THE GEOGRAPHICAL ECOLOGY OF MAMMALS

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This special feature is based on a symposium that paid honor to Robert MacArthur and his legacy. MacArthur's legacy is not so much a collection of basic principles as it a way of answering important questions in ecology. MacArthur's novel concepts, new perspectives, and superb insights integrated the fields of evolutionary and geographical ecology, and paved the way for many of today's most exciting discoveries.

Key words: biodiversity, coexistence, geographical ecology, Robert MacArthur

What is a legacy in science? A legacy may mean deducing general patterns, basic principles or scientific law. Boyle will always be remembered in physics for the ideal gas law that bears his name, even though the mechanical physics of Boyle and Newton have given way to quantum mechanics and relativity. The scientific approach leading to the discovery may have been surpassed, yet the legacy remains.

A second and equally impressive legacy emerges when an individual identifies and opens new and major avenues of research. Robert MacArthur's legacy includes the community matrix of population interactions, island biogeography, and optimal foraging theory. His legacy lives in current research on foraging theory, consumer-resource dynamics, niche partitioning, island biogeography, and large scale patterns of species diversity (all represented in this special feature).

When we are drawn to the same questions and areas of inquiry that MacArthur first identified, we extend his legacy. MacArthur's science grew from drawing on principles of evolution by natural selection to study population dynamics and community structure and from using patterns in space or time to infer processes past and present. Today, this approach resides within evolutionary ecology and recognizes that populations comprise interacting individuals whose traits have been shaped by natural selection. MacArthur advocated using simple strategic models to generate testable predictions for the population- and community-level consequences of optimal behaviors. The optimization research program (sensu Mitchell and Valone, 1990) may embody most closely MacArthur's legacy.

While not all of the aforementioned lines of research originated with MacArthur, they all comprised his science. We study many of these questions today because of him. Even when most of MacArthur's original theories have been superceded, his ideas, thought processes, and approach to evolutionary ecology will ensure that his writings continue to provide excellent reading. They provide a testament for where the field of evolutionary ecology has come from and a beacon for where we might go next.

The 1960s, largely because of Robert MacArthur, were one of the most creative and euphoric decades in the history of ecology. While ecologists scrambled to catch up with MacArthur's groundbreaking field research on niche partitioning, population regulation, and species coexistence (Mac-

Arthur, 1958), works such as Hutchinson (1959) and MacArthur and Levins (1964, 1967) already had set the stage for our current understanding of the evolution and dynamics of ecological niches and habitat selection. Levins's (1962) invention of fitness sets was an early application of optimization theory to what we now call evolutionary ecology. MacArthur and Wilson's (1963, 1967) seminal work energized the field of island biogeography, and through its concepts of r- and K-selection, revolutionized studies of life-history evolution. The work of Rosenzweig and MacArthur (1963) remains seminal on predator-prey population dynamics, and it underpins most research on the stability and community consequences of predator-prey interactions. MacArthur and Pianka (1966) and Emlen (1966) launched optimal foraging theory that now dominates most investigations of feeding behaviors and its ecological consequences (what Rosenzweig has recently termed "foraging ecology").

In the early 1970s, MacArthur's laboratory continued to steer ecology toward new horizons with studies on limiting similarity and the stability of complex assemblies (May and MacArthur, 1972). In "Geographical Ecology" (MacArthur, 1972), the deservedly famous summary of MacArthur's work, we see the origins of Tilman's (1982) consumer-resource theory, concepts of species assembly, and a clear exposition on history's role in ecological structure and subsequent evolution.

We hoped to capture some of the excitement of MacArthur's era by commemorating his approach to ecology at the Seventh International Theriological Congress (ITC). We chose the ITC because it marked the 25th anniversary of the publication of "Geographical Ecology" (and of MacArthur's death) and because many of the world's leading practitioners of MacArthur's approach have based their studies on mammals. Our goal was to invite scholars whose science represents extensions and outgrowths of Robert MacArthur's approach to geographical and evolutionary ecology (dare we call ourselves 'Neo-MacArthurians'!). The work of these scientists represent new perspectives, new initiatives, new analyses, new interpretations, new insights, and new concepts. We were delighted that most accepted our invitation to join us in Acapulco, although the ITC format meant that few were able to give oral presentations.

The papers that follow were by many of our guest speakers. We wish that all speakers, and participants whose superb posters were an integral part of our symposium, could have published their contributions here. But to do so would have required an entire issue of the *Journal of Mammalogy.* We take solace in knowing that the works undoubtedly will appear soon in the world's leading ecological publications.

In the first paper, Jim Brown looks at "The Big Picture." Brown's tribute tells us how MacArthur thought and about some of the things that he considered important. The message is just as important now as it was a quarter of a century ago. Brown follows through with a brief overview of macroecology, and an update of recent developments, including species-abundance and species-area relationships, relationships with body size, and latitudinal gradients.

Bruce Patterson's contribution emphasizes, as did MacArthur, the role of history. Patterson corrects the common misconception that the ecological and evolutionary outcomes of history, reflecting probabilistic events, produce unpredictable patterns in biodiversity. It is true that ecological communities, and the local and regional diversity from which they draw their membership, carry contingent scars of history. But some species (and clades) are more prone to extinction than are others, some are better colonists, and some possess greater potential for diversification. Resulting patterns are far from random and challenge us to think about mechanisms whose temporal and spatial scales appear to exceed our capacity for experimental tests. Patterson and

Atmar's (1986) concept of nested subsets, every bit as exciting now as were many of the ideas of the 1960s, guarantees a long legacy for island biogeography in the next millenium.

Burt Kotler and Joel Brown integrate several of MacArthur's contributions by demonstrating how one can use optimal behaviors of individual foragers to test mechanisms of coexistence. They extend their invention of giving-up-densities (GUDs) of resources in artificial foraging patches to examine, among other things, relative efficiencies of competitors on different kinds of food in different habitats. Kotler and Brown demonstrate the generality of their "optimization research program" by using it to evaluate distributions and competitive coexistence of taxonomically diverse granivores in desert ecosystems. Mechanisms of coexistence, a natural outgrowth of foraging theory and the community matrix, provide a potentially vibrant tool for understanding local and regional patterns of species diversity.

Differences among GUDs correspond, at equilibrium, to the respective differences in zero-growth isoclines that MacArthur used so effectively throughout his career to help understand species coexistence. But the patina of isoclines has faded as ecologists have, with very few exceptions, been unable to obtain reliable and unbiased measures of competition in the field. One of the most significant problems is that isoclines will frequently be warped by habitat selection (Rosenzweig, 1974, 1979) and consequently depart markedly from the linear caricatures of MacArthur's theories. Doug Morris shows us how to convert the apparent shortcoming to our advantage by using theories of habitat selection to measure competitive interactions and draw isoclines. Applying the approach to mice (*Peromyscus*), voles (*Clethrionomys*), and lemmings (*Dicrostonyx* and *Lemmus*), Morris discovers new forms of coexistence and habitat use that also may help us understand the enigmatic dynamics of northern mammals. Isolegs (Rosenzweig, 1981) and Morris's isodars represent a natural marriage of the MacArthur community perspective with Fretwell and Lucas's (1970) concept of density-dependent habitat selection within a species.

In the final paper, Joel Brown caps the series with a MacArthurian treatment of the "Ecology of Fear." Brown demonstrates by theory and example how the behavior of fierce predators and their prey can stabilize their joint dynamics. Brown's approach is a significant departure from classic theory. The persistence of fierce efficient predators is a paradox within the Lotka-Volterra framework because of instabilities that arise in predator-prey dynamics when the predator's isocline lies to the left of the hump in the prey's isocline. The paradox disappears when the ability of the predator to capture prey is linked directly to the way that prey respond to the threat of predation. The ontogeny of this and its predictions was MacArthur.

Would MacArthur be surprised by our emerging abilities to predict outcomes of large-scale processes, or to use optimal behaviors of individuals to understand species coexistence and patterns of biodiversity? We hope not. We suspect that he would be pleased by the progress.

Acknowledgments

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