

other distribution function that seems appropriate. Changes in the zero class of the distribution, that is, in the probability of extinction, will be caused by these parameter values, which can then be viewed as the relative measures of resilience. It will be important to explore this technique first with a number of theoretical models so that the appropriate distributions and their behavior can be identified. It will then be quite feasible, in the field, to sample populations in defined areas, apply the appropriate distribution, and use the parameter values as measures of the degree of resilience.

## APPLICATION

The resilience and stability viewpoints of the behavior of ecological systems can yield very different approaches to the management of resources. The stability view emphasizes the equilibrium, the maintenance of a predictable world, and the harvesting of nature's excess production with as little fluctuation as possible. The resilience view emphasizes domains of attraction and the need for persistence. But extinction is not purely a random event; it results from the interaction of random events with those deterministic forces that define the shape, size, and characteristics of the domain of attraction. The very approach, therefore, that assures a stable maximum sustained yield of a renewable resource might so change these deterministic conditions that the resilience is lost or reduced so that a chance and rare event that previously could be absorbed can trigger a sudden dramatic change and loss of structural integrity of the system.

A management approach based on resilience, on the other hand, would emphasize the need to keep options open, the need to view events in a regional rather than a local context, and the need to emphasize heterogeneity. Flowing from this would be not the presumption of sufficient knowledge, but the recognition of our ignorance; not the assumption that future events are expected, but that they will be unexpected. The resilience framework can accommodate this shift of perspective, for it does not require a precise capacity to predict the future, but only a qualitative capacity to devise systems that can absorb and accommodate future events in whatever unexpected form they may take.

### Literature Cited

1. Baskerville, G. L. 1971. *The Fir-Spruce-Birch Forest and the Budworm*. Forestry Service, Canada Dept. Environ., Fredericton, N. B. Unpublished
2. Beeton, A. D. 1969. Changes in the environment and biota of the Great Lakes. *Eutrophication: Causes, Consequences, Correctives*. Washington DC: Nat. Acad. Sci.
3. Cooper, C. F. 1961. The ecology of fire. *Sci. Am.* 204:150-6, 158, 160
4. Edmondson, W. T. 1961. Changes in Lake Washington following increase in nutrient income. *Verh. Int. Ver. Limnol.* 14:167-75
5. Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen
6. Fujita, H. 1954. An interpretation of the changes in type of the population density effect upon the oviposition rate. *Ecology* 35:253-7
7. Gilbert, N., Hughes, R. D. 1971. A model of an aphid population—three adventures. *J. Anim. Ecol.* 40:525-34

8. Glendening, G. 1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. *Ecology* 33:319-28
9. Griffiths, K. J., Holling, C. S. 1969. A competition submodel for parasites and predators. *Can. Entomol.* 101:785-818
10. Hasler, A. D. 1947. Eutrophication of lakes by domestic sewage. *Ecology* 28: 383-95
11. Holling, C. S. 1961. Principles of insect predation. *Ann. Rev. Entomol.* 6:163-82
12. Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48: 1-86
13. Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulations. *Mem. Entomol. Soc. Can.* 45: 1-60
14. Holling, C. S., Ewing, S. 1971. Blind man's buff: exploring the response space generated by realistic ecological simulation models. *Proc. Int. Symp. Statist. Ecol.* New Haven, Conn.: Yale Univ. Press 2:207-29
15. Huffaker, C. D., Shea, K. P., Herman, S. S. 1963. Experimental studies on predation. Complex dispersion and levels of food in an acarine predator-prey interaction. *Hilgardia* 34:305-30
16. Hughes, R. D., Gilbert, N. 1968. A model of an aphid population—a general statement. *J. Anim. Ecol.* 40:525-34
17. Hutchinson, G. E. 1970. Ianula: an account of the history and development of the Lago di Monterosi, Latium, Italy. *Trans. Am. Phil. Soc.* 60:1-178
18. Larkin, P. A. 1971. Simulation studies of the Adams River Sockeye Salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Can.* 28:1493-1502
19. Le Cren, E. D., Kipling, C., McCormack, J. C. 1972. Windermere: effects of exploitation and eutrophication on the salmonid community. *J. Fish. Res. Bd. Can.* 29:819-32
20. Lewontin, R. C. 1969. The meaning of stability. *Diversity and Stability of Ecological Systems, Brookhaven Symp. Biol.* 22:13-24
21. Loucks, O. L. 1970. Evolution of diversity, efficiency and community stability. *Am. Zool.* 10:17-25
22. MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533-6
23. May, R. M. 1971. Stability in multi-species community models. *Math. Biosci.* 12:59-79
24. May, R. M. 1972. Limit cycles in predator-prey communities. *Science* 177: 900-2
25. May, R. M. 1972. Will a large complex system be stable? *Nature* 238:413-14
26. Minorsky, N. 1962. *Nonlinear Oscillations*. Princeton, N.J.: Van Nostrand
27. Morris, R. F. 1963. The dynamics of epidemic spruce budworm populations. *Mem. Entomol. Soc. Can.* 31:1-332
28. Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. *J. Fish. Res. Bd. Can.* 9:450-91
29. Nicholson, A. J., Bailey, V. A. 1935. The balance of animal populations—Part I. *Proc. Zool. Soc. London* 1935: 551-98
30. Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11:559-623
31. Ricker, W. E. 1963. Big effects from small causes: two examples from fish population dynamics. *J. Fish. Res. Bd. Can.* 20:257-84
32. Roff, D. A. 1973. Spatial heterogeneity and the persistence of populations. *J. Theor. Pop. Biol.* In press
33. Rosenzweig, M. L., MacArthur, R. H. 1963. Graphical representation and stability condition of predator-prey interactions. *Am. Natur.* 97:209-23
34. Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-7
35. Rosenzweig, M. L. 1972. Stability of enriched aquatic ecosystems. *Science* 175: 564-5
36. Slobodkin, L. B. 1964. The strategy of evolution. *Am. Sci.* 52:342-57
37. Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. *J. Fish. Res. Bd. Can.* 25:667-93
38. Steele, J. H. 1971. Factors controlling marine ecosystems. *The Changing Chemistry of the Oceans*, ed. D. Dryssen, D. Jaquer, 209-21. Nobel Symposium 20, New York: Wiley
39. Walters, C. J. 1971. Systems ecology: the systems approach and mathematical models in ecology. *Fundamentals of Ecology*, ed. E. P. Odum. Philadelphia: Saunders. 3rd ed.
40. Wangersky, P. J., Cunningham, W. J. 1957. Time lag in prey-predator population models. *Ecology* 38:136-9
41. Watt, K. E. F. 1968. A computer approach to analysis of data on weather, population fluctuations, and disease. *Biometeorology, 1967 Biology Colloquium*, ed. W. P. Lowry. Corvallis, Oregon: Oregon State Univ. Press

42. Watt, K. E. F. 1960. The effect of population density on fecundity in insects. *Can. Entomol.* 92:674-95
43. Wellington, W. G. 1952. Air mass climatology of Ontario north of Lake Huron and Lake Superior before outbreaks of the spruce budworm and the forest tree caterpillar. *Can. J. Zool.* 30: 114-27
44. Wellington, W. G. 1964. Qualitative changes in populations in unstable environments. *Can. Entomol.* 96:436-51
45. Wellington, W. G. 1965. The use of cloud patterns to outline areas with different climates during population studies. *Can. Entomol.* 97:617-31