THE IMPACT OF ROBERT MACARTHUR ON ECOLOGY

❖4084

Stephen D. Fretwell
Division of Biology, Kansas State University, Manhattan, Kansas 66506

Every word of God is tested.

Proverbs 30:5

PROLOGUE

Scientists are responsible for truth, knowledge, wisdom, and understanding.

Truth is what is—it is the underlying reality of all existence. Knowledge is what we think we know about truth. Knowledge, however, is always an imperfect assessment, and is always subject to revision and improvement. The realization that there are discrepancies and weaknesses in knowledge is wisdom. Wisdom leads to a process, called the philosophy of science, through which knowledge is modified to better fit the truth. Philosophy means the love of wisdom, and doctors of philosophy are supposed, before all else, to be experts in wisdom. Understanding, as defined in Job (28:28), is the effort to avoid evil. We may think of understanding as what we use in order to adequately apply our wisdom and our knowledge in guiding our actions. While applied scientists seek understanding, basic scientists seek knowledge.

Dr. Robert MacArthur has made a dramatic impact on ecology because, to him, all of this was second nature.

INTRODUCTION

There are several ways of looking at what Robert MacArthur's life and work mean to ecology. First, he affected the way many other ecologists and students think and work, and so has had a broad, but indirect influence via their work. Second, his own work has directly affected the dogma and frontiers of ecology, so that discussions of many subjects are now incomplete without considering ideas that he advanced.

Third, MacArthur's lifestyle and attitude provided unique examples to guide ecologists in those dimensions of their lives that affect their work, but are usually not codified in print.

I look at these areas in order, mostly trying to recount my personal view of the history of his work and influence. My central thesis is that Robert MacArthur had a major impact on the way we do things, both as people and as ecologists, rather surpassing that which he taught us directly about the natural world. I attempt to express what I learned about his style, and his spirit of doing things, not only in what I say, but also in the way that I say it. There is a certain unfairness about this. I spent far less time with him than some, and I am less steeped in the details of his work than many. However, my personal perspectives are both mystical and broad, sufficiently so, I hope, to allow me to organize appropriately the experience I do have.

HIS EFFECT ON ECOLOGISTS

The Personal Touch

MacArthur's effect on other ecologists was both personal and indirect. My own conversations with him were (to me) significant and life-shaping. However, even when I had not met him, his published work reflected an attitude that was and is changing the field. I treat these two aspects separately, the first briefly, for fewer people have enjoyed his personal presence.

There is a mysterious connection between love and truth that almost borders on equivalence. Somehow, love is enlightening or mind brightening. MacArthur, in most of my personal encounters with him, was a very loving person. He was patient, kind, tactful, joyous, responsive, openly human. This had the effect, as J. T. Bonner put it, of making a conversation with him seem especially clear and significant, and of making one feel very bright (introductory remarks at the MacArthur Symposium, November 1973). I rarely thought so clearly as when I talked with MacArthur.

Robert clearly loved most of the things he encountered in life. He loved his family, nature, and any exchange of ideas that sought to resolve some honest and tangible confusion. He loved elegant mathematical structures, and patterns in nature. He wore his genius lightly, and shared it easily. He welcomed insights and abandoned inappropriate ideas. He honored the search for truth so deeply that digressions (small talk) were unwelcome; however, he accepted both honest confusion or a tangible discovery equally. This attracted me to visit with him, but only after I had developed some "good" questions, or could present a developed idea. The effect of all this on the careers of the scientists who knew Robert is difficult to estimate or discuss. Two things seem certain: each of us responded uniquely, becoming more ourselves. And, each of us became better at what we wanted to contribute. I believe this indirect influence on the careers of his colleagues and students was profound.

Hypothesis Testing and Fame

On a broader scale, MacArthur has helped transform American ecology by his effect on scientific attitude and methodology. I look at this transformation from the perspectives provided in part by H. R. van der Vaart and H. L. Lucas at North Carolina State University in Raleigh, who developed in me a great interest in the methods of science, especially the philosophy of science that is formally called the hypothetico-deductive (H-D) method. This method has had great success in many fields of science (physics, chemistry). But, prior to MacArthur's 1957 paper (13) on relative abundance, it had been little used in the study of natural history (about 5% of papers in *Ecology* from 1950–1956 tested predictions, compared to almost 50% nowadays). MacArthur accomplished two things with respect to furthering the use of this method: he provided acceptable examples of how one should do H-D science and he provided leadership and protection to those who wanted to work this way. As a result, many now proceed using this philosophical approach. The reader is invited to compare recent issues of *Ecology* with issues from, say, 1955, before MacArthur began publishing. Nowadays, almost half the papers contain tests of explicit or indirect predictions from theory.

I focus, in this section, on the way that MacArthur's influence was developed, rather than look too closely at his methods themselves. I take this emphasis because the methods are well known and established elsewhere (e.g. see Tricker, 37). MacArthur's main contribution here was his leadership in getting this approach accepted.

The issues were (and still, in part, are) these: Should scientists be allowed to make mistakes in print? How extensive is one's responsibility to previous literature and scholarship? The first issue is usually precipitated by so called "weak" tests of theories. These are insubstantial data contributions in response to a theoretical prediction, confirming the prediction but only raising the plausibility of the theory a modest amount. Critics claim that such "tests" mislead the naive into believing that the theory is proved. One hears that science reaches "conclusions," i.e. ideas are proved correct, and that then (and only then) should work be published. The second issue pertains to rejection of clever or interesting statements because they are not interpreted in light of most of the previously published reports that seem related.

MacArthur never really discussed these issues; he just took a position. The position he took was intellectually sound, but socially risky. He simply went ahead making and publishing predictions and weak tests of predictions. And so, like any good H-D scientist, he crawled out on a limb in print. His mathematics was sound and useful, but not so to the extent it might have been. And his data, although edifying and encouraging, were usually limited and open to a variety of interpretations. Nor did he overwhelm possible critics, or play citation politics, by including "all the right" references.

The rest of us did not have to wait until an endless debate on scholarly principles was settled before we dared to seriously consider using weak data to test loosely formulated models or to discuss a new idea without a lengthy library research. MacArthur was famous enough to silence most criticism and provided an outstanding example of success, doing just what he sensed needed doing to excite himself and his many reasonable colleagues. From a position of authority, he ignored, and so took responsibility for our ignoring, the reviewer of research who looks for and at mistakes instead of assessing progress. Thus his contribution to the people who let themselves be positively affected by him was both to point the way for a radically different perspective on how ecologists should proceed and to get famous enough so that we could follow this direction without undue harassment.

In order to understand this aspect of MacArthur's impact, we must first look at the process of publication, the fame-making machinery in the scientific community. There is a difference between the current system, by which scholarly papers are rejected and accepted, and the ordinary process of public censorship, where the expression of painful ideas is openly suppressed. But the difference varies from discipline to discipline, and from time to time, and is never as large as we would like to think. Too few reviewers of papers (for ecological journals, anyway) will advocate the acceptance of a paper they think is "wrong"; not many realize that, almost always, any innovative idea will be thought of as wrong by most other scientists. Not all wrong ideas are innovative, of course, but all truly innovative contributions must, on first reading, appear wrong. Scientific papers should never be rejected because someone is found who disagrees with the ideas presented. Quite the contrary, a truly scientific journal might reject as unnecessary any paper that failed to elicit such criticism. Too rarely, nowadays, are papers rejected for the right reasons (internal inconsistencies, unclear writing, or poor scholarship leading to redundancies); most are merely disagreed with.

MacArthur bypassed this problem, using some hints and some help from G. E. "Concluding remarks" Hutchinson. The National Academy of Sciences (NAS) once had the enlightened view that any idea that impressed one intelligent scientist (i.e. a NAS member) was worthy of publication. Many of MacArthur's significant ideas were expressed in the journal of that society (the Proceedings of the NAS) with Hutchinson's blessing. Having bypassed the normal review process, he was well on his way to becoming famous.

In appreciating MacArthur's rise to fame, we must never overlook the differences between his style of working and the style of most established ecologists. His papers began in speculation and ended in data, instead of the other way around. The math was often fuzzy or incomplete, and the data oversimplified and limited. It was easy for anyone with a lifetime commitment to the heavily descriptive or elegantly formal ecology of the times to be upset by the style. And, rejecting (I would say, censoring) one of his papers must have been easy, for there were plenty of flaws to catch. Without the Proceedings of the NAS, I wonder how far MacArthur would have gotten.

That he suffered at the hands of reviewers was obvious from several of his actions. Specifically, the formation of the Princeton Monograph Series was partially an effort to provide an outlet for the sort of research that he stimulated and encouraged. The *Journal of Theoretical Population Biology,* formed in 1970, was another effort
us from, as he put it, "all that gas." He once related to me the history of his 1967 paper with Levins (24) on limiting similarities, published in the *American Naturalist.* When the work was first submitted, it contained a mathematical mistake that completely reversed the conclusion. While the paper was being reviewed, MacArthur discovered the error, rewrote the paper and resubmitted. The editor meanwhile

had received the review of the erroneous draft. The error had not been caught, but the reviewer still recommended that the paper not be published. His grounds were that the conclusions (now known to be reversed) were intuitively obvious! The editor had no choice but to accept the corrected version, since its findings had been proved to be clearly counter-intuitive.

So, leaning on the Proceedings of the NAS and on "special" publications, MacArthur got to the top. Some called him a charlatan, others called attention to some of his mistakes. But many simply delighted in each new writing, encouraged to find such fresh air blowing in the top ranks of American ecology. With this sort of person leading, I, for one, felt more free to carry on the same way; we no longer needed to be so worried about criticism and rejection.

Some special comment should be made with reference to MacArthur's example in using the literature. We ask: how are we to use the literature? There is a great expanse between the minimal and the maximal number of references that are possible in a paper. Ecology as a whole has tended toward the maximal, but MacArthur leaned the other way, and reasonably so. The process of prediction making requires such strict logic that peripheral references merely distract. There is also the danger of high scholarship, which tries to settle issues by argument instead of by empirical testing. Few scientists realize how antithetic are scholarship and science. A Ph.D. who has been taught in a rich tradition of scholarship is tempted to use its techniques inappropriately, as an end in themselves, instead of using the literature just to clarify the process of making real-world tests. Consistent with his use of H-D science, MacArthur rarely used a broad literature base in his work.

In brief, MacArthur was a lover, in the highest sense of the term. Thus he attracted, enlightened, and stimulated many ecologists in personal exchanges. He gave his genius up, and it spread. He also accepted the intellectually sound but risky idea that science should proceed by the testing of hypotheses in print, even if it means that published mistakes may be made. He both provided examples of this idea and worked to silence or defeat the power of criticism that would prevent its wider adoption and acceptance. He became famous largely on his own authority, often bypassing the normal publication process, and thus provided leadership and support for those who agreed that H-D science was acceptable. He also freed us to use the literature in ways appropriate to predictive science.

IMPACT ON ECOLOGICAL THOUGHT

Although MacArthur's main contributions were (in my opinion) to the methodology (the wisdom, the philosophy) of science in ecology, the fact remains that what we call the body of knowledge of ecology has been significantly affected by his particular discoveries. I now look closely at these contributions. In order to do so, I first describe briefly the general classes of dogmatic ecological knowledge, and some of what may be called the frontiers of ecological knowledge. Then, armed with this overview of the field as a whole, we can look at MacArthur's explicit contributions.

The Dogma of Ecology

Some central concepts of modern ecology are:

1. *Succession, i.e. ecosystem ontogeny* So far, we think that succession proceeds because dominant life forms pollute their environment, making it unsuitable for their own continued existence, and inviting invasion from other species.
2. *Energy flow and nutrient cycling in ecosystems (ecosystem physiology)* The methods of systems analysis and the theories of multiple simultaneous causation allow us to discuss the flow of energy and nutrients through an ecosystem. This flow drives an ecosystem's dynamics and connects all of its elements. Some of the counter-intuitive consequences of environmental actions are discovered here.
3. *Community diversity* Information, opportunity, and glory are all to be found in species-rich communities. Why are some communities richer than others? They live in more structured environments and have different balances of immigration, speciation, and extinction rates. Intraspecific morphological variation plays a role, perhaps, and predation pressure.
4. *Population regulation* The population size at a particular time is the result of a sequence of previous increases and decreases in numbers. These changes in size are dependent, in turn, on changes in the growth rates. Growth rates are usually correlated with population size (density-dependence) through the effects of predation, disease, societal pressure, and contest or scramble competition. These factors may stabilize a population or drive it to extinction.
5. *Evolutionary ecology* Everything has evolved strategically to optimize fitness, and there is great beauty and wonder in coming to know "why" nature is shaped as it is.
6. *Population genetics* What do evolution and population regulation do to gene frequencies? They drive some to zero, others to "fixation," and leave still others at various intermediate levels, either by heterosis or by frequency-dependent selection.
7. *Ecological management* We want to understand ecology, to bring more desirable results from resource exploitation, and to minimize environmental impact. Also, we need to conceptualize (in the silence of God) what *is* desirable.

Now we can ask: how is the content of ecology different, having experienced Robert MacArthur's input? The dogma that appears to have been most heavily influenced by his writings is the area of community diversity or richness. The question of numbers of species, though earlier asked by Hutchinson (9), was given some substantial answers by MacArthur (17).

Second in importance, in my opinion, are MacArthur's contributions to the area of evolutionary ecology. Lack (11), with his clutch size research, had a great influence in establishing this field. But MacArthur also was an early leader in "strategic" analysis. One of his most important contributions in this area is the distinction between r versus k selection, which he was early (1961) in noticing (15). Also, his work on the evolution of generalist versus specialist feeders was seminal, although others were also contributing here.

In the field of population regulation, MacArthur mostly clarified the idea of scramble competition, a basic assumption in most of his serious diversity modeling (e.g. with Levins, 23). In the process of explaining diversity, he developed some clear statements of how competitors might reduce each other's resources. Andrewartha & Birch (1) had earlier raised questions that demanded the sorts of precise statements found in MacArthur & Levins (23).

Rosenzweig's predator-prey work, done with MacArthur (34), also made an important advance in population regulation theory by providing a needed analytical tool. It is interesting to note that Kolmogoroff (reviewed in Rescigno & Richardson, 32) had early accomplished a similar development. Kolmogoroff's work is rather more elegant, but was obscurely published. Still, there is a simplicity about the Rosenzweig-MacArthur formulation that makes it one of the most cited textbook graphs, one of the most explicitly tested predator-prey theories (Maley, 28), and a most useful theory for extending our grasp of new problems (e.g. see Rosenzweig, 33).

In ecosystem theory, only one idea of MacArthur's is much noticed: his 1955 paper (12) showing that diversity in an ecosystem enhances its intrinsic stability. This, it seems, was what everyone wanted to hear in the then-budding ecology movement, so MacArthur's "proof" was grabbed up. May (29) recently found some potential exceptions to this dogma. Still, this report by MacArthur is one of the most cited of all his papers. It appears, incidently, that MacArthur's early interest in diversity hinged around the relationship between diversity and stability (Hutchinson, 9; MacArthur & MacArthur, 25).

MacArthur only touched on community succession and his work may not significantly influence conventional treatment of that subject. He explored, with Wilson (27), the properties of good island colonizers, mentioning that the theories that were developing should apply to successional communities. He noticed that bird species of secondary mainland habitats, being the best colonizers, were most likely to appear on islands. He and Horn (8) showed that if there were a trade-off between competitive ability and colonizing ability, a so-called harlequin environment could be stably subdivided by two similar species, one sedentary and one mobile. In time, the sedentary species replaces the mobile, in a given habitat.

MacArthur said very little about energy flow and nutrient cycling. In his book with Connell (22, p. 179) there is a review of the subject with a clever and concise formulation relating relative biomasses in the links of a food chain to body sizes and turnover rates. This little model is an excellent one for dealing with inverted food chains, but is both little noticed and seldom used.

In population genetics, MacArthur made a couple of rather esoteric contributions (16; and with Wilson, 27) that are generally overlooked nowadays, although they foreshadowed much current research having to do with ecotypic selection and frequency-dependent selection. It is hard to pinpoint the specific impact on the field that these models made; yet one mention of them was in MacArthur & Wilson's widely cited book. The failure of many workers in this field (myself included) to cite this work may have been due to our inability to understand it fully, at least until after we had "rediscovered" similar ideas.

Generally, those of MacArthur's contributions that have appeared in textbooks concern diversity, stability, community dynamics, and *r* versus *k* selection. His work in nearly all other fields of ecology has been or should be helpful (or even seminal) in more complete treatments; yet his impact in these areas will probably be less recognized. However, MacArthur typically is one of the most cited authors in current ecology texts; usually only the author of a given text has more listings in the bibliography than MacArthur.

Frontiers of Ecology

It remains, then, to discuss MacArthur's "trend-setting" activities: his effect on "new" ideas not yet part of the dogma of ecology.

Some frontiers of ecological research today are:

(*a*) density-dependent versus density-independent factors in the evolution and regulation of populations;
(*b*) the nature of competition: social intolerance versus resource exploitation versus altruistic management as competitive mechanisms;
(*c*) species diversity: invadable versus "packed" communities; the shapes of extinction, immigration, and speciation curves;
(*d*) generalist versus specialist feeding strategies—who does which and why?;
(*e*) the response of ecosystems and populations to variable environments, including those that are seasonally (or predictably) variable and those that vary stochastically;
(*f*) genetic and morphologic variability *within* populations: ecotypic versus archetypic selection;
(*g*) models for population prediction and management;
(*h*) the structure of ecosystems—complex systems models for the prediction of counter-intuitive effects;
(*i*) material flux through ecosystems, limiting energy transfers;
(*j*) the evolution of reproductive rates and other life history parameters.

(May I be forgiven for those I have overlooked.)

MacArthur has had three sorts of effects on developing ideas in ecology: 1. He has provided didactic development and tests of certain ideas that were generally accepted by those who understood them, but were not widely understood. 2. He has asked questions that had not been asked before, and stimulated other ecologists to think about them. 3. He has discovered new patterns and relationships in nature that probably will become part of the dogma.

First, let us consider density-dependent versus density-independent sorts of population dynamics. This area received a good deal of attention from the nearly simultaneous publication of books in 1954 by Lack and Andrewartha & Birch, and is still painfully polarized. MacArthur first entered it by "showing" that warblers were regulated in a density-dependent fashion (14). He used a clever statistical analysis of runs of population increases and decreases to show that an increase was usually followed by a decrease, instead of another increase. This analysis foreshadowed Tanner's (36) extensive correlational analysis and all the statistical debate that has followed. For all its weaknesses, this sort of analysis of population fluctuations promises to unravel the way density-dependent and density-independent effects cooperate in regulating numbers, as is evidenced by the excellent analysis by Varley, Gradwell & Hassell (38).

MacArthur had very little to say about mechanisms of competition (21, pp. 25–28). As noted above for competition dogma, MacArthur clarified resource exploitation (scramble) competition theory, but he really said very little to contrast this theory with the alternatives. The major contributors here were Nicholson (30) and Wynne-Edwards (39). The work of the latter author is vastly underappreciated and misunderstood, due, I think, to some inappropriate attacks by evolutionary ecologists. MacArthur [with Connell (22, p. 140); see first quote in Appendix] was early in encouraging a temperate attitude towards Wynne-Edward's ideas.

Most of the people now working on species diversity are working on concepts that were first stated by MacArthur and his colleagues. Perhaps ten percent of the papers in recent issues of the Journal of *Ecology* deal with this subject. MacArthur's impact here is so conspicuous that it requires little analysis.

The problem of specialist and generalist feeding strategies was first raised by MacArthur & MacArthur (25). MacArthur & Pianka (26) then provided an early answer to that question, but others (e.g. Emlen, 5) reached similar conclusions at about the same time. Tests have been slow in coming, and few patterns have been discovered.

The problem of variable (both seasonal and stochastic) environments, which is another question of population regulation, was raised by Lack (11), who suggested that post-breeding survival (i.e. periods of negative population growth rates) regulated populations. Andrewartha & Birch (1) made a similar point, a bit less explicitly. However, MacArthur's widely imitated early study on warblers (14) emphasized coexistence and competition (i.e. regulation) in the breeding season (positive population growth rates). This emphasis was not conceptual, however, for MacArthur expended considerable energy studying wintering warblers as well as breeding ones. The winter studies were simply less productive and so received less attention. However, many of those following this study have worked only in the breeding season, assuming that populations are regulated or limited then. Hespenheide (7) has shown that these studies need not assume strict breeding limitation, but do require some breeding regulation. Few studies to date support even that assumption, except perhaps for nest sites (Fretwell, 3; Krebs, 10), which, however, are not usually emphasized in competition studies (but see Hespenheide, 6). Thus MacArthur somewhat inadvertently has led workers into making an a priori unlikely assumption, which has made an issue of seasonal regulation.

I have already touched on MacArthur's contributions to the archetypic versus ecotypic selection problem (reviewed by Rothstein, 35). I repeat it here, since population genetics arrives as theoretical dogma before it becomes an empirical frontier. MacArthur personally contributed to my report on this latter area (2, as cited), and even predicted some of the sorts of tests since confirmed by Rothstein (Fretwell, 4). (He successfully predicted that pygmy nuthatches would be less variable than brown-headed nuthatches, since the former have more competitors.)

MacArthur contributed almost nothing to the area of ecologic management. I believe he rather disapproved of using ecology theory for management, impact statements, and the like. He seemed to feel that nature enriched the naturalist, and hence the world, in spiritual ways, so that there was a greater harvest of peace and truth than of lumber in a forest.

I daresay, also, that few of the current systems modelers, including those working on nutrient cycling, are using MacArthurian theory or philosophy. In this area of research, descriptive thoroughness is optimized at the sacrifice, perhaps, of elegance, simplicity, and interest.

Research on life history evolution, although not begun by MacArthur, certainly was boosted substantially by his 1961 paper, "Population effects of natural selection," (15) and by his monograph with Wilson (27). This work developed the concepts of r and k selection. This distinction (actually it is a continuous dimension, see Pianka, 31) promises to play a significant role in most areas of ecology, since it is tied simultaneously to environmental stability, predator-prey interactions, and succession.

MISCELLANEOUS IMPACTS

My intent in this section is to present some things that I learned (or am learning) from the way MacArthur did things. I suspect that his spirit and/or example is affecting others similarly. Discussing these issues, all a bit subtle or personal, should accomplish one objective: by openly describing the example provided, it will be easier for others to follow. As many ecologists as possible should have access to these details, lest MacArthur's disciples unknowingly leave out something essential in developing a predictive ecology.

Leadership and Reform

MacArthur's position towards "the establishment," i.e. authority, and leadership in science was enlightening. He clearly trusted and respected the system and was hopeful that, with proper leadership, it could be made more effective in accomplishing science. Although he did things differently, he did try to move so that the system was not offended. So, he succeeded in having an impact. Insofar as optimism can be cultivated or passed on, his effect on what might be called "revolution" in ecological method was therefore a temperate one. I do not believe he thought much about this; yet I wonder at his brilliance in balancing innovation with conservatism.

Being Wrong or Awkward in Print

Conventionally, mistakes in print are regarded as disasters. Yet MacArthur made several published mistakes (18). He offended in many ways the sanctity of print, and was caught at it. Some of his best works are flawed in terms of style and symbolic or typographical error. We are inclined to forgive this, in deference to his great genius. I elevate it to the place of a lesson about misplaced emphasis. In all research reporting, over-attention to detail can obscure the spirit of curiosity and wonder upon which good basic research depends. MacArthur's work survived all these errors, which does not justify them exactly, but makes inexcusable the report that is deadly dull but otherwise correct. Better to spend (as MacArthur did) one's time and energy being interesting; if something has to be sacrificed, let it be the exactness. Clearly, one can contribute as much with such an approach.

How to Recognize a "Good" Ecologist

MacArthur thought highly of some of those ecologists that he knew, and he was concerned about the problem of identifying good ecologists. In a commentary (20), he emphasized the importance of field work. He later told G. Lark (personal communication) that a good test for an ecologist was to walk with the person through a field and see how many questions he asked. This, presumably, measures curiosity; love of and attention to nature. I doubt that this test should stand alone; but I do not doubt that the things it measures are generally neglected.

Open-Mindedness before Skepticism

The characteristics of a scientist are open-mindedness, empiricism, and skepticism. MacArthur advocated that these be in balance, re-emphasizing the importance of open-mindedness during a time when skepticism was dominant. However, he also put them in the above order, putting skepticism last, and only as a response after data had been gathered to test an idea (empiricism). I believe that his attitude towards these traits has helped restore, even in these competitive days, a very sweet mood of tolerance, widespread "wait and see" attitude. There was a bristling arrogance that once stalked meetings of ecologists with cries of "unwarranted speculation!" and "but what about. . .?" Such questions are now confined to private conversations among those coming in from the greatest distance.

Love Your Wife and Family First

Maybe I'm the only one affected by this example that MacArthur set, but it was the first and hardest thing he taught me. When I knew him (in 1968–1969) he was above all a family man; he spent much time at home, and he surely loved his wife and placed her first. This is, admittedly, a personal question, yet, it is one that must pervade every scientist's life: to marry or not, and, if married, how much of one's time that could be spent in research should be spent instead with one's family. And where does one's mind rest? I had the distinct impression that MacArthur worked on ecology mostly when his family got tired of his hanging around. I suspect that he had the freedom to do what he did for ecology, going against all convention, because it was all secondary to him anyway; or maybe he just spent so much time with his family that he never really had time to learn the conventions! Yet, even so, look at what he accomplished!

One can argue (I often do) that it was his genius that allowed him to so lightly toss off pieces of research and so to be home more. However, I am dissatisfied with this interpretation, which, in any case, gets me nowhere. Just as plausibly and much more usefully, I now believe that MacArthur's personal priorities (family before profession) were part of what made him so successful. For, in inspecting his work, the freedom is more conspicuous and more unique than the brilliance; the freedom, then, is the major contribution. And such freedom very cogently follows from lowering research and publication into a second (or lower) place.

The human and philosophical contributions of an eminent scientist's life are usually reserved for biographies, where their influence on other scientists is, at best, tardy. MacArthur's contributions here may be critical to a successful continuation of his style of ecology, and the science cannot move too quickly into a more effective and engaging method. So I discuss the attitudes and personal factors that I think were a part of his accomplishing what he did. I emphasize his respect for the "system," his emphasis on curiosity and open-mindedness, and his love of family, with the hope that other scientists seeking a worthy example will have a better view of the man.

SUMMARY

I have suggested that MacArthur's major impact was in methodology and spirit; he taught us how to be basic scientists, what to value, what to do. But he also contributed grandly to our science in increasing significantly our grasp of diversity and stability and community structure, with lesser impacts in most other areas of ecology.

Before he died in 1972, his work had drifted into some rather sophisticated mathematical structures. But his last book (21) written, in part, to summarize his life's work, proved that his heart was still in nature, and that both theory and data are merely tools to improve understanding of that on which the eye fell of its own accord.

APPENDIX

Some quotes of interest:

In a section titled *Group Selection:* "Perhaps the biggest unsolved problem of natural selection—the problem that more than any other makes evolutionists get angry and say something irrational—is concerned with whether . . . (individual selection) . . . is the only one possible" (in MacArthur & Connell, 22). "Much of modern ecology has to be done in the field, and should be taught there" (20). ". . . by no means all ecologists will favor such field stations and, as long as they aren't made to feel inferior by staying behind, will keep ecology one of the components of the community of scholars" (20).

"It is the purpose of this note to raise a problem, and to show by means of an example how interesting that problem is" (19).

Literature Cited

1. Andrewartha, H. G., Birch, L. C. 1954. *The Distribution and Abundance of Animals.* Chicago: Univ. Chicago Press. 782 pp.
2. Fretwell, S. D. 1969. Ecotypic variation in the non-breeding season in migratory populations: a study of tarsal length in some fringillidae. *Evolution* 23:406 20
3. Fretwell, S. D. 1972. *Populations in a Seasonal Environment.* Princeton, NJ: Princeton Univ. Press. 217 pp.
4. Fretwell, S. D. 1973. *Ecotypic versus archetypic selection, and the niche breadth of species.* Presented at the MacArthur Memorial Symposium, November 1973
5. Emlen, J. M. 1966. The role of time and energy in food preference. *Am. Nat.* 100:611–17
6. Hespenheide, H. A. 1964. Competition and the genus *Tyrannus. Wilson Bull.* 76:265–81
7. Hespenheide, H. A. 1973. Ecological inferences from morphological data. *Ann. Rev. Ecol. Syst.* 4:213–29
8. Horn, H. S., MacArthur, R. H. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749–52
9. Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many

kinds of animals? *Am. Nat.* 93:145–59
10. Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. *Ecology* 52:1–22
11. Lack, D. 1954. *The Natural Regulation of Animal Numbers.* Oxford: Clarendon. 343 pp.
12. MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533–36
13. MacArthur, R. H. 1957. On the relative abundance of bird species. *Proc. Nat. Acad. Sci. USA* 43:293–95
14. MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599–619
15. MacArthur, R. H. 1961. Population effects of natural selection. *Am. Nat.* 95:195–99
16. MacArthur, R. H. 1962. Some generalized theorems of natural selection. *Proc. Nat. Acad. Sci. USA* 48:1893–97
17. MacArthur, R. H. 1965. Patterns of species diversity. *Biol. Rev.* 40:510–33
18. MacArthur, R. H. 1966. Note on Mrs. Pielou's comments. *Ecology* 47:1074
19. MacArthur, R. H. 1968. Selection for life tables in periodic environments. *Am. Nat.* 102:381–83
20. MacArthur, R. H. 1969. Commentary: The ecologists' telescope. *Ecology* 50(3):352
21. MacArthur, R. H. 1972. *Geographical Ecology.* New York: Harper and Row. 269 pp.
22. MacArthur, R. H., Connell, J. 1966. *The Biology of Populations.* New York: Wiley. 200 pp.
23. MacArthur, R. H., Levins, R. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proc. Nat. Acad. Sci. USA* 51:1207–10
24. MacArthur, R. H., Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101:377–85
25. MacArthur, R. H., MacArthur, J. W. 1961. On bird species diversity. *Ecology* 42:594–98
26. MacArthur, R. H., Pianka, E. R. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603–9
27. MacArthur, R. H., Wilson, E. O. 1967. *The Theory of Island Biogeography.* Princeton, NJ: Princeton Univ. Press. 203 pp.
28. Maley, E. 1967. A laboratory study of the interaction between the predatory rotifer *Asplanchna* and *Paramecium. Ecology* 50:59–73
29. May, R. M. 1971. Stability in multispecies community models. *Math. Biosci.* 12:59–79
30. Nicholson, A. J. 1954. An outline of the dynamics of animal populations. *Aust. J. Zool.* 2:9–65
31. Pianka, E. R. 1974. *Evolutionary Ecology.* New York: Harper & Row. 350 pp.
32. Rescigno, A., Richardson, I. W. 1967. The struggle for life: I. Two species. *Bull. Math. Biophys.* 29:377–88
33. Rosenzweig, M. L. 1971. The paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–87
34. Rosenzweig, M. L., MacArthur, R. H. 1963. Graphical representation and stability conditions of predator prey interactions. *Am. Nat.* 97:209–23
35. Rothstein, S. I. 1973. The niche variation model—is it valid? *Am. Nat.* 107:598–620
36. Tanner, J. T. 1966. Effects of population density on growth rates of animal populations. *Ecology* 47:733–45
37. Tricker, R. A. R. 1965. *The Assessment of Scientific Speculation.* New York: American Elsevier. 200 pp.
38. Varley, G. C., Gradwell, G. R., Hassell, M. P. 1973. *Insect Population Ecology.* Oxford: Blackwell. 212 pp.
39. Wynne-Edwards, V. C. 1962. *Animal Dispersion in Relation to Social Behavior.* New York: Hafner. 653 pp.