Appendix 2.1

The following material is Appendix 2.1 for Chapter 2 of: Fowler, C.W. 2009. Systemic Management: Sustainable Human Interactions with Ecosystems and the Biosphere. Oxford University Press

1 Variety in patterns among species

1.1 Single species-level characteristics

There are many examples of published patterns among species; some are patterns not included in Figures 2.1–2.36 of Chapter 2, and some are further examples of these patterns. This appendix presents brief descriptions and graphic presentations of a selection of patterns. The objective of this appendix is not to be exhaustive. Its goal is much more than that of emphasizing the potential for further research on patterns with the view that, even in looking for undiscovered patterns, being exhaustive is not a realistic possibility. Such research is important, however, and will lead to better understanding of the complexity in ways we can measure species and approach management. For those cases where new measurements are found, the progress would accomplish two things of practical importance: (1) lead to new management questions regarding the sustainable fit of our species within ecosystems and the biosphere, and (2) add to correlative information that can be used to refine these management questions as introduced in Chapter 2.

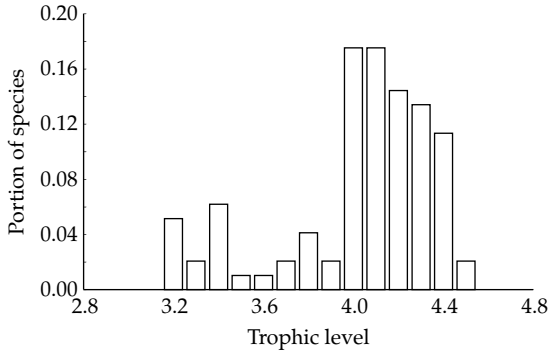
1.1.1 Trophic level

Specific taxonomic groups are often confined to subsets of the overall range of trophic levels observed among species. Appendix Figure 2.1.1 demonstrates this for the trophic levels of 97 species of marine mammals (from Pauley *et al.* 1998). Here we see a bimodal distribution in which the lower mode represents the large baleen whales (11 species) that are filter feeders. Marine mammal species at the higher trophic levels are fish or mammal predators. It is not rare to observe more than one mode in species-level patterns exemplified by this case.

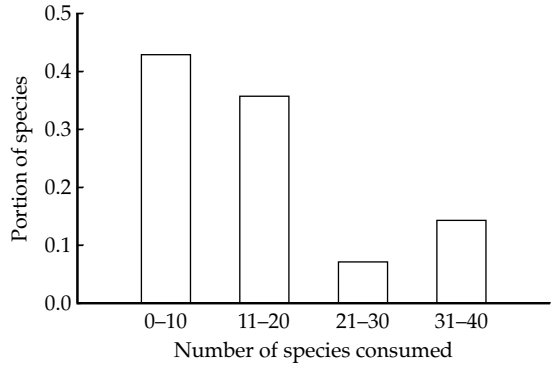
1.1.2 Symbiotic interactions

It is uncommon to see species that are completely interdependent (obligate dependence), wherein the extinction of either species results in the extinction of the other. The great majority of completely dependent symbiotic interactions that have been described involve no more than two species. One factor involved in producing this situation is the fact that the extinction rate (a risk) of any dependent species is always higher than that of the species upon which it depends. When the dependence is mutual, and the risk equivalent, it is always higher than would be the case without the dependence. With more than two species the risk is even more extreme.

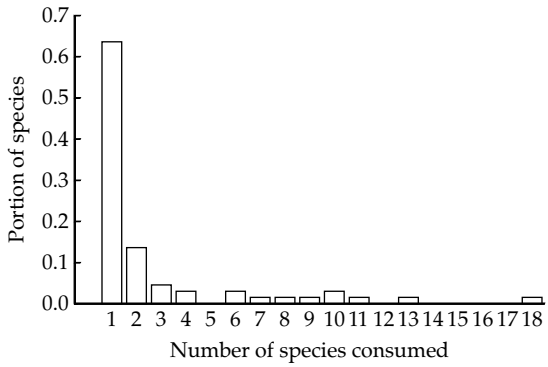
Obviously, interdependence could conceivably entail three or even more species if it were simply a random phenomenon. The structure of the webs of such interdependence would have a variety of potential forms, the simplest being linear. Rings or cycles of dependence (e.g., species A depends on species B, B depends on C, and C depends on A) are known to occur (e.g., Reagan and Waide 1996). However, obligate interdependence (A depends on B, etc. so that the extinction of one guarantees that of all others) in rings is not common and may not exist in natural systems. Even rings that are not obligate are not common (Berendse 1993, Cohen *et al.* 1990, Hall and Raffaelli 1993, Lawton 1989b, May 1973, Pimm 1982), but they do exist (see Reagan and Waide 1996, Thompson 1982 and references therein).



Appendix Figure 2.1.1 The distribution of species across trophic level for 97 species of marine mammals, from Pauley *et al.* (1998).



Appendix Figure 2.1.3 Frequency distribution of 14 species of grasshoppers in Colorado according to the number of species of plants they consume (from Thompson 1982 and Ueckert and Hansen 1971).



Appendix Figure 2.1.2 Frequency distribution of species according to the number of prey they consume based on species from 95 insect-dominated food webs (from Schoenly *et al.*, 1991).

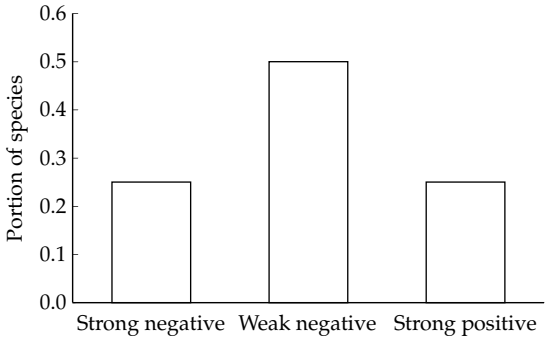
1.1.3 Specialization—number of prey species

Science includes observations that have led to the conclusion that most species tend to be consumers of only a small portion of the resource species available to them. Complete specialization may be common in some samples of species, but not all, and consumption of all available species is never observed. This tendency is demonstrated in the pattern in Appendix Figure 2.1.2 (Schoenly *et al.* 1991). In this sample of insect-dominated food webs, there are few extreme generalists compared to the numbers of more specialized species.

Care must be exercised in conclusions regarding general species-level patterns based on local samples. Over the entire geographic range of most species, more prey species are available, and consumed, than in more confined regions (see, Fox and Morrow 1981). In other words, with increasing area the diversity of diet (number of species consumed for the area in which dietary diversity is being measured) also increases.

In spite of what might be the results of some forms of natural selection, complete specialization may not be the most prevalent form of interaction (Bleiweiss 1990, Futuyma 1983, Orians and Kunin 1990). For example, of seven species of grasshoppers (Thompson 1982, from Ueckert and Hansen 1971) none feed on only one species of plant and five of the seven feed on more than ten species. The complete set of data shows a decline in consumer species numbers with greater diversity in diet (Appendix Fig. 2.1.3), consistent with the tendency shown in Appendix Figure 2.1.2.

Both natural selection at the individual level and risk of extinction are likely involved as explanatory factors in the complexity behind these patterns and, therefore, reflected by the patterns. There is less chance of extinction when risk is spread over a number of resource species than is the case for specialization in spite of the fact that specialization can result from natural selection among individuals. This may be a case, as will be seen in Chapter 3, of natural selection among individuals and natural selection among species acting in opposition.



Appendix Figure 2.1.4 The proportion of eight populations of seven species of marine intertidal invertebrate species categorized according to the strength of their effects on the population-level recruitment of algal species they consume (from Paine 1992).

The balance is part of what contributes to the emergence of pattern. However, we must remain mindful of the fact that the origin of patterns involves many factors in addition to two forms of natural selection working against each other.

1.1.4 Interaction strength

Appendix Figure 2.1.4 shows the results of early work on interaction strength. In this work the majority of intertidal marine consumers had either very little or only intermediate influence on resource species. Some had small positive effects (see also Lawton 1992).

It is highly likely that the pattern of interaction strength shown in Appendix Figure 2.1.4 is a general pattern in being characterized by an intermediate maximum surrounded by fewer species toward the extremes—representing natural variability (Power *et al.*, 1996) within bounds. Single-tailed patterns could occur for interactions that are confined to measures of either positive or negative effects.

1.1.5 Predation/consumption rates

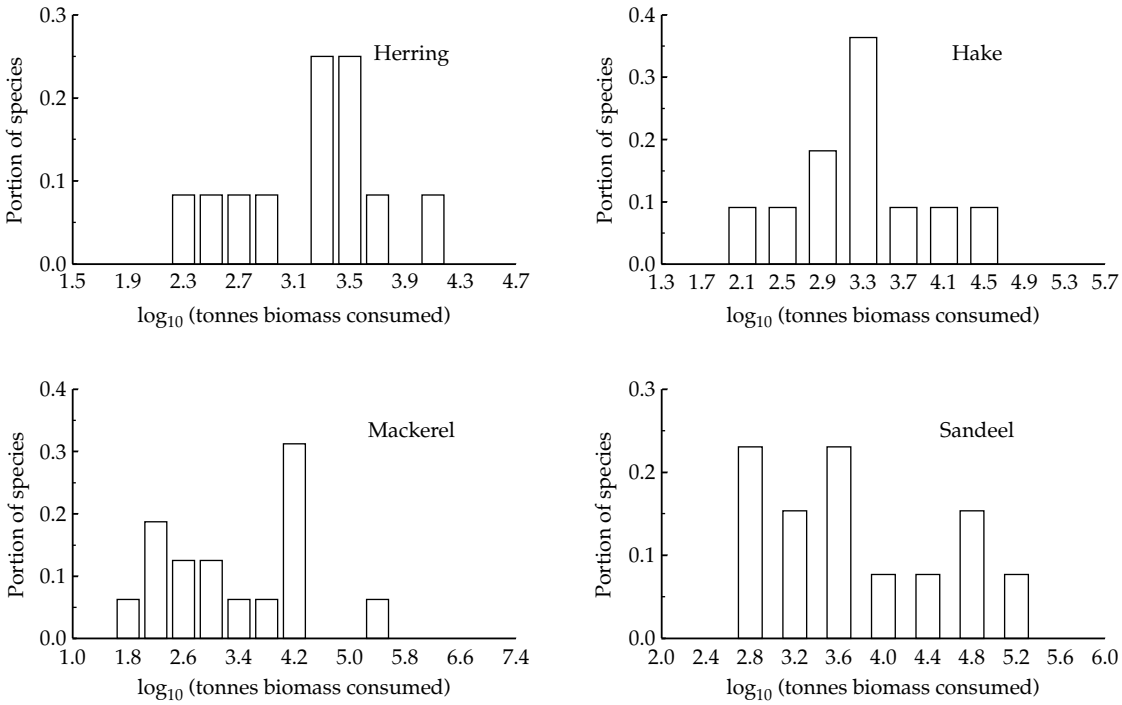
Appendix Figure 2.1.5 illustrates patterns in consumption rates among nonhuman vertebrate predatory species in the northwestern Atlantic Ocean in their take of four prey species. Data in this graph are presented in terms of total biomass consumed rather than portion of the standing stock (as was used in Fig. 2.6). As with previous examples in Chapter 2, these do not include the microconsumers such as disease organisms and parasites and do not reflect the pattern representative of the entire geographic range for these species. They pertain to a specified ecosystem at a specific time (and under specific conditions) as with the data for walleye pollock in Figure 2.6.

Another ecosystem for which there are data regarding consumption rates is the Benguela ecosystem off the southwest coast of Africa. Appendix Figure 2.1.6 shows the consumption rates by avian predators on a single resource species (anchovy), from a group of resource species (lantern fish, *Lampanyctodes hectoris*; lightfish, *Maurolicus muelleri*; anchovy, and hake, *Merluccius* sp.), and from the entire ecosystem (from Crawford *et al.* 1991).

1.1.6 Population variability

Rothschild (1986) examined a pattern in population variation for at least 12 species of fish. Rothschild's data demonstrate, as do those of Appendix Figure 2.1.7, that the bulk of species sampled occur at the low end of the range of population variability. The ecosystems in which the species of Rothschild's study occur are subject to several identifiable abnormal human impacts. Fishing is known to contribute to variation in fish populations (Anderson *et al.* 2008). Observed patterns, therefore, are subject to both these and the indirect effects of all human influence whether abnormal or normal. Thus, human influence is behind the levels of observed variability as in the case of many agricultural systems and disturbed systems in general (Apollonio 1994). Also involved is the nonrandom nature of the sample of fish species in Rothchild's work. Commercial fisheries concentrate on productive fish species with life histories associated with high variability. In spite of these caveats, Rothschild's (1986) work shows that there are few species that show high population variation compared to the numbers of species that exhibit intermediate population variation—the pattern we would expect.

Also consistent with what we would expect, there is rarity among species showing extremely low population variation. This is shown in Appendix Figure 2.1.7B. This particular pattern is based on measurements of the ratio of largest to smallest observed population levels (N_{max}/N_{min})

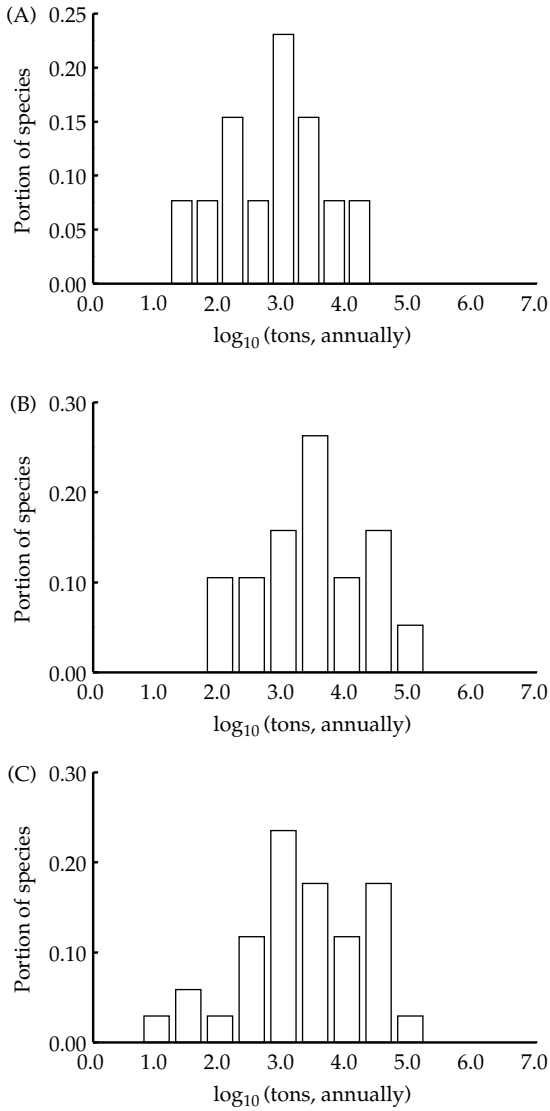


Appendix Figure 2.1.5 Frequency distributions among nonhuman vertebrate species that consume hake (*Merluccius bilinearis*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and sand eel (*Ammodytes americanus*) in the northwestern part of the Atlantic Ocean according to the biomass they consume ($\log_{10}$ metric tons per year, Overholtz *et al.* 1991).

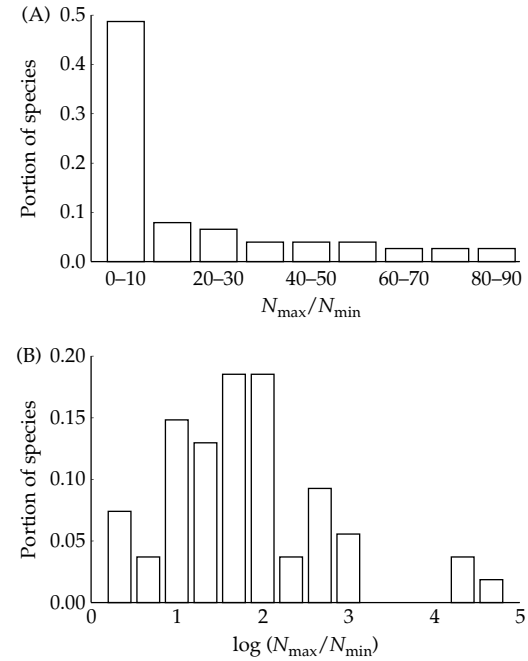
for a variety of species, from Hassell *et al.* (1976). The fact that some insect species may have originally been specifically chosen for study is a potential source of bias, as would be varying length of time periods over which observations were made. Species we humans consider to be pests are more likely to experience outbreaks in agricultural monocultures and may account for much of the long right-hand tail of the distribution. Seventeen percent (13) of the species are not included in the top panel (A) of this graph because they exhibited variability beyond the range shown and obscure the nature of the remaining part of the distribution when included. Eleven of these excluded species are insects.

A population above or below its carrying capacity can behave in a variety of ways. It may return to typical levels through a smooth monotonic trajectory, or it may change so rapidly as to result in "overshoot" and experience diminishing cyclic fluctuation (damped oscillations) in approaching stability. Alternatively, the population might undergo continued oscillations (stable limit cycles), or, in the extreme of variation, exhibit chaotic fluctuations. Hassell *et al.* (1976) examined data for a number of populations and categorized species according to their dynamic behavior (Appendix Fig. 2.1.8). The pattern is consistent with that shown by other data. Species with monotonic damping are the least variable and most numerous. At the other extreme, stable limit cycles and chaotic behavior represent more variability and the fewest species fall into these categories.

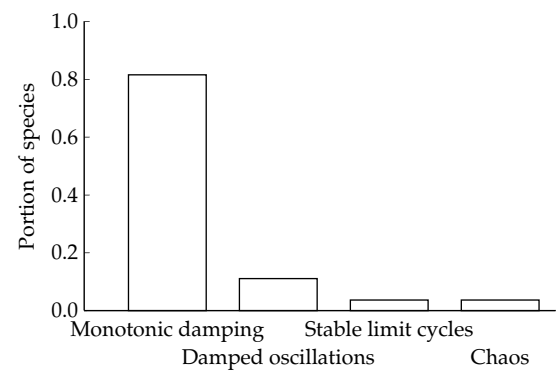
Another measure of population variation is displayed in Appendix Figure 2.1.9 based on measures of the standard deviation of observed rate of change for various mammal populations (thus different from, but related to, the extent of population change). This distribution shows another example of bimodal character.



Appendix Figure 2.1.6 Patterns in the consumption rates among avian predators in the Benguela ecosystem: (A) the consumption rates on anchovy (*Engraulis capensis*), (B) the consumption rates on four species of fish, and (C) the consumption rates from the entire ecosystem (compare to Fig. 1.7; from Crawford *et al.* 1991, Fowler and Perez 1999).



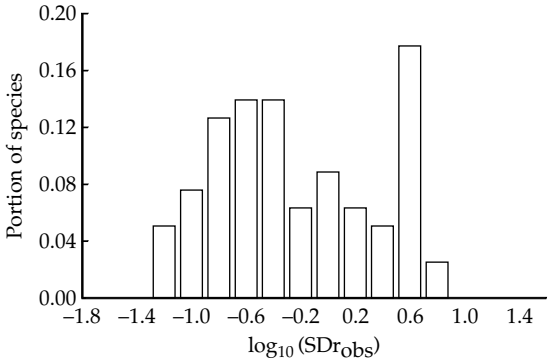
Appendix Figure 2.1.7 The frequency distribution of species of terrestrial insects, aquatic and marine invertebrates, birds, fishes, and small (nonmarine) mammals distributed over an index of variability calculated as the largest population level (N_{max}) divided by the smallest population level (N_{min}) observed over time (Hassell *et al.* 1976). Thirteen species of insects (17% of the total) showed N_{max}/N_{min} values beyond 90 and are not included in panel A (raw numbers) but are shown in panel B wherein the measure of fluctuation in population numbers is expressed as the $\log_{10}$ transformations of N_{max}/N_{min} from panel A.



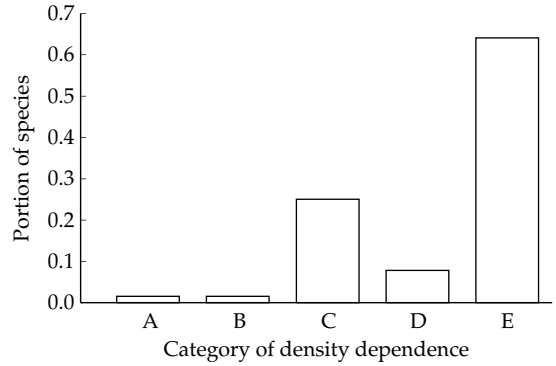
Appendix Figure 2.1.8 The frequency distribution of 24 insect species by population variability. Categories of increasing variability in population change are monotonic damping, damped oscillations, stable limit cycles, or chaotic fluctuations (from Hassell *et al.* 1976).

1.1.7 Density dependence

Other measures of density dependence might result in distributions different from that shown in Figure 2.21. However, they would not remove the characteristic intermediate mode if they cover



Appendix Figure 2.1.9 Population variation observed for 55 species of mammals worldwide, expressed as the $\log_{10}$ transformation of the standard deviation of the observed instantaneous rate of change (r_{obs}, based on data from Sinclair (1996).



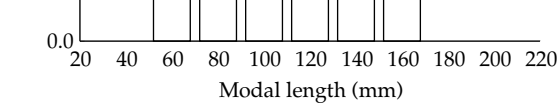
Appendix Figure 2.1.10 The frequency distribution for a collection of 64 species of invertebrates, fish, birds, and mammals by level of density dependence from Tanner (1966, see also Pimm 1982). Density dependence is measured by the slope of the correlation between $(X_{t+1} - X_t)/X_t$ and X_t according to five categories: A—positive and statistically significant; B—positive but not significant; C—negative but not significant; D—negative and significant at the 0.10 significance level; E—negative and significant at the 0.05 significance level.

the full spectrum of density dependence. A mode at one extreme is the only option for the pattern shown in Appendix Figure 2.1.10 because information on the magnitude (rather than statistical significance) of negative slope in the relationship between population density and rate of change is missing for the species as displayed in this sample. This pattern is based on data from a combined variety of metazoan taxa (Pimm 1982, Tanner 1966). This figure does demonstrate a lack of species with little density dependence. Very uncommon are species with positive slopes—the antithesis of density-dependent population regulation. Most species show intermediate levels of density dependence in which recovery from reduced population levels actually happens but without leading to extreme population fluctuation (Appendix Fig. 2.1.8).

1.1.8 Other factors

1.1.8.1 Age/size composition of consumed resources

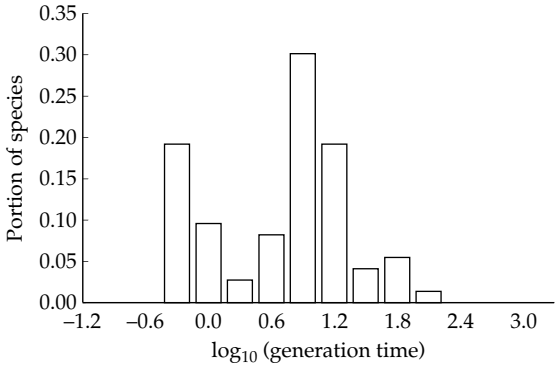
Allocation over different phenotypic categories among the individuals of a resource species is also a matter for management. Patterns with units defined by relevant management questions are exemplified by Appendix Figure 2.1.11 which shows how 12 species of sea birds allocate their consumption of sand eel near the Shetland Isles, across the various size classes of this resource species.



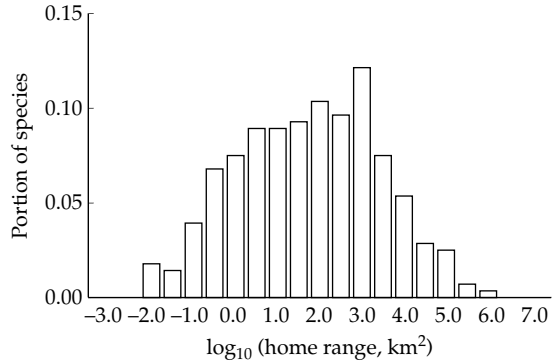
Appendix Figure 2.1.11 The frequency distribution of modal size (mm) for sand eel (*Ammodytes marinus*) consumed by 12 species of sea birds that forage near Shetland Island (Furness 1990).

1.1.8.2 Generation time

Sinclair (1996) presented estimated generation times (in years) for 73 species of mammals; these are displayed in Appendix Figure 2.1.12. As with intrinsic rate of increase (Fig. 2.22), generation time shows a bimodal pattern when expressed in $\log_{10}$ values, keeping in mind that these are for a group of species in a specific taxonomic category. A similar



Appendix Figure 2.1.12 A species frequency distribution showing the generation times (years) for 73 species of mammals in $\log_{10}$ scale (from Sinclair 1996).



Appendix Figure 2.1.13 The frequency distribution for home range size ($\log_{10}$ km^2) for 280 species of terrestrial mammals (from Kelt and Van Vuren, with data provided by D. A. Kelt).

pattern could, at least in theory, be determined for the full set of species from an ecosystem. The characteristics of such a pattern would represent attributes of the ecosystem, just as would the characteristics of other patterns presented in Chapter 2 if they represented all (or a large random sample) of the species of any particular ecosystem. As shown by Makarieva and Gorskov (2004), the generation times of larger systems span four orders of magnitude or more.

1.1.8.3 Home range size

Distinct from the geographic range of an entire species is the home range or the area used by individuals in their foraging and reproductive activities. The frequency distribution for the home ranges of a sample of mammalian species is shown in Appendix Figure 2.1.13. The mammalian species within any ecosystem would have their own distinctive pattern as would the full collection of animal species for any such system.

1.1.8.4 Biomass partitioning/body structure

Species frequency distributions regarding the allocation of biomass within individuals are another example of species-level patterns often seen as ecosystem structure. Examples are found in the distribution of above-ground compared to below-ground components of plants (Enquist and Niklas 2002). Clear patterns of biomass allocation are seen in the correlations between biomass of plants found in their leaves, stems, and roots when compared across a wide variety of species. Similar patterns are found in animals as exemplified by the correlations among various body parts and body size (e.g., Peters 1983). All such patterns are of relevance to the nutrient and energy dynamics of ecosystems and the patterns in such dynamics as ecosystem-level attributes.

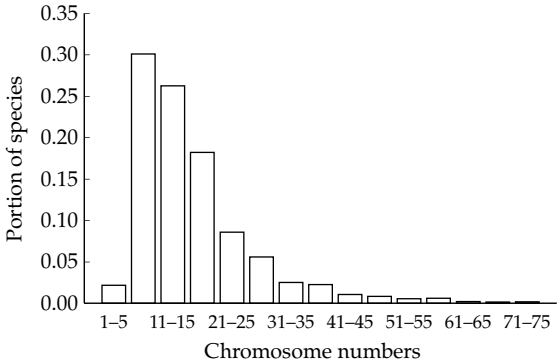
1.1.8.5 Chromosome count

Another example of a single-feature pattern among species involves the quantity of DNA material. Polyploidy and chromosome counts (Appendix Fig. 2.1.14, shown as chromosome number) vary among species and may relate to evolutionary plasticity. As treated and reviewed by Masterson (1994), Osmond *et al.* (1980), and Rosenzweig (1974, 1995), many plant species show evidence of more than one set of chromosomes and their frequency distributions in this regard are similar to that of Appendix Figure 2.1.14. This, again, is a taxonomically restricted sample and patterns will undoubtedly differ among taxa. In particular, animals show much less polyploidy than do plants (Rosenzweig 1995).

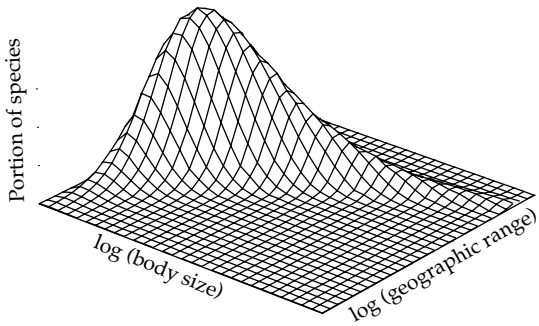
1.2 Two species-level characteristics

1.2.1 Body size and geographic range

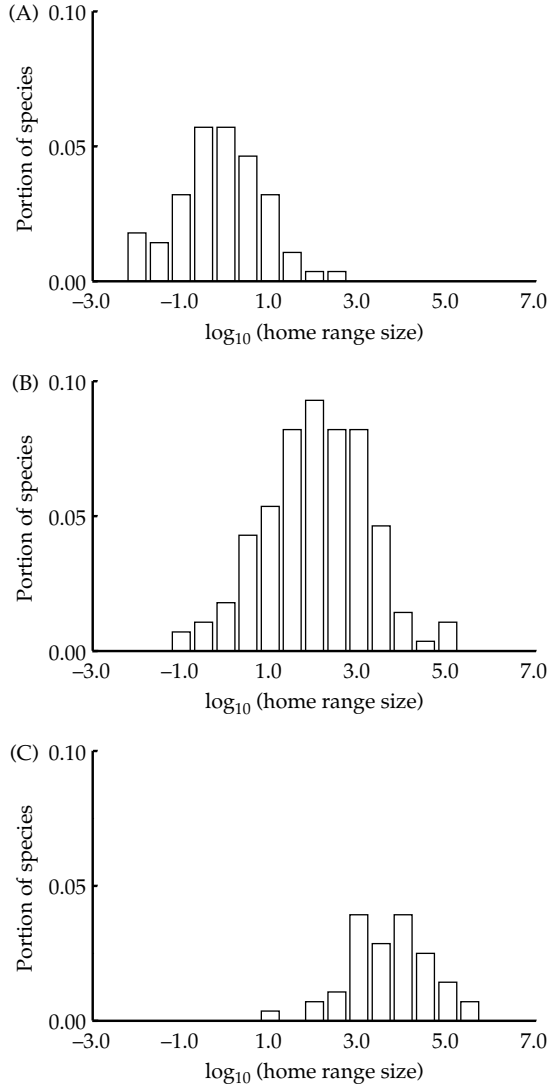
Based on the patterns of Figures 2.27 and 2.28, a fitted continuous surface representing species



Appendix Figure 2.1.14 The pattern in haploid chromosome numbers among 19,680 species of angiosperm plants (based on guard cell size in fossil plants and expressed as a portion of the total of 19,838 species including those with over 75 chromosomes) from Masterson (1994, and personal comm., 1996).



Appendix Figure 2.1.15 The general shape of the pattern expected for geographic range as related to body size (both in log scale) for a hypothetical and large samples of species, based on patterns consistent with those shown in Figures 2.27 and 2.28.



Appendix Figure 2.1.16 Three component patterns from that shown in Figure 2.1.29. These frequency distributions display the species in body size categories corresponding to ranges of $\log_{10}$ mass (g) from 0 to 2.5 (A), from 2.5 to 4.5 (B) and from 4.5 to 7 (C).

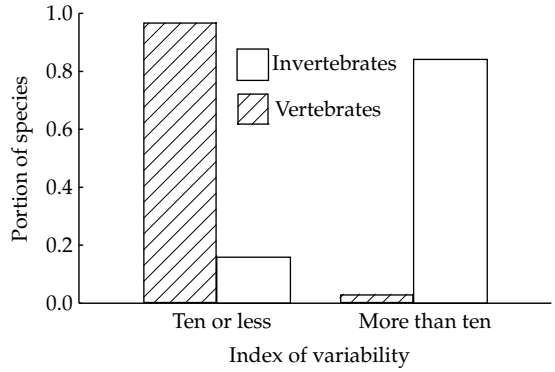
numbers over body size and geographic range might appear as shown in Appendix Figure 2.1.15 for the complete set of species within an ecosystem. The shape, but not necessarily the position, of such distributions may be expected to remain consistent from habitat to habitat (e.g., marine to terrestrial).

1.2.2 Body size and home range size

An alternative means of viewing the bivariate relationship of Figure 2.29 is shown in Appendix Figure 2.1.16. Any of the body size-specific patterns would be relevant to management questions framed to deal with body size directly. This would include home range. Management questions dealing with home range as the focal issue, of course, must make use of data such at those in Appendix Figure 2.1.16 and can, therefore, simultaneously account directly for body size.

1.2.3 Body size and population variability

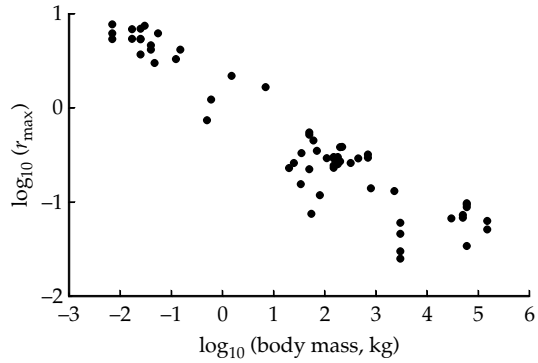
Appendix Figure 2.1.17 shows a pattern among species illustrating the correlative relationships between body size and population variation. A larger portion of the invertebrates (small bodied species) show high population variability in comparison to vertebrates (larger species). This is consistent with Figure 2.30 and the difference between Figures 2.19A and 2.19B.



Appendix Figure 2.1.17 The frequency distribution of vertebrates (large species) and invertebrates (small species) according to population variability, from Hassell *et al.* (1976).

1.2.4 Body size and intrinsic rate of increase

One of the patterns commonly cited in studies of relationships between body size and other species-level characteristics involves the maximum rate of increase (r_{max}, e.g., Blueweiss *et al.* 1978, Peters 1983). An example of this relationship is shown in Appendix Figure 2.1.18 based on data for 61 populations of 43 species of mammals from Sinclair (1996). The bimodality of Figures 2.22, and Appendix Figure 2.1.12 are now explained on the basis of what appears to be a real break, or gap, in the species representing this relationship (at about 1 kg; see Holling 1992 for consideration of "lumps" and gaps within taxonomic groups, and Caughley 1987 in regard to ecological type). Do such gaps occur more among taxonomic groups than among sets of species representing an entire ecosysem? Is there an explanation for such gaps; are they related to human influence?

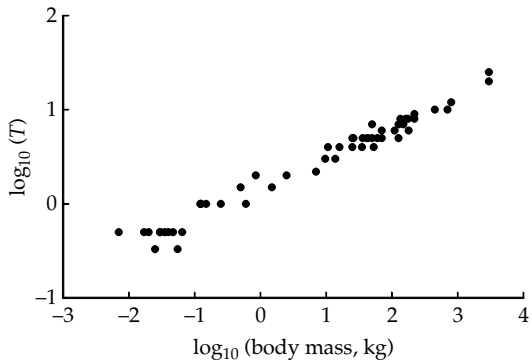


Appendix Figure 2.1.18 The correlation between the intrinsic rate of increase, $\log_{10}(r_{max})$, and body mass ($\log_{10}$ kg) based on data for 61 populations of 43 species of mammals, from Sinclair (1996).

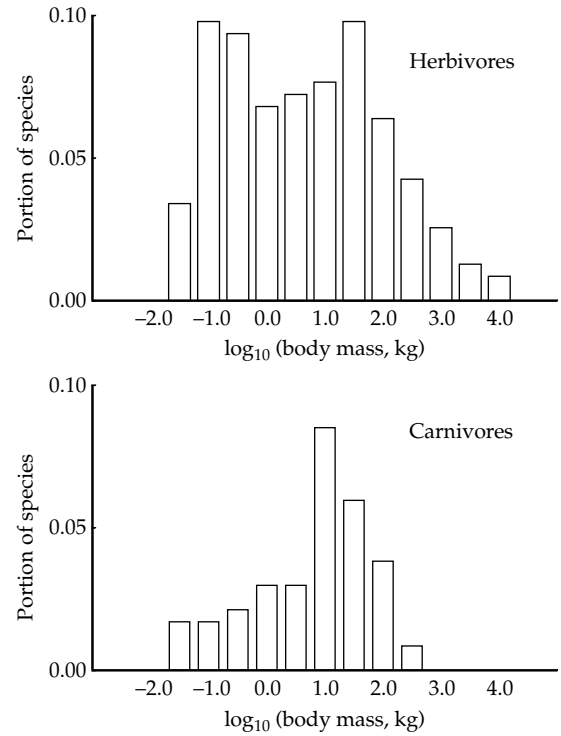
1.2.5 Body size and generation time

There is a correlation between time to maturation and body mass (Peters 1983) making it no surprise that there is a relation between generation time and body mass. Generation times, such as those shown in Appendix Figure 2.1.12, show a correlation with the body mass of the corresponding species. This is a relationship exemplified by the sample of species displayed in Appendix Figure 2.1.19. The distribution of species across generation time falls within a fairly narrow range for any particular body mass compared to that for the entire sample.

What portion of the geographic range of a species with a generation time of 20 years should be set aside as areas from which humans are excluded? This management question would direct research toward patterns involving overlaps in geographic ranges for an answer (e.g., Fig. 2.15 as it would apply for species such as the northern fur seal that occupy all of the eastern Bering Sea). However, the pattern chosen for guidance would also have to involve generation time (to be consonant with the question). Because of the relationship shown in Appendix Figure 2.1.19, body size would be accounted for automatically, even though the question might be refined a bit more by asking about specific species that have a body size within the variation observed to a generation time of 20 years. The same would hold true for home range sizes, rates of increase, and other features correlated with body size—consistency (Management Tenet 4, Chapter 1).



Appendix Figure 2.1.19 The correlation between generation time ($\log_{10}$ years) and body mass ($\log_{10}$ kg) for 79 populations of 55 species of mammals from Sinclair (1996).



Appendix Figure 2.1.20 Data for two sets of mammals divided according to their trophic level to show a comparison of the frequency distribution for body size for 72 species of carnivores and 163 species of herbivores (from Kelt and Van Vuren 2001).

1.2.6 Body size and population size

Based on the decline of density with body size, we might expect total population size to also show a decline in correlation with body size. This pattern was observed by Greenwood *et al.* (1996) for non-volant wild mammals in Britain (see also, Gaston and Blackburn 2000). Freedman (1989) lists species with body size similar to that of humans and corresponding approximations of population sizes. According to this information, crabeater seals may number between 15 and 30 million, kangaroos (at least two species) 19 million, ringed seals 6–7 million, caribou or reindeer 3 million, harp seals 2–3 million, dolphins more than 2 million, northern fur seal 2 million, and wildebeest 1.4 million. Other than humans, these species seem to represent the upper extremes of population size for this range of body size. The mean of population size for Appendix Figure 2.1.8 (about 300,000) is clearly less than most total populations for species of smaller organisms, such as bacteria, that often occur in numbers that are many (e.g., 20, Makarieva and Gorshkov 2004) orders of magnitude larger. The general shape of the two-dimensional species frequency distribution of body size and total population size has yet to be clearly described with empirical information for a large set of species for populations measured for their entire geographic ranges (e.g., all species within an ecosystem but with geographic ranges including areas outside the ecosystem).

1.2.7 Body size and trophic level

The patterns for body size (Figs 2.1 and 2.2) and trophic level (Fig. 2.3) lead to the prediction that we would see few large-bodied species at high trophic levels. Appendix Figure 2.1.20 illustrates a set of empirical data showing that the variance of body size is larger among herbivores than carnivores with a higher upper limit to the body size of herbivores than for carnivores. Most species at high trophic levels are small and exemplified by hyperparasites (Fowler and MacMahon 1982). These patterns are consistent with expectations based on consideration of risks of extinction coupled with energy flow within food chains. Consideration of species frequency distributions in the two-dimensional space of body size and trophic level, as well as factors contributing to the patterns are found in Anderson (1977), J. Brown (1971, 1981),

Brown and Maurer (1987), Glazier (1987a), Grayson (1977), Lawton (1995), and Terborgh (1974).

1.2.8 Body size and metabolic rate

Metabolic rate, one of the earliest of recognized species-level properties, is correlated with body size (generally body mass to the 3/4 power, Peters 1983). Based on the patterns of Figures 2.1 and 2.2, we would expect a concentration of species among those with lower metabolic rates (a pattern similar in shape to the pattern in Fig. 2.1). The bivariate pattern, therefore would resemble Figure 2.31 with a positive rather than negative slope. The opposite (but equal) slopes lead to a lack of correlation between energy consumption per unit area and body size (Damuth 1987, 2007). Such relationships are basic to patterns in energy flow within ecosystems.

1.2.9 Body size and other species-level characteristics

Within the pattern for reproductive mode, few species are asexual reproducers (0.1% for animals[8]). But there is also a pattern related to body size. Most asexually reproducing animal species are small bodied while nearly all large-bodied species are sexual reproducers.

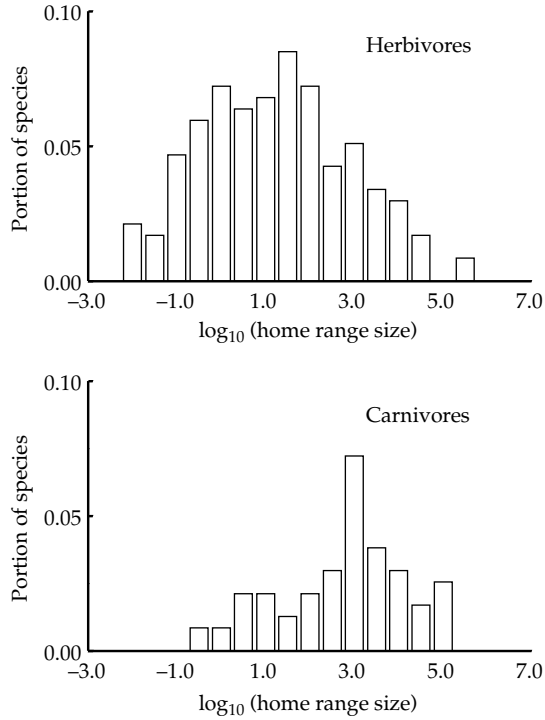
Most of the examples of specialization are found among smaller-bodied species such as insects (Gaston 1988, Hanski 1990, Niemalä *et al.* 1981, Woiwood and Hanski 1992) and lower trophic levels (especially plants). Most large mammals are generalists rather than specialists, although there are rare exceptions, such as the giant panda (notably endangered) and koala. Indeed, as indicated by Lawton and MacGarvin (1986) large-bodied species such as mammals are generally more polyphagous than insects.

In regard to mobility, birds, as a relatively mobile group of species, have a significantly greater proportion of large genera than do mammals of the same body size ("large" here, meaning numbers of species per genus, Glazier 1987a).

1.2.10 Other patterns involving two dimensions

1.2.10.1 Home range size and trophic level

Appendix Figure 2.1.21 shows patterns involving trophic level and home range size (Kelt and Van Vuren 2001). Holling (1992) considers home range size in relation to trophic level and shows similar patterns with references regarding the history of related studies.



Appendix Figure 2.1.21 A comparison of the frequency distribution for the mean home range size of herbivores and carnivores among 163 species of mammals from Kelt and Van Vuren (2001).

1.2.10.2 Intrinsic rate of increase and trophic level

Most consumer species have higher intrinsic rates of increase (r) than their resources (Hassell and Anderson 1989, May 1982). Among large species (i.e., low r), most of the species that serve as consumers are pathogens or parasites (higher r) rather than conventionally defined predators.

1.2.10.3 Geographic range and density

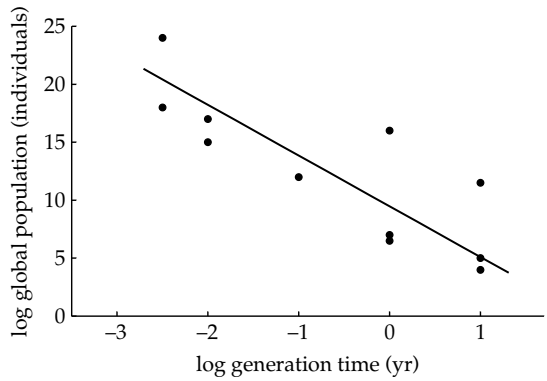
Both Bock and Ricklefs (1983) and Gaston and Lawton (1988a) found that (for their sample of birds and insects, respectively) species that are widely distributed also are generally locally abundant. As shown by Gaston and Blackburn (2000) this is a general pattern; however, there are examples

of species with large range size that are no more abundant than species with small range sizes. The infrequency of species at high density and small range size is clearer for insects than for birds.

1.2.10.4 Geographic range and population size
Gaston and Blackburn (2000) show examples for birds wherein species with larger range size exhibit larger populations. Concluding that this is a general pattern may be premature, however, because, across a broad spectrum of body size, density declines (Fig. 2.31) and range size increases in rough correlation with body size (Fig. 2.28).

1.2.10.5 Geographic range and population variation
Gaston and Lawton (1988a) found that a greater fraction of species with large ranges show high levels of population variability compared to species from more restricted geographic ranges. Whether or not this is generally true remains to be shown. The reverse may be expected given the relationships between body size, population variation, and geographic range size. Counter to this would be the extinction of highly variable populations in small geographic ranges. Observed patterns would, of course, be the result of all contributing factors (Fig. 1.4) to include the balance among such opposing forces.

1.2.10.6 Global population and generation time
Makarieva and Gorshkob (2004) presented a set of data with information regarding a variety of species-level characteristics important to processes involved in evolution and extinction. Among these are approximations for generation time (spanning about four orders of magnitude) and global population size (spanning about 28 orders of magnitude). These are shown in Appendix Figure 2.1.22 to illustrate the pattern involving these two species-level characteristics, even though the data represent groups of similar species rather than individual species. When reliable estimates of global population size are produced for numerous individual species, covering the full span of body size, we will see a clear pattern involving these two variables, owing to the pattern involving body size and generation time (e.g., Appendix Fig. 2.1.19) combined



Appendix Figure 2.1.22 The correlative pattern involving total global population (individuals) and generation time (yrs.) for a variety of species ranging from bacteria and diatoms to vertebrates, all spanning several trophic levels (in $\log_{10}$ scale for both variables). When original data (from Makarieva and Gorshkob 2004) involved a range of options in $\log_{10}$ scale, the midpoint was plotted in this figure. The line is based on a fit using geometric mean regression.

with that for density and body size (Fig. 2.31). Although it is clear that species with small bodies will usually be most numerous globally, it is also likely that the variance among estimates of total population size will also be correlated with body size. This expectation is based, in part, on consideration of the pattern involving geographic range size and its variation for small-bodied species, compared to larger species (e.g., Figs 2.27 and 2.28). Collectively, this information leads to the conclusion that evaluating the total (global) population size for any species is a process that must account for generation time (and/or body size) when we are addressing management questions about a sustainable global population.

1.2.10.7 Additional patterns
Further examples of patterns in bivariate frequency distributions abound. Charnov (1993) presents many graphically. These relationships are often specific to particular taxa but are represented by graphs of species-level characteristics in which each point represents a species (as in Figs 2.31 and 2.33). Examples include pairwise correlations among species-level attributes such as mortality rate, somatic growth rate, reproductive rates, age at first reproduction, sex ratios (and changes in them), rates of increase (including rate of increase per generation),

body size, and life spans. Work on patterns involving body size seems to predominate (e.g., see the early synthesis in Peters 1983). Other studies in the ecological literature present further treatment of a variety of species-level attributes, often including body size (see Anderson 1977; Brown 1995; Gaston and Blackburn 2000; Gaston and Lawton 1988a,b, 1990a,b; Glasier 1986; Hassell and Anderson 1989; Holling 1992; Hutchinson and MacArthur 1959; Kelt and Van Vuren 2001; Lawton 1990; Marzluff and Dial 1991; Patterson 1984; Sinclair 1996; Sugihara *et al.* 1989; Wilson and Willis 1975; plus the many papers spawned by these). Patterns that are not related to body size should not to be forgotten (e.g., Figs 2.32 and 2.33 and anything correlated with rate of increase per generation time, and the shape of productivity curves). Other patterns not correlated with other specific species-level attributes are to be sought in macroecological research.

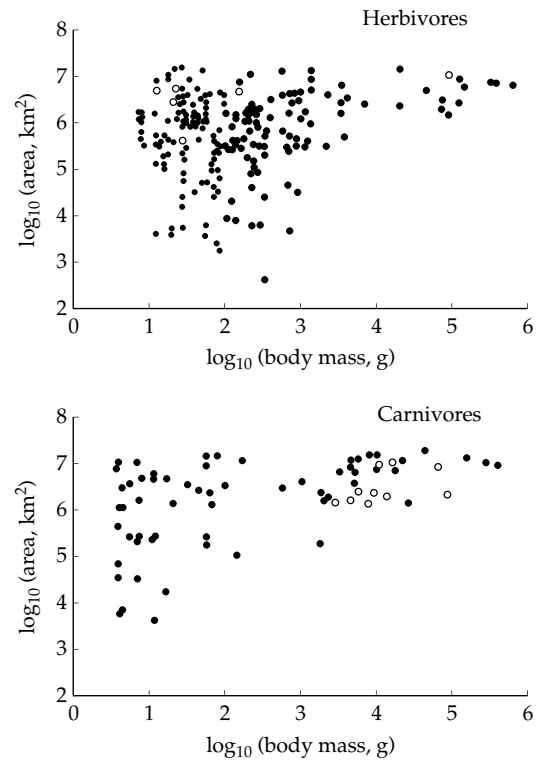
1.3 Three species-level characteristics

1.3.1 Body size, trophic level, and geographic range

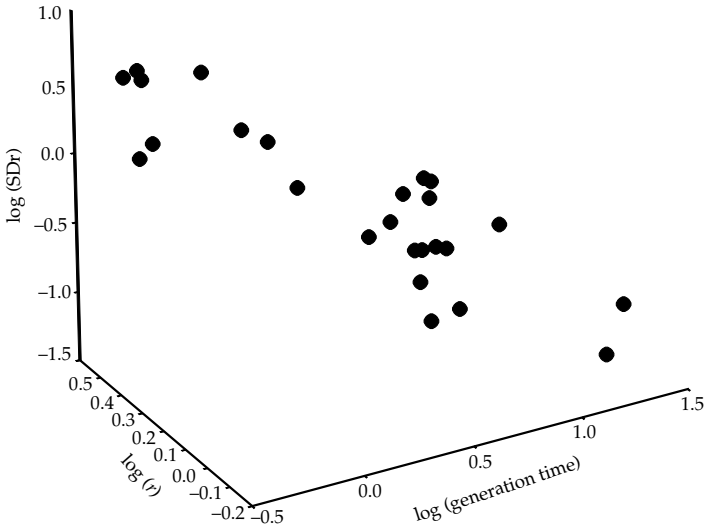
Appendix Figure 2.1.23 represents the separation of North American mammal data for geographic range and generation time (Brown 1981, Fig. 2.28) into two trophic categories: herbivores and carnivores. Few species represent the combination of long generation time, high trophic level, and small geographic range (all of which contribute to elevated risk of extinction). Within the three-dimensional space of these characteristics, the density of species is maximum at an intermediate level of geographic range, small body size and low trophic level. From this peak species density declines in progressing toward combinations of small range size, large body size, and higher trophic level. Species numbers also diminish toward the opposite extremes of large range size, small body size, and lower trophic level. These patterns are not surprising based on the combined patterns in body size (May 1978, 1986, Fig. 2.1), trophic level (Fig. 2.3), and energy consumption (Fig. 2.11) along with the relationships of the latter two with body size.

1.3.2 Other three-dimensional patterns

In spite of the potential for hundreds of three-way patterns among recognized species-level characteristics (Table 2.1), graphic examples such as Appendix Figure 2.1.23 are rare in the literature. Carbone and Gittleman (2002) explore various three-way relationships among the density, numbers, and body mass of carnivores in correlation with prey biomass and productivity. Marquet (2002) showed information regarding the pattern involving trophic level, body size, and population density. Gillooly *et al.* (2001) present information on relationships among body size, temperature, and metabolic rates. Other similar data undoubtedly exist; their graphic presentation would help see informative structure within the relevant biotic systems—in particular for ecosystems where the species would be the entire set of species represented by populations in those systems. Qualitative descriptions for three or more characteristics are far fewer than for one or two characteristics (e.g.



Appendix Figure 2.1.23 The distribution of North American mammals over geographic range and body size (log transformed) according to trophic level, from Brown (1981).



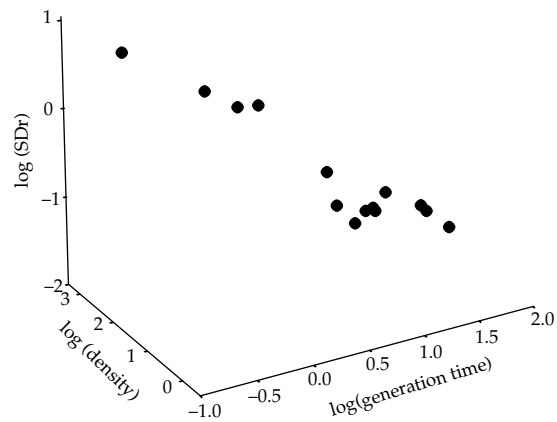
Appendix Figure 2.1.24 The correlations among generation time (years), intrinsic rate of increase (r_{max}, year^{-1}), and standard deviation of observed r (SDr), all in $\log_{10}$ scales, for 26 species of mammals from Sinclair (1996).

Gaston and Lawton 1988a,b; Hanski 1990; and Orians and Kunin 1990).

The next sections present more examples of data that hint at the three-dimensional patterns one would expect for entire ecosystems or the biosphere.

1.3.2.1 Generation time, rate of increase, and population variation

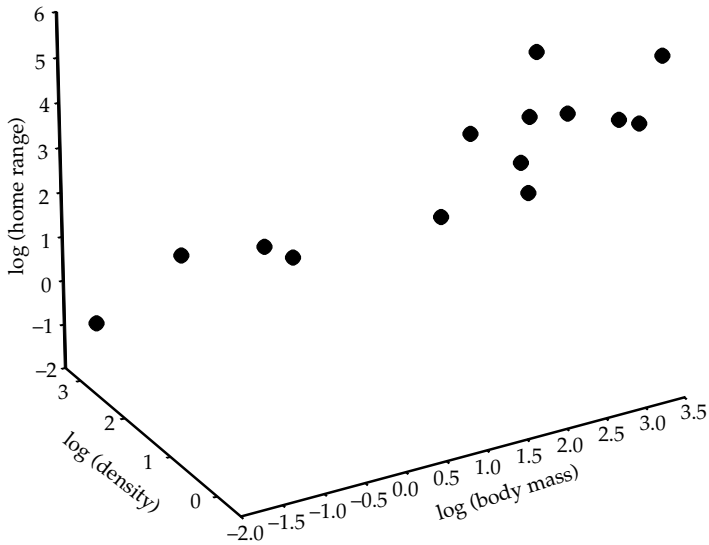
Appendix Figure 2.1.24 shows the interrelationships among generation time, rate of increase, and population variation for a sample of mammal species to demonstrate the general shape of patterns one would expect on the basis of the correlations between these variables and body size (Fig. 2.30, Appendix Figs 2.1.18 and 2.1.19). The overall shape of the relationship is one thing, the density of species within the relationship is another. Within this seemingly log-linear cloud of points the density of species is probably misleading owing to the lack of species with high population variation, short generation times, and high intrinsic rates of increase, especially outside the range of each of these variables as covered by this graph. The density or distribution of species within this pattern is important to the matter of distinguishing the abnormal from the normal for purposes of implementing Management Tenet 5 (Chapter 1).



Appendix Figure 2.1.25 The correlative relationships among density, population variation, and generation time for a sample of 14 mammal species in the combination of data from Damuth (1987), and Sinclair (1996).

1.3.2.2 Density, population variation, and generation time

Appendix Figure 2.1.25 illustrates the relationship between population density and variation in correlation with generation time. It is based on 14 species of mammals from Sinclair (1996) with density estimates from Damuth (1987). As with Figure 2.35 and Appendix Figure 2.1.24, there is



Appendix Figure 2.1.26 The relationships among body mass, population density, and home range size for 14 species of mammals common to the data sets from Damuth (1987), and Kelt and Van Vuren (2001).

an under-representation of the numbers of species with high population variation, short generation times, and high densities because such species are under-represented in relevant published research.

1.3.2.3 Density, body size, and home range size

Appendix Figure 2.1.26 is similar to Appendix Figures 2.1.24 and 2.1.25 above in showing three-dimensional relationships, here among body mass, population density, and home range size. There is no surprise in seeing a decline in density with an increase in home range size, although overlapping home ranges within a species would be a factor in determining the slope of this relationship.

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