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Robert MacArthur

ROBERT HELMER MACARTHUR

April 7, 1930–November 1, 1972

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“IN NOVEMBER 1972 a brief but remarkable era in the development of ecology came to a tragic, premature close with the death of Robert MacArthur at the age of 42,” wrote Martin Cody and Jared Diamond in the 1975 memorial volume, *Ecology and Evolution of Communities*.

MacArthur will be remembered as one of the founders of evolutionary ecology. It is his distinction to have brought population and community ecology within the reach of genetics. By reformulating many of the parameters of ecology, biogeography, and genetics into a common framework of fundamental theory, MacArthur—more than any other person who worked during the decisive decade of the 1960s—set the stage for the unification of population biology.

MacArthur was the youngest son of John Wood MacArthur, a professor of genetics at the University of Toronto and Marlboro College in Vermont. After completing his undergraduate education at the latter institution and taking a master's degree in mathematics at Brown University, Robert MacArthur took a Ph.D. in 1957 at Yale University, under the direction of G. Evelyn Hutchinson. In order to receive additional training in field ornithology, he spent the academic year 1957–1958 with David Lack at Oxford University. Hutchinson, Lack, and an older brother, the physicist John

W. MacArthur, Jr., were dominant influences in shaping MacArthur's unique blend of mathematical and ecological interests. From 1958 to 1965, MacArthur advanced from assistant professor to full professor at the University of Pennsylvania. He then moved to Princeton University, where he ended his career as Henry Fairfield Osborn Professor of Biology. In 1952 he married Elizabeth Bayles Whittimore, with whom he had four children (Duncan, Alan, Elizabeth, and Donald).

MacArthur began his career with three articles that revealed an unusual power and originality of approach. The first (1955) was the proposal of a way to measure community stability taken from information theory, formalizing for the first time a concept that, until then, could only be expressed through verbal description.

Soon afterward (1957) came the celebrated "broken-stick" model of the relative abundance of bird species. Although the specific hypothesis of competition embodied in the broken-stick distribution has been disputed and the approach was later dismissed as obsolete by MacArthur himself, we should not overlook the real significance of this contribution, which did indeed appear to describe what happens in nature in some as yet imperfectly studied circumstances. In three short pages, MacArthur audaciously confronted a central problem of community ecology that previous writers had scarcely formulated in words. He characterized the issue in such a way as to suggest that the deepest remaining mysteries of natural history can be reached by leaps of the imagination—so long as such efforts are disciplined by the postulational-deductive method.

Reviewers sometimes forget that the broken-stick hypothesis was only one of three frequency distributions presented in the article, each derived from a different, competing set of biological hypotheses. The method of multiple working

hypotheses was thereby introduced to this branch of ecological theory. The 1957 article set the tone for all of MacArthur's later work. Inevitably, his approach was condemned by some ecologists as oversimplification, but—right or wrong in particular applications—it energized a generation of young population biologists and transformed a large part of ecology.

MacArthur's third early contribution was an elegant analysis of niche division in warblers (1958). For this somewhat more conventional study, he received the Mercer Award of the Ecological Society of America. The warbler study revealed the real secret of MacArthur's success, his almost unique status as a mathematician-naturalist. He was a mathematician of professional grade, having been trained in the discipline before commencing the formal study of ecology. He shared the conviction of pure mathematician G. H. Hardy, whom he resembled very much in temperament and philosophy, "that a mathematician was a maker of patterns of ideas, and that beauty and seriousness were the criteria by which his patterns should be judged."

In conversation, MacArthur would say that the best science comes, to a great extent, from the creation of *de novo* and heuristic classification of natural phenomena. "Art," he enjoyed quoting Picasso, "is the lie that helps us to see the truth." But MacArthur was also a born naturalist. He watched birds with the patience and skill of a professional ornithologist, visited the tropics as often as he could, and delighted in the endless facts of natural history, which were temporarily exempted from his cartesian scalpel. The store of random information thus accumulated and the shadowy play of its many patterns were the real inspiration of his theoretical work.

The decade of the 1960s was a period of intense activity for Robert MacArthur. While serving on the faculty of the

University of Pennsylvania and then at Princeton, he began a parallel series of investigations, many in collaboration with colleagues and students, that touched on a wide range of topics around the central problem of species diversity. Part of his special genius was an ability to work closely with persons of widely varying talents and interests, to turn them into fast friends, and to bring out the best in their scientific labors. One of them, E. O. Wilson, who coauthored this memoir, recorded the following impression of him:

He was medium tall and thin, with a handsomely angular face. He met you with a level gaze supported by an ironic smile and widening of eyes. He spoke with a thin baritone voice in complete sentences and paragraphs, signaling his more important utterances by tilting his face slightly upward and swallowing. He had a calm understated manner, which in intellectuals suggests tightly reined power. Because very few intellectuals can keep their mouths shut long enough to be sure about anything, MacArthur's restraint gave his conversation an edge of finality he did not intend. In fact he was basically shy and reticent. He was not a mathematician of the first class—very few scientists are, otherwise they would become pure mathematicians—but he joined superior talent in that field with an extraordinary creative drive, decent ambition, and a love of the natural world, birds, and science, in that order.¹

MacArthur and his coworkers analyzed the evolution of the demographic parameters, established the environmental correlates of bird diversity, and formulated and partly solved the species packing problem. One of his most influential works, *The Theory of Island Biogeography* (1967), written with Wilson, created species equilibrium theory. This theory explored the many ramifications of a balance of species number on islands and on “habitat islands,” any sharply demarcated habitat—such as a lake, or even, for insects at least, a tree in

¹ E. O. Wilson, *Biophilia* (Cambridge, Massachusetts: Harvard University Press, 1984), p. 68. A further account of MacArthur's collaborative work and its impact on ecology has been given by Sharon E. Kingsland in *Modeling Nature: Episodes in the History of Population Ecology* (Chicago: University of Chicago Press, 1985).

the middle of a field. During colonization, the extinction rate in species/unit time rises as the number of species on the island rises and the immigration rate falls. When the two converge, a dynamic equilibrium is attained in which the continuing turnover varies according to the speed with which the colonization took place. The models predict an increase in species numbers with larger island area and greater proximity to the mainland. Other investigators have added many refinements to this basic theory. Experimental tests have also been performed on isolated habitats, from bottles of nutrients to full-scale islands and island habitats in the Florida Keys and the Brazilian Amazon.

The current theory of island biogeography, while still very inadequate for the largest and most complex systems, has worked well enough to become an important part of both ecology and biogeography. It is also a cornerstone of the new field of conservation biology because of its relevance to the study of the extinction process and the planning of natural reserves.

As time passed MacArthur spoke of himself increasingly as a biogeographer and made the subject the focus of his teaching at Princeton. In 1971, when he learned he had only a year or two left to live, he quickly brought the many threads of his work together in the single book, *Geographical Ecology: Patterns in the Distribution of Species*. The clarity and incisiveness of this synthesis show him at the height of his power. *Geographical Ecology* is both the reflective memoir of a senior scientist and the prospectus of a young man whose creative effort ended at the point of its steepest trajectory.

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