

central output pattern. The possibility that a fully learned motor pattern may become independent of peripheral control is of considerable neurological interest. It will be difficult to test this conclusively in the case of chaffinch song since it would require the elimination of all relevant proprioception accompanying song production.

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References and Notes

1. S. J. McNaughton and L. L. Wolf, *Science* **167**, 131 (1970).
2. The index is of the form:

$$W = \left[\frac{\sum (y_p \cdot p^2) - (\sum y_p \cdot p)^2 / \sum y_p}{\sum y_p} \right]^{1/2}$$
 where p is the position of the community ordered on an environmental gradient from 1 to 10, y_p is the importance of the species in that community, $\sum y_p$ is the total importance of the species for all its occurrences, and W is an index of niche width of the species [Erratum, *Science* **168**, 455 (1970)].
3. B. Maguire, Jr., *Amer. Natur.* **101**, 515 (1967).
4. K. Fujii, *Syst. Zool.* **18**, 151 (1969).
5. I thank an anonymous reviewer for his comments.

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Community Ordering and Niche Width

McNaughton and Wolf (1) proposed an index of niche width based upon both the importance and position of species along one-dimensional environmental gradients. A simple example illustrates a possible danger in using this technique in certain environmental orderings.

In community ordination, the performance of such elementary operations as multiplication and addition requires that mapping numbers (for example, values for the position of a community in an environmental ordering running from 1 to 10) are isomorphic to some numerical structure which includes these operations. When communities are ranked with numerical scores and these scores are manipulated by addition and division [as is the case for the McNaughton and Wolf index (2)], then it is assumed that the ranking technique is isomorphic to arithmetic. Since community ordination is usually not isomorphic with arithmetic, different ordination techniques can produce very different indices of niche width.

For example, assume that an investigator has ordered a secondary successional gradient by ranking ten communities from 1 to 10 according to their differences and that the communities are evenly spaced along this ordination. Two hypothetical species, A and B, occur in the different communities such that A has an importance of 36 in community 1 and an importance of 1 in communities 2, 3, 4, and 5, and B has an importance of 36 in community 10 and an importance of 1 in communities 6, 7, 8, and 9. Importance can refer to such measures as biomass, density, summated home range (for animals), or coverage (for plants). With the McNaughton and Wolf index, the niche width (W) for these two species is the same under this ordination scheme ($W = .8291$). However, let us

further assume that the investigator notes that community 1 occurs after 10 years of succession, that community 10 occurs after 100 years, and that each of the other communities occurs after the respective ordinal rank of the community squared plus 10 years. Thus, by dividing the age of the community by 10 a new ordination with ranks running from 1 to 10 can be devised. With the new ordination ranks for the communities, the niche width of species B ($W = 1.1103$) is more than twice that of species A ($W = .4759$).

Since the niche width formula given by McNaughton and Wolf (1) weights the importance of the species according to their positions in the environmental gradient, one can easily see from the above example that the parameter used for ordering should not be arbitrary. Niche-width indices (W 's) based upon ordinations of community ages, differences, temperatures, altitudes, amounts of moisture, and other ecological factors can differ in both magnitude and proportion. Selecting one ordination technique from the virtually infinite set of possible techniques is almost by necessity arbitrary.

If one uses positions along a community ordination to ascertain niche width, he should be certain that his niche-width index does not require the ordination to be isomorphic to arithmetic. One such index has been used for protozoa (3). An alternative is to use individual- or population-level data in conjunction with statistical techniques currently common in numerical taxonomy, thus circumventing the need for any community ordination (4).

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In his comment on our discussion of niche width (1), Shugart correctly points out a possible difficulty in using our index (2). An important question that arises is whether environmental ranges should be subdivided arbitrarily for the purposes of niche-width calculation or according to characteristics of the organisms involved. A major conclusion of our article was that different species tend to specialize on different environmental parameters, thus making it highly unlikely that one can divide any environmental gradient symmetrically for all species. Shugart's example converts communities 1 to 5 to 1 to 3.5 and 6 to 10 to 4.6 to 10 or vice versa, depending upon which ordination is most appropriate. We assume that few ecologists would, as Shugart suggests, arbitrarily order a successional sequence by 10-year intervals since succession is obviously nonlinear on time. The problem of asymmetry in ordination has been so thoroughly discussed (3) that we felt ecologists employing our index would be aware of pitfalls of the type pointed out by Shugart. With the data available to us, more refined techniques seemed unnecessary and unwarranted. Other niche-width indices may be found preferable as more data become available for the definition of niche parameters. As we said in our introduction, "it is hoped that we will stimulate tests of the relevance of the model proposed to such carefully defined niches."

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