Correction to One of MacArthur's Species-Abundance Formulas

Abstract. *The expected relative abundances of the commoner species in a biological population are less if the niches are overlapping than if they are nonoverlapping. MacArthur's mathematical arguments, which lead to the opposite conclusion, are incorrect.*

MacArthur (*1*, *2*) has discussed and compared certain hypotheses that might account for the relative abundance of the several species constituting a natural population of organisms. This work has aroused great interest among ecologists and has been widely quoted. According to one of his hypotheses [hypothesis II: overlapping niches (*1*)], the abundances of the species are independent of one another; each abundance is treated as proportional to the length of the segment lying between a pair of points placed at random on a line of unit length. The segment length, x, is then a random variate with frequency function $f(x) = 2 - 2x$; distribution function $F(x) = 2x - x^2$; and mean $E(x) = 1/3$. On this hypothesis the expected abundance of the rth rarest species in a population of n species is proportional to the expected value of x_r, the rth value from the bottom in a sample of n values of the variate x. MacArthur (*2*) gives this expectation as

$$[(n - r + 1)^{\frac{1}{2}} - (n - r)^{\frac{1}{2}}]n^{-\frac{1}{2}}$$

We wish to point out that this is incorrect.

The desired result may be derived as follows: The frequency function of x_r is

$$g(x_r) = \frac{n!}{(n - r)!(r - 1)!}(2x_r - x^2_r)^{r-1} \times (1 - 2x_r + x^2_r)^{n-r}(2 - 2x_r)$$

and

$$E(x_r) = \int_0^1 x_r g(x_r) dx_r$$

Putting $x_r = 1 - (z)^{\frac{1}{2}}$ we obtain

$$E(x_r) = \frac{n!}{(n - r)!(r - 1)!} \times \left\{ \int_0^1 z^{n-r}(1 - z)^{r-1}dz - \int_0^1 z^{n-r+\frac{1}{2}}(1 - z)^{r-1}dz \right\}$$

$$= 1 - \frac{n!}{(n - r)!} \times \frac{\Gamma(n - r + 3/2)}{\Gamma(n + 3/2)}$$

The values of $E(x_r)$ for $r = 1, 2, \cdots, n$ are most easily obtained from the recurrence relation

$$\frac{1 - E(x_{r+1})}{1 - E(x_r)} = \frac{n - r}{n - r + 1/2}$$

with $E(x_0) = 0$.

As a check on calculations it may be noted that

$$\sum_{r=1}^{n} E(x_r) = nE(x) = n/3$$

The formula given by MacArthur is not that for $E(x_r)$ but represents something entirely different. If the possible range of x, namely (0 to 1), is subdivided into n intervals such that the probability that a randomly chosen value of x is equally likely to fall into any of them, the rth such interval is

$$\{1 - [(n - r + 1)/n]^{\frac{1}{2}}, 1 - [(n - r)/(n)]^{\frac{1}{2}}\}.$$

The width of the interval is therefore

$$[(n - r - 1)^{\frac{1}{2}} - (n - r)^{\frac{1}{2}}]/n^{\frac{1}{2}}$$

and this is MacArthur's formula (see *3*). These widths, however, do not correspond with anything in his hypothesis.

MacArthur has compared this hypothesis with another [his hypothesis I: nonoverlapping niches (*1*)] according to which it is assumed that the abundances of the n species are dependent on one another; they are taken to be proportional to the lengths into which a unit line would be divided if $n - 1$ points were placed at random upon it. On this hypothesis the abundance of the rth rarest species is proportional to

$$\sum_{i=1}^{r} [1/(n - i + 1)]$$

In comparing these hypotheses with empirical data hypothesis I sometimes gives a very good fit (*1*, *2*), while in other cases (*1*, *2*, *4*) it underestimates the observed abundances of the common species and overestimates those of the rare species. Hypothesis II has been assumed by MacArthur (*1*) to predict greater abundances of the common species.

Using the correct formula for hypothesis II we find that this is not so; in fact it exaggerates both the defects of hypothesis I; that is, the abundances of common species are even more markedly underestimated and of rare species, more markedly overestimated. This is demonstrated in Fig. 1 which shows the predicted abundances, under both hypotheses, of the individuals in populations of 25 and 100 species, respectively. Hence, for the empirical data that have thus far been examined, hypothesis II is wholly inferior to hypothesis I.

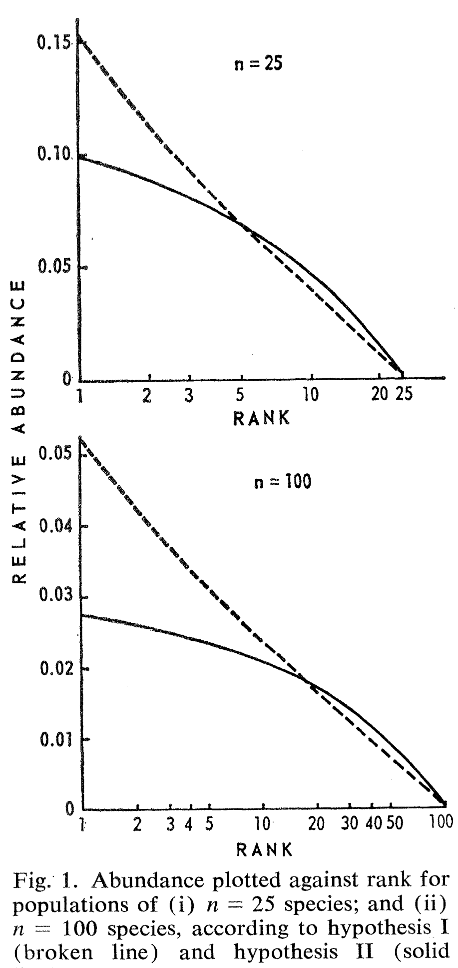

Fig. 1. Abundance plotted against rank for populations of (i) $n = 25$ species; and (ii) $n = 100$ species, according to hypothesis I (broken line) and hypothesis II (solid line).

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References and Notes

1. R. H. MacArthur, *Proc. Nat. Acad. Sci. U.S.* **43**, 293 (1957).
2. ———, *Amer. Natur.* **94**, 25 (1960).
3. The formula here quoted is that given in (*2*), and is the width of the rth interval. The formula in (*1*) is different since it actually refers to the $(r + 1)$th interval, not the rth.
4. M. Lloyd and R. J. Ghelardi, *J. Anim. Ecol.* **33**, 217 (1964).

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