Renaming the "Henneman Size Principle"

The principle that the orderly recruitment of motoneurons is based on variation in size, with the smaller neurons activated first, is credited to Harvard University physiologist Elwood Henneman, who first published a description of this theory in *Science* (Reports, 27 Dec. 1957, p. 1345). Having recently been asked to annotate an early basic science paper by the late eminent experimental neurologist Derek Denny-Brown, who was one of C. S. Sherrington's last students, we were surprised to find the "Henneman principle" clearly stated in a 1938 article Denny-Brown wrote with J. B. Pennybacker (*1*) which demonstrated that electromyography could be used to distinguish various involuntary muscle contractions such as fibrillations, fasciculations, and cramps in patients: "A particular voluntary movement appears to begin with discharge of the same motor unit. More intense contraction is secured by the addition of more and more units added in a particular sequence. This 'recruitment' of motor units into willed contraction is identical to that occurring in certain reflexes. The early motor units in normal gradual voluntary contraction are always in our experience small ones. The larger and more powerful units, each controlling many more muscle fibers, enter contraction late" (*1*, p. 324).

The article by Denny-Brown and Pennybacker was not cited in Henneman's 1957 paper, nor in later works (*2*), although it clearly should have been. Apparently, Henneman was unaware of the Denny-Brown and Pennybacker paper, because he stated in 1968, "The enormous differences in cell size found in various types of neurons in the central nervous system intrigued early histologists and provoked many speculations, but the functional significance of cell size did not become apparent until recently," (*3*). This omission is particularly perplexing given the fact that Denny-Brown and Henneman were contemporaries at Harvard. Regardless, we suggest that if an eponym is to be associated with the "size principle," the correct association should be with Denny-Brown and Pennybacker.

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References and Notes

1. D. Denny-Brown and J. B. Pennybacker, *Brain* **61**, 311 (1938).
2. E. Henneman, G. Sonjen, D. Carpenter, *J. Neurophysiol.* **28**, 581 (1965).
3. E. Henneman, in *Medical Physiology*, V. Mountcastle, Ed. (Mosby, St. Louis, MO, 1968), p. 1724.
4. We are grateful to D. Stuart and R. Enoka for discussion of this issue. Supported by PHS grant NS33782, which also supports our efforts at cataloging the Denny-Brown Research Collection [J. A. Vilensky, S. Gilman, E. Dec, *Ann. Neurol.* **60**, 247 (1994)].

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Populations as "Species-in-Waiting"?

Given the importance of populations in ecosystem function and stability, attempts to estimate the total number of populations on the planet are critical for science and public policy. However, the report "Population diversity: Its extent and extinction" (24 Oct., p. 689) by J. B. Hughes *et al.* has two problems.

First, the estimate of the number of populations per area of a sample of species should have used the arithmetic mean of populations per area, $\langle P \rangle$, not the geometric mean (*1*). Second, because the number of populations per species, *Z*, must be at least 1, *P* must negatively covary with the species' range, A, which invalidates their method. This problem can be corrected.

With the use of the data provided directly by J. B. Hughes, I calculated an estimate of Z (*2*) assuming independence between A and P of 5×10^5 and a minimum bound for <Z> assuming maximal negative correlation of 6×10^2. One should compare these values with that stated in the report, 2.2×10^2. My analyses (*3*) show that a linear relationship between accumulation (or loss) of species and area is supported when population ranges are much smaller than the area lost. Because <Z> is so large, <P> must also be large, and linearity is likely. The minimum estimate of population loss rate is 4.4×10^7 populations per year, which is 2.7 times greater than the estimate stated in the report. Even the corrected method produced results (such as values of Z less than 1 or support for the negative correlation) that suggested problems and biases in the data. An estimate of <Z> requires direct estimates for many taxa; an indirect method that relies on the variables <A> and <P> is not appropriate.

The implication of a negative correlation between A and P is a biological constraint on Z, most simply explained by populations contributing to "speciation potential" [species with more genetically isolated populations are more likely to speciate, as discussed in the accompanying Perspective "Mass extinction and evolution" (24 Oct., p. 597) by N. Myers]. Thus, populations could be understood as "species-in-waiting," which has consequences for the topology of phylogenies (*3*). Population diversity is important to evolution as well as to ecology.

The simplest explanation of the data is that isolation alone is sufficient for speciation potential, in which case the evolutionary importance of population diversity can be approximated by simple population richness. This is not the case for the ecological importance of populations. Differences between populations may be ecological or genetic, or both. If solely ecological, populations are fungible. If solely genetic, populations are ecologically fungible. Only when populations differ in both respects are the differences of ecological importance. In this ecological sense, population richness (as discussed in the report) is only the crudest measure of population diversity. Further efforts to measure the ecological contribution of population diversity should account for both ecological and genetic fungibility.

Some believe that when the extinction debt is paid, the planet will be reft of most species and that we must preserve speciation potential. Preserving population diversity would be a good place to start.

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1. R. R. Sokal and F. J. Rohlf, *Biometry: The Principles and Practice of Statistics in Biological Research* (Freeman, New York, ed. 3, 1995).
2. A more complete explanation of the estimate of <Z> is available at www.eeb.princeton.edu/ ~kaichan/letter_to_sci.html
3. K. M. A. Chan, in preparation; ——— and B. R. Moore, in preparation.

Response: Chan correctly points out that our estimate of average populations per area of a species was calculated as a geometric mean, so that, all else being equal, we underestimated the planet's population diversity in our report. We deliberately used orders of magnitude to estimate populations per area so that our bias was toward the low end, because there is more uncertainty at the higher end and because we wanted to be conservative in our estimate of global population diversity.

A separate and interesting issue that Chan raises is whether the area occupied by a species and the number of populations per area are independent. Because a species must consist of at least one population, the average populations per area of a species cannot be less than 1 divided by the species' range size. In other words, there are impossible combinations of ranges and numbers of populations per area (where both are small). This constraint is not sufficient to deduce a negative correlation between the variables.

We also caution against drawing conclusions about a correlation from our data. Although the data are suitable to make a conservative, first approximation of population diversity, there are at least two biases that could make correlations calculated from them inaccurate or spurious. First, the species range estimates are inflated to unknown degrees. Range maps delimit the extent of occurrence of a species, but often much of the area will not be "filled-in" by populations. Second, our estimate of population differentiation is a lower bound. The number of sites sampled in each study limits the estimate of populations per area.

Of course, there may actually be a negative correlation. Using information in the literature on population differentiation and range size for the same species would help resolve the covariance question if sufficient data were available. One potential bias with this method, though, is that researchers studying population differentiation may sample narrowly distributed species more intensively (at smaller geographic intervals) than species with larger ranges.

Finally, we agree with both Myers (in his Perspective) and Chan that preserving the evolutionary potential of a species is important, yet we doubt that this argument will provoke major changes in policies. On the other hand, the costs of ecosystem service losses that accompany population extinctions are measurable and increasingly appreciated (*1*). It may be that another level of biodiversity besides that of populations better captures the quality of ecosystem services, but the loss of genetically distinct populations will certainly be positively correlated with their decline. Our main concern is that species extinction rates, which are those almost exclusively cited, do not fully capture the loss of the benefits of biodiversity (*2*).

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1. G. C. Daily, Ed., *Nature's Services: Societal Dependence on Natural Ecosystems* (Island, Washington, DC, 1997).
2. J. B. Hughes, G. C. Daily, P. R. Ehrlich, in *Nature and Human Society*, P. Raven, Ed. (National Academy Press, Washington, DC, in press).

Corrections and Clarifications

■ The photograph of the large comet on page 1533 of the 5 June issue should have been credited as follows: "Julian Baum/SPL/Photo Researchers, Inc."

■ The Research News article "New role for estrogen in cancer?" by Robert F. Service (13 Mar., p. 1631) referred to work reported in *Carcinogenesis* by Tom Sutter of Johns Hopkins University and his colleagues. The work was performed by David Spink at the New York State Department of Health in Albany, Sutter, and their colleagues.

Letters to the Editor

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