</i>	271.5	<0.01	0.5	-0.268
<i>Eumetopias jubatus</i>	185.2	76.00	140.7	2.148
<i>Megaptera novaeangliae</i>	5.5	29.00	1.6	0.206
<i>Mesoplodon stejnegeri</i>	5.8	10.00	0.6	-0.240
<i>Orcinus orca</i>	16.1	65.00	10.5	1.020
<i>Phoca fasciata</i>	70.7	54.00	38.2	1.582
<i>Phoca hispida</i>	256.7	85.00	218.2	2.339
<i>Phoca largha</i>	89.1	96.00	85.5	1.932
<i>Phoca vitulina</i>	43.3	75.00	32.5	1.512
<i>Phocoena phocoena</i>	1.0	85.00	0.8	-0.072
<i>Phocoenoides dalli</i>	169.0	50.00	84.5	1.927
<i>Physeter macrocephalus</i>	952.8	18.00	171.5	2.234

**Appendix Table 11.** List of 20 species of predators that feed on walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea showing the percent of the estimated standing stock biomass of pollock that is consumed by each predator species annually, along with the  $\log_{10}$  transformation (from Livingston 1993, and Livingston, personal comm., Alaska Fisheries Science Center, Seattle, WA).

Species	Percent of pollock biomass consumed	$\log_{10}$ (percent biomass)
<i>Callorhinus ursinus</i>	1.460	0.164
<i>Eumetopias jubatus</i>	0.594	-0.226
<i>Phoca vitulina</i>	0.187	-0.729
<i>Phoca larga</i>	0.117	-0.931
<i>Phoca hispida</i>	0.299	-0.525
<i>Erignathus barbatus</i>	0.036	-1.439
<i>Uria aalge</i>	0.912	-0.040
<i>Uria lomvia</i>	1.294	0.112
<i>Fulmarus glacialis</i>	0.276	-0.559
<i>Oceanodroma furcata</i>	0.021	-1.673
<i>Larus tridactyla</i>	0.127	-0.895
<i>Fratercula corniculata</i>	0.021	-1.673
<i>Lunda cirrhata</i>	0.233	-0.632
<i>Gadus macrocephalus</i>	2.143	0.331
<i>Atheresthes stomias</i>	0.140	-0.853
<i>Hippoglossoides elassodon</i>	0.019	-1.710
<i>Pleuronectes bilineatus</i>	0.000	-4.732
<i>Pleuronectes asper</i>	0.011	-1.972
<i>Reinhardtius hippoglossoides</i>	0.010	-2.002
<i>Hippoglossus stenolepis</i>	0.006	-2.192

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