

gest that a possible test of the stability of an observed temporal correlation would be operant reinforcement of its dissociation (11).

On the other hand, successful dissociation does not disprove a possible functional relation between the precentral cell and muscles; it merely demonstrates the flexibility of that relation. As others have already noted, the activity of single precentral cells (1, 2) or specific motor units (12) may be quite variably related to similar force or position trajectories in successive motor responses. To what extent our EMG recordings are representative of the activity of these and synergistic muscles remains to be documented. These preliminary results suggest that a useful approach to investigating relationships between central cells and muscles is to study the activity of the same elements under as many different behavioral conditions as possible, including operant reinforcement of specific response patterns.

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3. W. T. Thach, *J. Neurophysiol.* **333**, 527 (1970).
4. Under isometric conditions integrated EMG activity has been demonstrated to be proportional to muscle tension [V. T. Inman *et al.*, *Electroencephalogr. Clin. Neurophysiol.* **4**, 187 (1952); O. C. J. Lippold, *J. Physiol.* **117**, 492 (1952); B. Bigland and O. C. J. Lippold, *ibid.* **123**, 214 (1954)].
5. A seven-channel FM tape system recorded the activity of the precentral cell and four arm muscles, the position of the elbow during passive and active movements, and a delayed trigger pulse 1 second after the occurrence of each reinforced response pattern. Playing the tape backward, we used these delayed pulses to trigger a Nuclear-Chicago Data Retrieval Computer, which computed averages of the full-wave rectified EMG activity of each muscle and time histograms of unit activity over 2-second intervals around the reinforced responses.
6. A small, brief EMG response of biceps during passive elbow extension, seen on close inspection of single trials, was probably due to the myotatic stretch reflex; this response was not large enough to appear on the averages at the same gain used for active movements.
7. Active elbow extension was accompanied by some triceps activity, but due to unequal loading, required somewhat less force than active flexion. Note that cell activity accompanying active extension was negligible compared to the response evoked by comparable rates of passive extension.
8. While voltage pulses triggered by the cell's action potentials drove the integrator voltage toward reinforcement threshold, activity of any muscles drove the integrator voltage away from threshold. The relative contribution of the EMG activity was minimized initially so that only those unit bursts accompanied by lesser amounts of EMG activity were reinforced. As the monkey emitted less EMG activity with successive unit bursts the gains on the EMG channels were gradually increased to require further EMG suppression for reinforcement.
9. After a rest period, however, the monkey still performed the active flexions and extensions of the elbow. The actual sequence of the described observations was: passive movements of elbow and wrist; isometric contraction of biceps, triceps, extensor carpi radialis, flexor carpi radialis; reinforced unit bursts; unit bursts with EMG suppression; biceps bursts with unit suppression; passive elbow movements; active elbow movements.
10. Eight of these cells were identified as pyramidal tract (PT) cells on the basis of an invariant antidromic response to stimulation of the medullary pyramids. Three cells did not respond to PT stimulation, and five cells, including the one illustrated, were studied before the pyramidal tract electrode was implanted.
11. By showing that specific components of the visual evoked response may be altered by operant reinforcement, S. S. Fox and A. P. Rudell [*J. Neurophysiol.* **33**, 548 (1970)] demonstrated that consistent correlations between neural responses in a sensory system and the evoking stimulus may be operantly dissociated.
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## Redwoods: A Population Model Debunked

In his article Bosch (1) gives license to lumber companies to harvest 50 percent of all redwoods under 800 years old, claiming that the trees would still "survive and flourish." He states that "there is a trade-off between a model so complex as to defy analysis and one so simple that no real conclusions can be drawn from it." His model for *Sequoia sempervirens* forests falls in the latter class; its deficiencies must be made known because of the possible danger that someone might take his recommendations seriously.

To begin with, the concepts of population biology employed are faulty. The redwood "belt" of central and northern California actually consists of a series of disjunct populations, each subjected to somewhat different environmental conditions. For example, in central California *Sequoia sempervirens* forms nearly pure stands in deeper canyons and ravines, but it is associated with Douglas fir (*Pseudotsuga menziesii*) in drier areas (2). That the age distribution, seed set, and survival are identical or even comparable between these two habitats is unlikely. Moreover, it is even more unlikely that these characteristics are the same for the Big Sur population as they are for populations in Humboldt County. To make a model for "the redwoods" based on data from one virgin stand in one locality is at best naive.

Furthermore, the application of a model based on data from an undisturbed stand to predict the effects of harvesting is unlikely to produce con-

clusions even vaguely approaching reality. The redwoods are often logged by clear-cutting. By no stretch of the imagination can the combination of 500 acres of virgin forest and 500 acres of clear-cut forest be expected to have the same population dynamics as a 1000-acre stand logged very carefully by selective cutting. Indeed, even a selectively cut stand should not be expected to replace its losses at rates comparable to those of an intact stand.

Finally, the model is not even appropriate to describe the dynamics of one virgin stand in Humboldt County. This model uses fecundity and survival values inappropriate even for the intact stand, much less for a logged area. For example, the assumption is made that, in each 50-year period, 18 percent of the class 2 trees (ages 200 to 800 years) will go on to class 3 (800 years and up), and that 92 percent will remain in class 2. Without even an allowance for deaths, this has accounted for 110 percent of the class 2 trees.

More crucial, the estimate that, in each 50-year period, 30 percent of the class 1 trees will graduate to class 2 is five to ten times the correct value. The numbers of individuals in each age class in a population are a function of both advancement from the previous class and deaths occurring within the new class. This is very critical, because the overstatement of survivorship is exactly what leads to the erroneous conclusions. Since no more than 10 percent of the class 1 trees are going to be between 150 and 200 years (accord-

ing to 1, table 1), this must serve as a (very conservative) upper bound to the fraction that can graduate to class 2 in the next 50 years. Moreover, the conclusion that 75 percent of class 1 trees remain in class 1 after 50 years (which is to be added to the 30 percent which went on to class 2) is based on the oversimplified argument that "since class 1 is a 200-year period, in 50 years three-fourths of the class 1 trees are still in class 1." That statement ignores both the age structure, which includes the fact that 58 percent of the class 1 trees are in the high risk 0- to 20-year age group, and the exceedingly high mortality of class 1 trees.

This confusion with the age classes has led to a plethora of errors. One cannot be sure what the result of further analysis of the data would show, but we do not agree that "meaningful conclusions may be drawn" from this model and must dismiss out of hand the conclusions regarding harvesting.

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1. C. A. Bosch, *Science* 172, 345 (1971).
2. J. H. Thomas, *Flora of the Santa Cruz Mountains of California* (Stanford Univ. Press, Stanford, Calif., 1961).

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Bosch's article has serious errors both in basic logic and execution. He tries to deduce, from empirical observations on redwoods, the long-term population dynamics of the species. However, he only uses information about the birth of trees from seeds and sprouts, and the age distribution at one point in time (his tables 1 and 2). As a matter of principle, this does not contain enough information to make a model about the behavior of age distribution with time unless one makes some additional explicit or implicit assumptions. For instance, although not explicitly stated, trees do not die before an age of 800 years in the author's model. (His diagonal elements  $b_{11}$ ,  $s_{22}$  describe only loss from an age group by growing out of it). Since one can also extract from his table 3 (reproductive characteristics), and how the author uses it, that each tree during the time from age 0 to 800 years produces 376 new trees, none of the conclusions drawn by the author

are surprising. Although this, all by itself, seems enough to invalidate the analysis that leads to the author's conclusions, there are other serious flaws in this paper. To quote two examples:

1) In the calculation of  $s_{21}$  and  $s_{32}$  on p. 347 the calculated values are in no way related to the time period the matrix is supposed to describe. To make it obvious how meaningless the chosen values for these matrix elements are, one can make the following consideration: If one uses the values of  $s_{21}$  and  $s_{32}$  given by the author, as well as his diagonal elements, and if one furthermore, for the purpose of this argument, ignores the birth of trees (that is, setting  $b_{11} = 0.75$ , and  $b_{12} = b_{13} = 0$ ), one comes to the following conclusion: Without the birth of any new trees, the total population of the three age groups grows during a period of 50 years from 2263 to 2369 trees!

2) Even if the above-mentioned shortcomings were corrected, the basic mathematical formulation contains another inconsistency. The author states correctly that elements 31 and 23 of  $M$  have to be zero. The reason given applies equally to  $M^2$ , describing a 100-year period; but the 31 and 23 elements of  $M^2$  are clearly not zero. This contradiction is a consequence of describing a time period with  $M$  that is smaller than the time interval of the age classes.

Ecological problems are currently subjects of great public and political interest. Bosch's paper will undoubtedly receive considerable attention, and may even be widely quoted. Although it is clearly worthwhile and possible to study the topic under discussion, it seems to me that publication of this particular paper can do great harm to the public, and also may well reduce the credibility of the scientific community.

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The article by Bosch (1), contains serious errors and the underlying model is conceptually incorrect.

In Bosch's article, the matrix  $M$  (1, p. 348) has  $s_{22} = 0.92$  and  $s_{32} = 0.18$  where  $s_{22}$  is the proportion of class 2 trees that stay in class 2 during a time interval of 50 years, and  $s_{32}$  is the proportion of class 2 trees that graduate to

class 3 during the 50-year interval. Since, during a 50-year period a class 2 tree either stays a class 2 tree, becomes a class 3 tree, or dies ( $s_{22} + s_{32}$ ) must be  $\leq 1$ . As given by Bosch,  $s_{22}$  and  $s_{32}$  sum to 1.10. His errors are as follows. He computes  $s_{22}$  by noting that the class 2 interval is 600 years, and therefore  $550/600 = 0.92$  of the trees in this interval stay in it every 50 years. This is based on an assumption that the age distribution of class 2 trees is uniform over the interval 200 to 800 years. A glance at Bosch's table 1 (1) shows that this is not the case. In computing  $s_{32}$ , the author notes that 82 out of 485 class 2 trees reach class 3 (see 1, table 2) and hence  $s_{32} = 82/485 = 0.18$ . The problem here is that not all those 82 trees got to be class 3 trees during one 50-year period. Hence  $s_{32}$  should be smaller than 0.18.

There is no way to make the above calculations correctly because the model is conceptually wrong. One of the essential features of predicting future population sizes by the iteration of matrices is that the population structure at time  $n + 1$  must be completely determined by the population structure at time  $n$  and not also be dependent on the structure at times previous to  $n$ . Since the length of Bosch's age classes is not the same as the time unit, this feature is not present in his formulation. For, in order to know what proportion of class 2 trees become class 3 trees during the 50-year period, the age distribution within class 2 must be known, and this in general does depend on preceding 50-year periods.

Finally, even if the model were correct conceptually, it is inappropriate to compute the parameters for 50 percent harvesting by dividing natural environment parameters by 2, as Bosch does to obtain the matrix  $M_h$  (1, p. 348). Once 50 percent harvesting starts, the forest environment changes radically and parameters must be recomputed from data obtained by observations made under the new conditions.

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## Redwoods: A Population Model Debunked

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