

## CHAPTER TWO

# On Current Theories of Relative Species Abundance

No other general attribute of ecological communities besides species richness has commanded more theoretical and empirical attention than relative species abundance. Commonness, and especially rarity, have long fascinated ecologists (Rabinowitz et al. 1986, Hubbell and Foster 1986a, Gaston 1994), and species abundance is of central theoretical and practical importance in conservation biology (Soulé 1986). In particular, understanding the causes and consequences of rarity is a problem of profound significance because most species are uncommon to rare, and rare species are generally at greater risk to extinction.

Given its central importance, it is surprising that relative species abundance is missing entirely from MacArthur and Wilson's theory of island biogeography. This is all the more surprising because there is a lengthy discussion of extinction and its relationship to population size in their 1967 monograph. Just a few years earlier, MacArthur (1957, 1960) published his two famous theoretical papers on relative species abundance. These papers were steeped in niche-assembly theory and did not fully break out of the static, equilibrium mode of thinking about ecological communities. However, MacArthur's broken-stick hypothesis did raise the possibility of random community assembly by asking what relative species abundances would be if they were set by randomly apportioned limiting resources.

Before attempting to extend the theory of island biogeography, it is useful to outline the major theoretical and

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empirical milestones in the study of relative species abundance. More detailed reviews can be found elsewhere (Engen 1974, Pielou 1966, 1975, May 1975, Engen 1978, Gray 1987, Tokeshi 1993, 1997). Two major approaches to the study of the distribution of individuals per species have been taken: inductive and deductive. In the early years, when the study of relative species abundance was in its infancy, an inductive approach dominated. Observed distributions of the numbers of individuals per species in collections were fit to statistical distributions with little or no attempt at theoretical explanation or at defining the sampling universes from which the collections were made.

A milestone of the inductive approach was the publication of Corbet (1941) and, two years later, of Fisher, Corbet, and Williams (1943). The entomologist Steven Corbet had collected abundance data on 620 species of butterflies in Malaya. Williams (1939, 1940) had similar data on the abundance of moths collected over a four-year period at light traps at Rothamsted Experimental Station in England. When the number of species was tallied into abundance classes, i.e., species represented by a single individual, by two individuals, and so on, they noticed that the series was a relatively smooth hyperbolic progression, with many rare and few common species. Corbet and Williams took their data to Ronald Fisher, who assumed that the "true" relative abundances of species in nature would be well described by a gamma function. However, this distribution would be sampled, and Fisher assumed that the number of individuals collected of a given species would be Poisson distributed because most species were rare and represented by only a few individuals in the samples of Corbet and Williams. The resulting compound distribution was negative binomial. However, there was a problem because the zero abundance class (species too rare to be sampled) was obviously not observable, so Fisher truncated the negative binomial to eliminate the zero class. Then, having no way of estimating

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how many species were not sampled, Fisher assumed the number of species in the community was effectively infinite. Fisher obtained a one-parameter distribution that he dubbed the logarithmic series, derived from the negative binomial as a limiting case (shape parameter set to zero).

According to the logseries, as it is now generally called, the number of species in a collection having  $n$  individuals will be given by  $\alpha x^n/n$ , where  $x$  is a positive constant  $0 < x < 1$  and  $\alpha$  is a measure of diversity, which in the expectation is equal to the number of singleton species divided by  $x$ . Thus, the number of species with 1, 2, 3, 4,  $\dots$ ,  $n$  individuals will be given by

$$\alpha x, \quad \alpha x^2/2, \quad \alpha x^3/3, \quad \alpha x^4/4, \dots, \alpha x^n/n, \quad \text{for } 0 < x < 1.$$

Adding all terms, the total number of species,  $S$ , is expected to be  $\alpha[-\ln(1-x)]$ , and the total number of individuals in the collection,  $N$ , is  $\alpha x/(1-x)$ . The parameter  $\alpha$ , known as Fisher's  $\alpha$ , is a widely used measure of species diversity because it is theoretically independent of sample size (Fisher et al. 1943). However, empirically  $\alpha$  is only approximately constant, changing slowly over large ranges in sample size (Hairston 1959, Magurran 1988, Condit et al. 1996). Fitting the logseries always results in the singleton category having the most species (fig. 2.1).

A few years later, Preston (1948) criticized the logseries on the grounds that it was not a good fit to data that he had assembled, primarily on bird species abundances. Preston argued that relative abundance distributions were more often bell-shaped curves, such that species having intermediate abundances were more frequent than very rare species. Preston also noted that the distributions were nonnormal. However, when he log transformed his species abundance data, he discovered that the relative species abundance curve could then be normalized (fig 2.2). Preston introduced a simple way to display the lognormal distribution of relative

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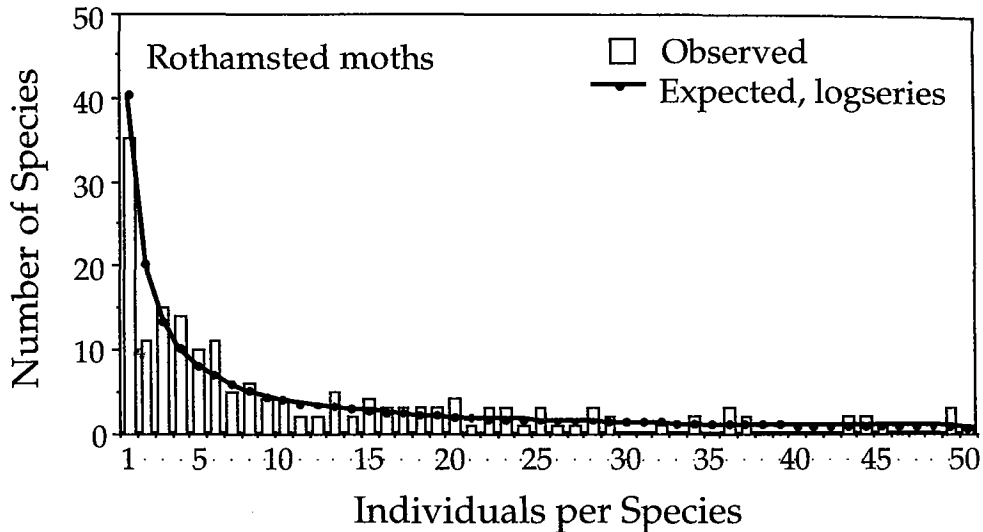


FIG. 2.1. An example of the use of the logseries distribution to fit data on species abundance in collections of moths at light trap over a 4-year period at Rothamsted Field Station, U.K. The logseries always predicts that the abundance class of singleton species will be the largest class.

species abundance. He erected doubling categories of abundance (1, 2, 4, 8, et seq.), and counted the species having abundances falling in each category. Species having exactly 1, 2, 4, 8, . . . individuals were divided equally between adjacent abundance categories. He called these doubling classes "octaves" in analogy to octaves of a musical scale, which represent a doubling of the frequency of musical pitch. This classification of species into doubling abundance classes effectively log transforms the relative abundance data to the log base 2. He chose log base 2 for the simple practical expedient of spreading the distribution of species abundances over more categories to make its shape more apparent. Using any larger number for the base of log transforming the distribution would only reduce the number of categories displayed, depending on the range in relative species abundances.

The lognormal distribution is continuous, not discrete as in the case of the logseries. However, Preston's method of categorizing abundances provides a simple way to approx-

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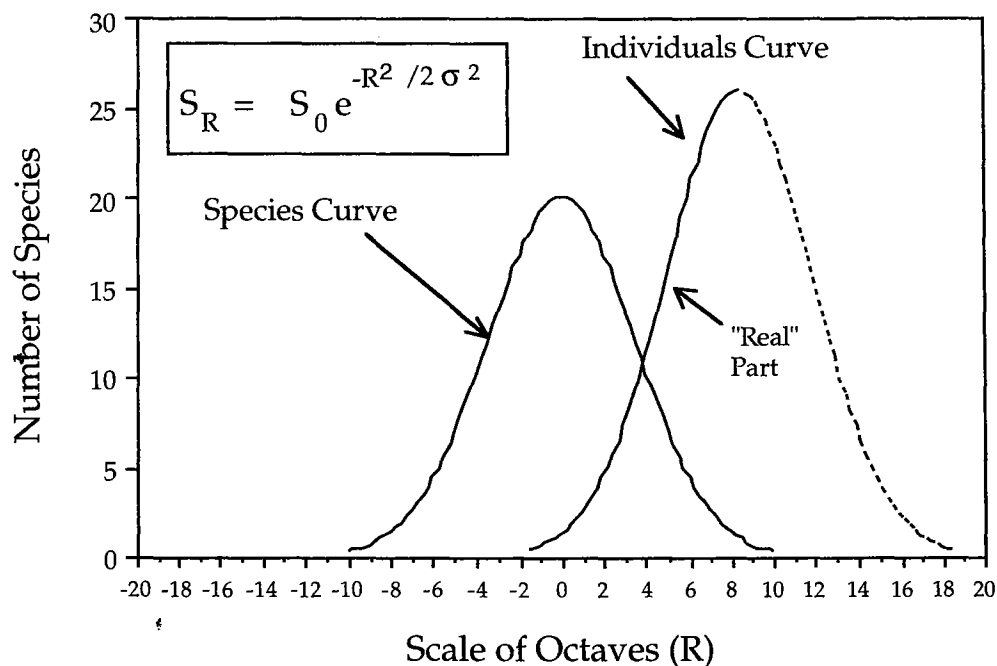


FIG. 2.2. Preston's "canonical lognormal" hypothesis. Preston argued that rare species were less numerous than species of middle abundance, and that species abundances were lognormally distributed. He counted species in doubling classes of abundance called "octaves." He further argued that there was a special relationship between the Species Curve and the Individuals Curve (discussed later), summed over all species in each octave. This canonical relationship predicted that the Individuals Curve would reach its modal value in the octave containing the most common species in the community. Redrawn from MacArthur and Wilson (1967).

imate the distribution by a discrete-valued function, as follows. Let  $S_0$  be the number of species in the modal octave of abundance. Let  $S_R$  be the number of species in the  $R$ th octave (or doubling abundance class) to the left or right of the modal octave. Then the so-called Species Curve can be written as

$$S_R = S_0 e^{-a^2 R^2}, \quad R = 0, 1, 2, \dots,$$

where  $a$  is a constant that depends on the variance of the lognormal,  $a = 1/\sqrt{2\sigma}$ . Note that the distribution is symmetrical about the mode, located at  $R = 0$ . Fitting the Species Curve can be done approximately by taking natural logs, and regressing  $\ln(S_R)$  on  $R^2$ , a regression having slope  $-a^2$

and intercept  $\ln(S_0)$ . More accurate fitting of the continuous lognormal distribution to the data on individual species abundances requires using a maximum likelihood technique for a truncated lognormal (Bulmer 1974, Slocumb et al. 1977). Over the past half century, the lognormal distribution has been fit successfully to a far larger number of relative species abundance distributions than has the logseries distribution, particularly as larger sample sizes have become available (Sugihara 1980).

Of almost equal importance to Preston's discovery of the widespread lognormality of the distribution of individuals per species was his recognition of the effect of sample size on the distribution. The importance of sample size had generally been overlooked because of the theoretically expected constancy of Fisher's  $\alpha$  in collections of different sizes (Hairston 1959, Routledge 1980). Preston argued that the shape of the relative species abundance distribution observed by Fisher et al. (1943) was an artifact of small sample size. In the logseries, the expected number of species is always largest in the rarest abundance category, consisting of singleton species. However, in a small sample, one should observe only a truncated distribution of relative abundances—one comprising only the most common species. This is because common species are generally collected sooner than rare species.

As sample size increases, Preston (1948) predicted that more and more of the lognormal distribution would be revealed. He conceptualized the unveiling of the underlying lognormal distribution by the leftward movement of a "veil line" across the distribution (fig. 2.3). For any given sample size, the veil line is positioned just to the left of the rarest abundance category that is observable (i.e., species represented by a single individual). Species whose expected relative abundances are fractional for a given sample size on average are unobserved and lie to the left of the veil line because they are still too rare to have been collected

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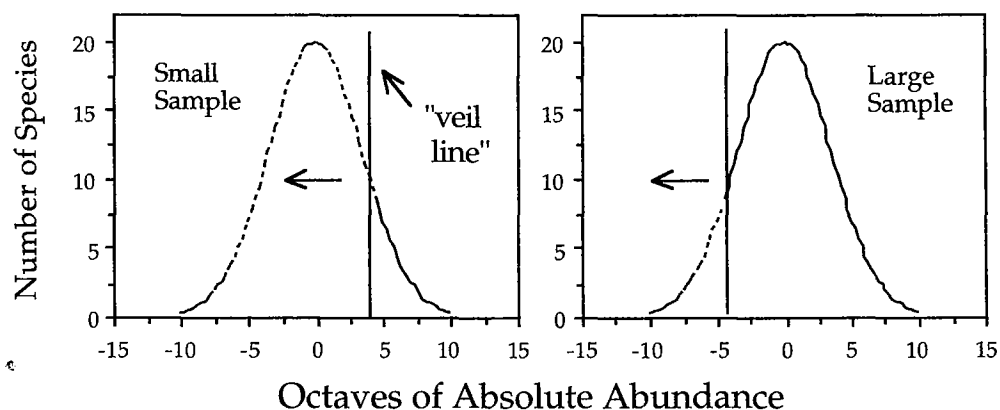


FIG. 2.3. The effect of increasing the sample size on the apparent distribution of individuals per species. As the sample size is increased, the category of rarest species, represented by singletons, moves farther and farther to the left. As more octaves of abundance are expressed in the sample, the mode is eventually seen. Thereafter, increasing sample sizes produce decreases in species number in the octaves containing the rarest species. This effect was described as an “unveiling” of the distribution, and the sampling cutoff at just below one individual per species was called the “veil line.”

even once (fig. 2.3). The mode of the distribution is eventually revealed when further increases in sample size result in decreasing rather than increasing species counts in the rarest abundance category. The prediction of the existence of an interior mode to the distribution was borne out for the Rothamsted moth data after more collection years were added (Williams 1964) (fig. 2.4). Routledge (1980) would later note that the logseries distribution can easily be mistaken for the right-hand tail of a lognormal distribution.

Another useful way of graphically presenting relative species abundance data was popularized by Whittaker (1965), who named his plot the dominance-diversity curve (fig. 2.5). This curve is a graph of the logarithm of the abundance of a species on the  $y$ -axis against the rank in abundance of the species on the  $x$ -axis. Common species are assigned low ranks and appear to the left. On such a plot, the logseries appears linear, whereas the lognormal is curvilinear, at first steep over the low ranks of the commonest species, then shallower over species of middling abundance, and finally

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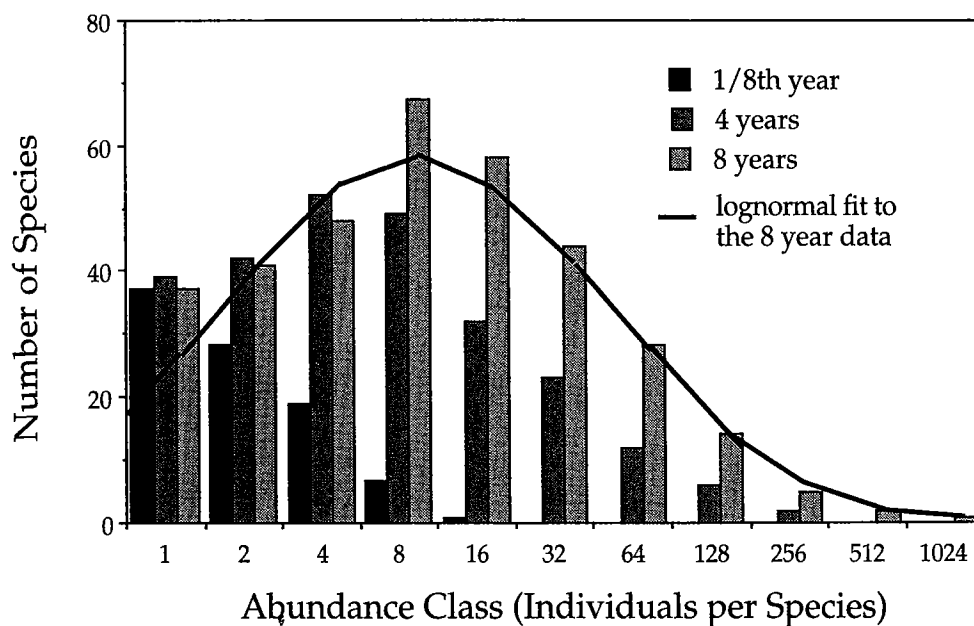


FIG. 2.4. As the survey of months at light traps at Rothamsted Field Station was extended over more years, the distribution of individuals per species became lognormal, as Preston predicted. Modified from Williams (1964).

becoming steep again over the rarest species at high ranks. Examples of such dominance-diversity curves were presented in the first figure of this book (fig. 1.1).

The logseries and lognormal were the principal “inductive” approaches to the study of relative species abundance. These were followed by theoretically inspired “deductive” approaches based on hypotheses about how ecological communities were organized.

In 1957 MacArthur published a paper in the *Proceedings of the National Academy of Sciences* critical of the inductive or “statistical” approach to studying the distribution of individuals per species in communities. This was followed by a second paper a few years later (1960). MacArthur’s papers ignited a decade of great interest in deductive theoretical models of relative species abundance. He believed that the lognormal patterns of relative species abundance were so ubiquitous that there had to be an underlying general mechanism that theory could elucidate. MacArthur once confided



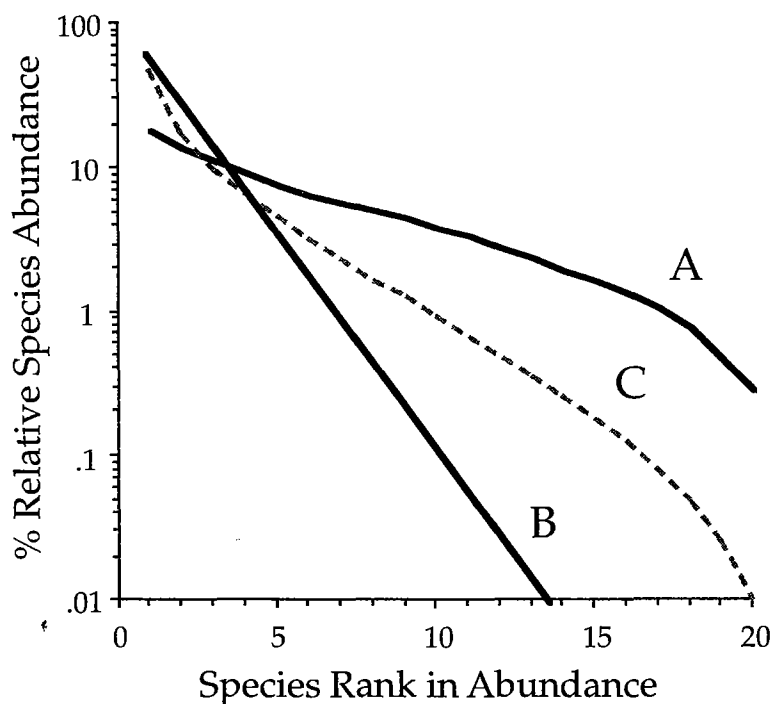


FIG. 2.5. Dominance-diversity curves, popularized by Robert Whittaker. The logarithm of percent relative species abundance is plotted on the  $y$ -axis against the rank of the species in abundance on the  $x$ -axis, with the commonest species at low rank. Curve A is the shape characteristic of MacArthur's "broken-stick" hypothesis, and is flatter than the typical lognormal observed for natural communities. Curve B is the "niche-preemption" model of Motomura, which produces a straight-line dominance-diversity curve on a semilog plot, as does the logseries distribution of Fisher et al. (1943). Curve C has the characteristic S-shape of lognormal distributions of relative species abundance. See text for further explanation. Figure redrawn from Whittaker (1975).

in me that he began by looking for a simple niche-based theory that would produce an S-shaped dominance-diversity curve like that of the lognormal. What if, MacArthur reasoned, groups of trophically similar species in ecological communities simply randomly divide up a common pool of limiting resource and their relative abundances were proportional to the fraction of total resource each utilizes? MacArthur idealized the resource pool as a stick of unit length. Suppose a community of  $S$  species randomly divides up the common resource. Now randomly partition the resource pool by throwing  $S - 1$  random points onto the

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unit stick. Then, break the stick at each random point, and rank the fragments from shortest to longest. The expected relative abundance of the  $i$ th rarest (shortest) species,  $y_i$ , should then be given by

$$E(y_i) = \left(\frac{1}{S}\right) \sum_{x=i}^S \left(\frac{1}{x}\right).$$

This is MacArthur's "broken-stick" hypothesis. Reasonably good fits to the broken-stick model have been found in narrowly defined communities of closely related species of birds (MacArthur 1960), minnows and ophiuroids (King 1964), and *Cornus* gastropods (Kohn 1969). The distribution of fragment lengths of a randomly broken unit line segment was previously known (Whitworth 1934), but the theory of relative species abundance was a new application of the distribution. In his 1960 paper, MacArthur added embellishments to the broken-stick model, such as allowing niches to "overlap"; but the resulting relative abundance distributions agreed less well with the empirical data and were not pursued. As it turned out, the relative abundance distribution predicted by the original broken-stick model was itself not a lognormal, although it did predict an S-shaped dominance-diversity curve. The predicted distribution was often too even (fig. 2.5): common species were not common enough, and rare species were too common.

Meanwhile, Whittaker (1965) had rediscovered a much earlier deductive approach in the work of the Japanese ecologist Motomura (1932), which had been inaccessible to most Western ecologists because it was published in Japanese. Motomura studied a series of simple plant communities characterized by high dominance. He found that a steep geometrical distribution characterized relative abundances in these communities quite well. Whittaker (1965) dubbed Motomura's model the "niche-preemption" model. It was conceptually similar to the broken-stick hypothesis,

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except that the partition of limiting resources was nonrandom. Suppose that the community is characterized by strict hierarchical dominance. Expected relative species abundances were found by applying the following rule: Let the most dominant species sequester fraction  $k$  of the total resource pool (e.g., space for space-limited plants), leaving fraction  $1 - k$  for all other species. Then let the second most dominant species sequester the same fraction  $k$  of the remaining resource, leaving fraction  $(1 - k)^2$  for all remaining species, and so on. This distribution produces a straight line on a dominance-diversity plot. May (1975) suggested that this model might be one theoretical explanation for the logseries of Fisher et al. (1943), which also produces a linear dominance-diversity plot. The assumed constancy of the fraction  $k$  in the niche-preemption model has never been adequately justified, however.

These theoretical efforts still left the lognormal unexplained. This was an unsatisfactory situation because the lognormal is one of the best documented empirical generalizations in community ecology. For a time after the apparent failure of deductive approaches, the general opinion was that the lognormal was of little or no biological interest (Boswell and Patil 1981). It was repeatedly pointed out that lognormals could arise simply as the result of the multiplicative interaction of many normal random processes affecting the growth of populations (e.g., May 1975, Caswell 1976), or that lognormals could arise by combining unrelated samples (Routledge 1980).

However, interest in the lognormal was rekindled again when Sugihara (1980) argued that the lognormals that describe relative species abundance were not just any lognormals, but were a special class of so-called canonical lognormal, a term coined by Preston (1962) eighteen years earlier. By *canonical*, Preston meant that there was a special relationship between the Species Curve, discussed earlier, and the Individuals Curve for the same community. The Individuals

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Curve is constructed by summing the abundances of the species in each octave of the Species Curve. Suppose there are  $n_0$  individuals per species in the modal octave. Then the number of individuals per species in the  $R$ th octave to the right of the mode,  $N_R$ , is  $n_0 2^R$ , and the number in the  $R$ th octave left of the mode is  $n_0 2^{-R}$ . Thus, the Individuals Curve is given by

$$N_R = S_0 n_0 2^R e^{-a^2 R^2},$$

which can be rewritten

$$N_R = S_0 n_0 e^{(\ln 2/2a^2)^2} \cdot e^{-a^2 [R - (\ln 2/2a^2)]^2},$$

which demonstrates that the Individuals Curve is also a log-normal with the same variance but with a mode displaced by  $\ln 2/2a^2$  to the right (MacArthur and Wilson 1967) (fig. 2.2). Most or all of the right half of the Individuals Curve is missing, however, because the distribution cannot extend beyond abundance octaves that still have species. It is truncated at or near its mode, which tends to be located in the octave containing the most abundant species in the community (fig. 2.2). This is not a necessary relationship, but it is empirically found in a wide variety of communities (Sugihara 1980).

With sufficiently large samples, and assuming relative species abundances are indeed lognormally distributed, essentially all species in the community will be tallied over the octaves in which  $S_R \geq 1$  (or  $1/2$  if one divides the count of singleton species between  $S_R = 1/2$  and  $S_R = 1$ ). The total  $J$  of all individuals in the community is  $J = \sum N_R$ . Taking the functional relationship between the Species Curve and the Individuals Curve as a postulate, Preston could then show that once  $J$  was specified (or more precisely  $J/n_r$  where  $n_r$  is the abundance of the rarest species, typically set to unity), then all the other parameters of the log-normal could be calculated, including the total number of

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species, the variance of the distribution, the modal number of species, and the modal species abundance (Preston 1962). Because of this parameter interdependency, Preston called this ensemble of relationships "canonical."

The importance of the canonical relationship to Sugihara (1980) was much more than the fact that the lognormals of relative species abundance were somehow special. Sugihara revisited the broken-stick model, following a comment of Pielou (1975) that repeatedly or sequentially breaking the broken stick would eventually produce a lognormal distribution of fragment lengths. The sequential breakage procedure is as follows. Take the stick and make the first random break. Choose one of the two fragments at random and break it randomly. Then choose one of the three fragments at random and break it, and so on. What Sugihara discovered was that the resulting distribution was not only lognormal, but it was also canonical *sensu* Preston (1962). Sugihara (1980) made the analogy of sequential breakage to the action of a rock-crushing machine, which produces a lognormal distribution of particle sizes (Pielou 1975).

With the wisdom of hindsight, one can identify many shortcomings of these attempts to derive a theory of relative species abundance from first principles. Not the least of the shortcomings are the supposed first principles themselves. In MacArthur's broken-stick model, for example, it is unclear what the competitive mechanism would be that was supposed to randomly partition resources, nor is it clear what spatial and temporal scales pertain to this partitioning. Moreover, the number of species in the community is a free parameter that cannot be derived from the first principles in the theory. Expected relative species abundances are only determined once the number of species partitioning the resource base has been specified. In the niche-preemption model, the assumed perfect constancy of the fraction of remaining resources that is preempted by each succeeding

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species in the competitive hierarchy remains unexplained by any biological mechanism, and borders on the mystical. In the sequential breakage model, which does at least generate canonical lognormal distributions, there has not been a satisfactory biological interpretation of the rock-crushing analogy. One proposal is that sequential breakage is somehow analogous to multidimensional niche partitioning. However, the biological analog to what is done mathematically in sequential breakage is still obscure. Moreover, there is no "stopping rule" inherent in the theory that fixes how many sequential breaks to carry out. This means that the number of species in the community is once again a free parameter that does not follow from the theory. Finally, all of these models can also be faulted for having little or nothing to say about sampling issues or how they might be tested with data from real communities (Pielou 1975, Tokeshi 1993, 1997). To its credit, the statistical approach of Preston (1948, 1962), while inductive, at least was firmly grounded in a sampling theory. The greatest conceptual weakness of all these theories, however, is that they are static and do not arise in any clear way as a necessary dynamical consequence of birth, death, and dispersal processes in natural populations. Thus, it is little wonder that there is no connection between these theories and the dynamical theory of island biogeography of MacArthur and Wilson.

One might therefore have expected classical dynamical theory in community ecology to have attempted to explain relative species abundance. However, when we turn to this extensive body of theory for assistance, we find that it is almost totally silent on the subject of relative species abundance. On reflection one can understand why this is so. The edifice of theory in community ecology is constructed largely on the foundation of the classical Lotka-Volterra equations of competition (Levins 1968, Rose 1987), or on their mechanistic, resource-based counterparts (Hsu et al. 1977, Tilman 1982). In the equilibrium analysis of mul-

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tispecies Lotka-Volterra competition, the focus has been almost exclusively on community stability and species coexistence, not on relative species abundance. No one to my knowledge has ever found any compelling theoretical basis for lognormal relative abundances in this body of theory. Lotka-Volterra theory is sufficiently parameter rich that no doubt someone could cleverly choose carrying capacities and competition coefficients that would yield a canonical lognormal distribution at equilibrium. A comparable exercise could be carried out in the context of resource-based competition theory. In either case, however, the choice of parameter values would be completely gratuitous. The parameter values would have no basis in theory, let alone have empirical necessity. Such an exercise would be even less justified than the theories of relative species abundance we just reviewed. For these reasons, I have little confidence that the current mainstream theoretical approaches to resource competition in communities will ever produce a successful dynamical theory of relative species abundance. At the end of the day, current niche-assembly theories of relative species abundance fail to explain either the lognormal or the universality and invariance of Fisher's  $\alpha$ .

In recent years, as larger sample sizes of relative species abundance have become available and the abundances of very rare species have become better known, it has become increasingly apparent that observed distributions of relative species abundance are in fact, seldom lognormally distributed. Observed distributions appear to be lognormal to the right of the mode in the right-hand tail representing common species. But they almost always show strong negative skewness, manifest as a large excess of rare and extremely rare species over that predicted by the symmetrical lognormal. This phenomenon is exemplified by the distribution of relative abundances of British breeding birds (Gibbons et al. 1993, Gregory 1994) (fig. 2.6). The right-hand tail looks like a perfectly respectable lognormal dis-

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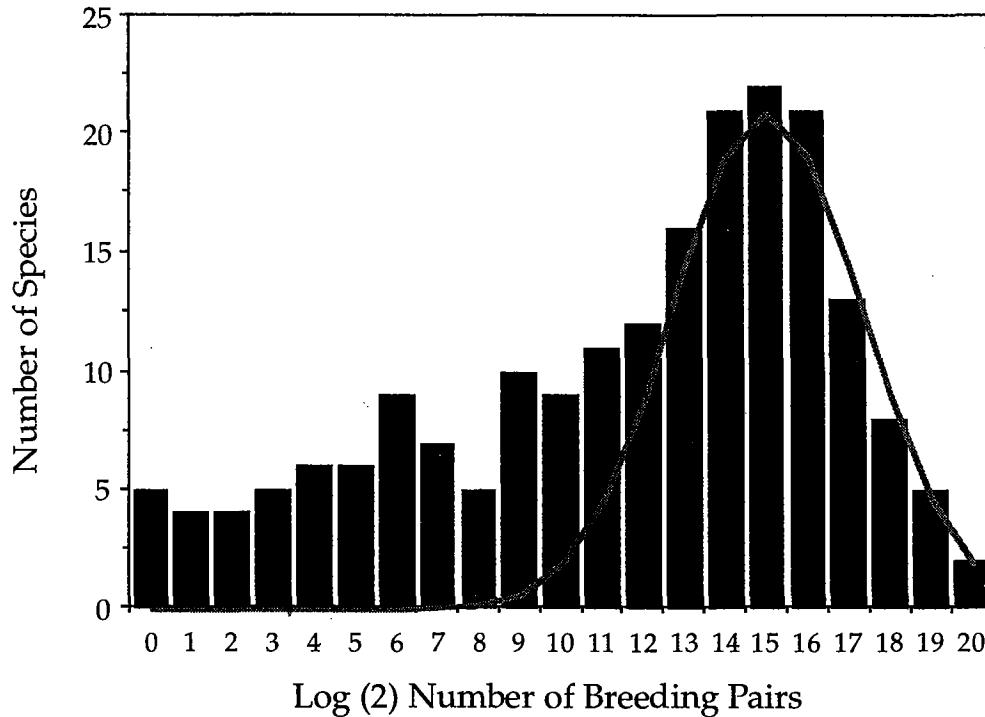


FIG. 2.6. Negatively skewed distribution of relative species abundance for all British breeding birds. Note the poor fit of the lognormal to the left-hand tail of rare and extremely rare species. Data extracted from Gibbons et al. (1993). See also Gregory (1994).

tribution, but when the lognormal is fitted only to data from the right-hand tail, the lack of fit to the left-hand tail is immediately apparent. Anticipating a result that will be proven later in this book, the unified theory predicts the existence of a new statistical distribution of relative species abundance, called the *zero-sum multinomial*. This new distribution also exhibits negative skewness, the extent of which depends upon local community or island size and the immigration rate.

Preston (1962) entertained the hope of estimating the total number of species in a community from subsamples short of a total count. He reasoned that if distributions of relative species abundance were indeed lognormal, then one only had to collect sample sizes large enough to find the mode of the distribution. One would simply add the



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number of species in the modal octave to twice the number of species in higher octaves of abundance. However, the asymmetry of observed distributions of relative species abundance means that Preston's method will always underestimate the actual number of rare species in the community. As we shall demonstrate, the new zero-sum multinomial distribution will enable us to estimate the total number of species as well as their relative abundance in arbitrarily large geographic regions. All the necessary parameters of the distribution can be estimated from relatively small samples. Thus, the unified theory provides a powerful new method for estimating the total biodiversity in a given community or taxon over a large biogeographic region, filling a critical need in conservation biology for improved estimates of regional biodiversity and relative species abundance.

### SUMMARY

1. The earliest theories of relative species abundance were inductive and based on fits to statistical distributions with no underlying ecological theory. Examples are Fisher's logseries and Preston's lognormal. Fisher's logseries distribution generates a diversity parameter known as Fisher's  $\alpha$ . This parameter relates the number of species in a sample to the number of individuals in the sample. Fisher's  $\alpha$  is widely used to characterize species diversity in collections because it is nearly invariant with increasing sample size.
2. Preston criticized Fisher's logseries because it always predicted that the rarest species would be the largest category of abundance (singletons). Preston's data produced distributions of relative species abundance with an interior mode. Preston argued that Fisher's logseries was an artifact of small sample size, which has generally proven in later years to be correct. However, the log-

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normal left unexplained the apparent universality and invariance of Fisher's  $\alpha$ .

3. Later theories of relative species abundance were deductive and based on one or another ecological theory of community organization. Each of these theories, such as MacArthur's broken-stick hypothesis, proposed simple a priori rules for how limiting resources would be apportioned among competing species in a community.
4. These deductive theories of relative species abundance can be faulted with the wisdom of hindsight. Their most serious problem is that they do not derive in any straightforward way from fundamental birth-death-migration processes in population dynamics. Also, the number of species in the community is a free parameter that cannot be predicted from first principles in any of the deductive theories.
5. Newer and much larger data sets on relative species abundance indicate that virtually all distributions have long and negatively skewed tails of very rare species. None of the current theories of relative species abundance, including Preston's lognormal, satisfactorily explain this negative skewing. This skewness means that the lognormal will always underestimate the number of rare species. It also means that relative abundance distributions are not canonical in the sense that there is no special relationship between the Individuals Curve and the Species Curve, as postulated by Preston.
6. The unified theory predicts the existence of a new distribution of relative species abundance called the *zero-sum multinomial*, which exhibits negative skewness, the extent of which depends on island size and the immigration rate.