ON THE RELATIVE ABUNDANCE OF BIRD SPECIES

By Robert H. MacArthur

DEPARTMENT OF ZOÖLOGY, YALE UNIVERSITY

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One approach to the study of the structure of animal communities for which there is a considerable amount of raw data is the comparison of abundances of the species of a group of organisms in a given locality. The basic information is a list of species found and the abundance of each. This can best be plotted by ranking the species from commonest to rarest along the abscissa and plotting their abundances along the ordinate. For convenience, the abscissa is graduated logarithmically. Earlier investigations,[1] discussed elsewhere,[2] fit known statistical curves of uncertain biological meaning to the data. A more fruitful approach seems to be to predict curves on the basis of simple biological hypotheses and to compare these with the data. Three such hypotheses will be discussed here. First, however, the evidence cited by Lack,[3] combined with the observation that censuses yield similar results when taken in the same habitat either at the same time in different places or in the same place in different years, indicates, for birds at least, that the observed populations are not under the control of very local or rapid temporal processes; i.e., they are in a near-equilibrium state. The hypotheses will therefore be ones which yield an equilibrium or near-equilibrium population.

Hypothesis 1: Nonoverlapping Niches.—The environment is compared with a stick of unit length on which $n - 1$ points are thrown at random. The stick is broken at these points, and the lengths of the n resulting segments are proportional to the abundances of the n species. This comparison is legitimate, since the mathematical part of the derivation can be used unchanged for spaces of higher dimension. The most complete discussion of the resulting distribution is given by Barton and David.[4] The expected length of the rth shortest interval is given by $(1/n) \sum_{i=1}^{r} [1/(n - i + 1)]$, so that the expected abundance of the rth rarest species among n species and m individuals is $(m/n) \sum_{i=1}^{r} [1/(n - i + 1)]$. This is plotted in Figure 1. Bird censuses from tropical forests[5] and many temperate regions fit this hypothesis almost perfectly. Quite frequently, however, the resulting curve is too steep; i.e., common species are too abundant, rare species too rare. These steep curves can be duplicated by considering the community as composed of two sticks of very different lengths (totaling unit length), each broken randomly into $n/2$ pieces. This is easily generalized to communities which are composed of several smaller ones, each obeying the original hypothesis. These composite communities are heterogeneous. The divergence from the ideal curve may, in fact, be regarded on this hypothesis as a measure of heterogeneity. Experimentally, for bird communities, this appears to explain most of the "steep" curves. For example, the census of Quaker Run Valley in Pennsylvania[6] yields a curve which is much too steep. When the censuses of the small pieces of the valley are plotted separately, they are in good agreement with the hypothesis. Some other populations of species, as of trees, do not seem to have this composite property and may require a different explanation.

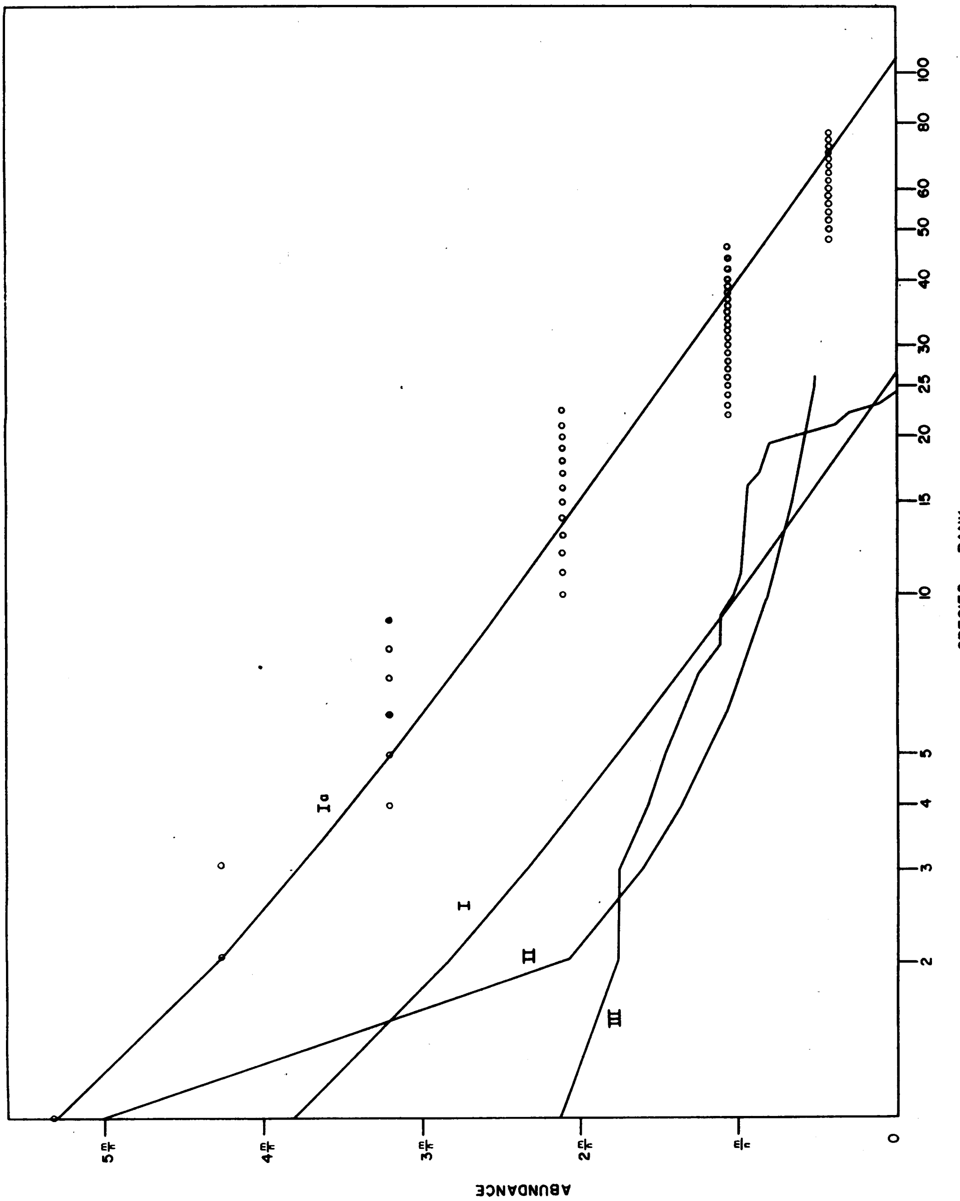

FIG. 1.—Comparison of the hypotheses. Curve *I* is the curve, on Hypothesis I, for 25 species, and curve *Ia* that, on the same hypothesis, for comparison with a census of 106 species. Curve *II* represents Hypothesis II for 25 species. Curve *III* is the mean of three sets of random tosses of 76 particles into 25 categories, illustrating Hypothesis III. The total number of individuals, is *m*; the total number of species, *n*.

Hypothesis II: Overlapping Niches.—The environment is again compared with a stick, but each species is now independent of the others. In other words, the abundance of any species is determined by the distance between a pair of points thrown at random onto the stick, *n* such pairs being thrown and the distances ranked and plotted as before. The probability density that the two points are separated by distance x is given[7] by $2 - 2x$, and, by a theorem of Mood,[8] the expected abundance of the rth rarest species is obtained by breaking the area under the curve into n equal parts by vertical lines and taking the rth shortest length along the abscissa of the resulting segments. The result is $(\sqrt{n - r} - \sqrt{n - r - 1})/\sqrt{n}$. This is plotted in Figure 1 and is seen to predict commoner common species, commoner rare species, and scarcer species of intermediate abundance than does Hypothesis I. Since rare species appear never to be commoner than is predicted by Hypothesis I, the second hypothesis seems false. Higher-dimensional models have poorer fit. This hypothesis may have some truth for species in an environment with superabundant resources.

Hypothesis III: Niches Particulate, Not Continuous.—The abundance-determining factor is accumulated as independent discrete units by the various species. That is, the species can be compared with urns into which particles (units of "abundance") are tossed on independent random throws, each urn having equal probability. This hypothesis involves an extra independent variable, namely, the number of "tosses." When this number of tosses becomes infinite, by the law of large numbers, all species become equally abundant, since the number of individuals is bounded. When plotted by the Monte Carlo method for smaller numbers of tosses, the curve seems always to drop off at the right more suddenly than that of Hypothesis I, although the left end may vary in shape. While it may be possible to adjust the variables here to fit observed census data, the predictions based upon a priori biological postulates seem to fail. Furthermore, the variance seems much greater than that observed.

Conclusion: Hypothesis I—nonoverlapping, continuous niches—is much closer to observations than the other hypotheses. Since it has no parameters other than number of individuals and number of species, it is a much simpler hypothesis than previous ones, at least for "homogeneous" communities. The precise nature of the heterogeneity giving rise to the steeper curves sometimes observed seems obscure, but it can apparently be eliminated by breaking the community into small components. The failure of Hypotheses II and III suggests that, at least as a rough approximation, niches do not overlap much and are more continuous than discrete.

The author wishes to thank G. E. Hutchinson, who suggested the problem several years ago and who has encouraged continued interest in it. A fuller discussion will be given in a later paper.

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[1] A distribution due to Motumura is discussed by K. Shinozaki and N. Urata, *Researches on Population Ecology. II* (Kyoto University, 1953); see also R. A. Fisher, A. S. Corbet, and C. B. Williams, *J. Animal Ecol.*, **12**, 42, 1943; F. W. Preston, *Ecology*, **29**, 254, 1948; M. B. Brian, *J. Animal Ecol.*, **22**, 57, 1953.

[2] G. E. Hutchinson, *Proc. Acad. Nat. Sci. Phila.*, **105**, 1, 1953; K. Shinozaki and N. Urata, *op. cit.;* R. Margalef, *La diversidad de especies en las poblaciones mixtas naturales* (Barcelona, 1956).

[3] D. Lack, *The Natural Regulation of Animal Numbers* (Oxford, 1954).

[4] D. E. Barton and F. N. David, *J. Roy. Stat. Soc., B*, **18**, 79, 1956.

[5] L. I. Davis, *Aud. Field Notes*, **9**, 425, 1955, and earlier censuses by the same author.

[6] A. A. Saunders, *N.Y. State Museum Handbook No. 16*, 1936.

[7] M. Loève, *Probability Theory* (New York: D. Van Nostrand Co., 1955).

[8] A. M. Mood, *Introduction to the Theory of Statistics* (New York: McGraw-Hill Book Inc., 1950).