

The Paper Trail

“The Paper Trail” contains essays on classic papers by an ecologist who has a particular interest in that subdiscipline of ecology. The essay will both identify a paper or papers that were important in catalyzing future developments, at least to the writer of the essay, and will also be a personal viewpoint. The editor hopes that other ecologists will be encouraged to submit their own appreciations and analyses of papers that have had a special significance for them.

The second article in this new series is Michael Kaspari’s study of R. H. MacArthur’s classic paper on the community ecology of Northeastern warblers. The original paper can be viewed at: MacArthur, R. H. 1958. Population ecology of some warblers of Northeastern coniferous forests. *Ecology* 39:599–619. Stable URL: <http://links.jstor.org/>

Knowing Your Warblers: Thoughts on the 50th Anniversary of MacArthur (1958)

This past spring I was on sabbatical in New England in time to enjoy the spring migration. As I was getting my first good look at a Bay-breasted Warbler, it occurred to me that I was on Robert MacArthur’s old stomping grounds for the 50th anniversary of MacArthur (1958), henceforth “the warbler paper.” This is a paper I find myself re-reading on a regular basis.

My choice of MacArthur’s warbler paper for repeated study might seem to ignore some low-hanging fruit (e.g., optimal foraging (MacArthur and Pianka 1966), species abundance distributions (MacArthur 1957), diversity–stability relations (MacArthur 1955), diversity and habitat structure (MacArthur et al. 1962), or island biogeography (MacArthur and Wilson 1967)). The proximate reason I do so is that the warbler paper is a staple of my community ecology course and my lectures in undergraduate ecology. The ultimate reason is that it is laden with well-articulated ideas, a great back-story, and object lessons on how some habits and practices stick, and others transform or disappear. If one wants to start a discussion on the nature of ecological science, publication, and communication, the warbler paper bears rereading. Here I touch upon a few of the lessons that keep me going back.

History

MacArthur already had a degree in mathematics when he went searching for a Ph.D institution. An avid birder, he applied to the University of Illinois to work with the ornithologist Charles Kendeigh, whose descriptions of bird communities in northern forests (Kendeigh 1945, 1947) would later be mined in the warbler paper. In a committee decision that likely shaped the future of ecology, Illinois rejected his application, ostensibly because he was trained as a mathematician, not a biologist (T. Martin, *personal communication*). Yale did not, and the relationship between G. E. Hutchinson and R. H. MacArthur was joined.

MacArthur was drafted soon after to serve two years in the Army at Arizona's Fort Huachuca. Ramsey Canyon, where he lived with his family, is not a bad place for an ornithologist to spend two years. After his requisite 40 hours a week calculating cannon trajectories was up, MacArthur would bird, read, and work on manuscripts, including his first (!), an exploration of the relationship between food web stability and species diversity (MacArthur 1955). MacArthur also spent time planning his thesis research. He would later tell colleagues that, upon returning to New England, he had the basic story of warbler foraging ecology after two weeks in the field. All told, the field work spanned the summers of 1956 and 1957, and an intervening winter trip to Costa Rica.

The paper, "Population ecology of some warblers of Northeastern coniferous forests," spans some 20 dense pages with an impossibly tiny font. In later years, MacArthur would puzzle as to why it received so much attention relative to what he thought was much stronger work. The answer may lie in the fact that it was a paper drenched in natural history—giving him considerable street cred among muddy boot ecologists, many of whom, if not outright ornithologists, knew their birds. Moreover, MacArthur motivated, quantified, and organized the data in a compelling and soon to be characteristic fashion based on the hypothetico deductive method. The warbler paper won the Mercer award "for an outstanding ecological research paper published within the past two years by a younger researcher."

I first encountered the warbler paper in 1979 as a freshman in Tony Joern's Intro Bio lectures at the University of Nebraska. Having discovered birding in high school, the notion that someone could do something useful while staring at birds appealed. Joern's summary first lured me into the cool dark canyons of the science library. I photocopied the paper and read it later that day. I was pleased, when researching this essay, to find that Henry Horn had had a similar reaction to mine, under similar circumstances, 20 years before.

I was immediately seduced into ecology by MacArthur's elegant combination of conceptual analysis, inventive data-gathering, and reveling in the details of outright natural history" (Pianka and Horn 2005).

The Paper

The warbler paper codified a particular style: start with a big question, propose hypotheses, choose the ideal system to answer the question, unpack the theory to generate testable predictions, and collect a variety of types of data to evaluate those predictions. Unlike most Mercer Award-winning papers today, it was not experimental. It more resembled Darwin's "one long argument": some provocative ideas supported by a variety of evidence.

MacArthur's previous papers (MacArthur 1955, 1957) had explored patterns of species diversity and their consequences. The warbler paper continued the run, testing mechanisms underlying the maintenance of local diversity. In a one-paragraph Introduction, MacArthur succinctly lays out the problem: five species of *Dendroica* coexist in mature boreal forest, so similar in form and food that leading ornithologists note they may be an

...interesting exception to the general rule that species either are limited by different factors or differences in habitat or range.

The warbler paper focused on a small, evolutionarily bounded community: five *Dendroica* flitting around New England's 20-m fir and spruce trees (Fig. 1). These species would already be expected to be similar through common descent. What better way to test what was already a popular conjecture in ecology, Gause's principle, than by attacking an apparent exception? The warbler paper was thus a great example of using a system appropriate to your question, in this case, a hyperdiverse group that, on the face of it, looked like Christmas ornaments differing only in their paint job (Fig. 1). When I was a graduate student in the 1980s, this was a powerful meme. We didn't study organisms. We studied *questions* and then searched for an appropriate system. (Nowadays, there is a growing appreciation for taxon-based research careers [Wilson 1989]. An intimate knowledge of a taxon allows one to ask a *variety* of questions, at different levels of organization. Of course, MacArthur also really knew his warblers.)

What follows is a 2-page section titled "Logical Nature of Population Control." Paragraph by paragraph, MacArthur builds upon one central theme: that species diversity as a community property emerges from the life history of that community's populations. The first paragraphs summarize, with avian examples, density-independent and density-dependent regulation. The next paragraph is a tour de



Fig. 1. The five warblers from MacArthur (1958). Clockwise from bottom, Bay-Breasted (*Dendroica castanea*), Myrtle (*D. coronata*), Cape May (*D. tigrina*), Blackburnian (*D. fusca*), and Black-throated Green (*D. virens*) Warblers.

force. It starts by saying the mere documentation of species differences in support of Gause's principle is not enough.

...such differences, if found, are then cited as the reason competition is not eliminating all but one of the species. Unfortunately, however, differences in food and space requirements are neither always necessary nor always sufficient to prevent competition and permit coexistence. Actually, to permit coexistence it seems necessary that each species, when very abundant, should inhibit its own further increase more than it inhibits the other's.

This text is ironic, of course. Years later, much of the criticism heaped upon the warbler paper and its many copycat studies was that they did precisely that: document differences as consistent with Gause. But this is where MacArthur the mathematician drew the line; science strives for evidence both necessary and sufficient. Those three words endure today as perhaps the best criteria for identifying great science. Drawing on the Lotka Volterra model, MacArthur gets to the crux of his thesis: that understanding the relative power of intra and interspecific density dependence, as modulated by differences in resource and space use, is key to placing Gause on firm footing as a scientific hypothesis.

But there is another jewel here. Hiding in plain sight (page 600) is a prescient paragraph submitted as an alternative hypothesis.

As has often been pointed out...birds may emigrate or disperse from the most suitable areas where reproduction is successful into marginal habitats. Consider such a species which will be called A. Let B be a species that lives only in the area that is marginal for species A. Now, even if in an unlimited environment of this type, species B would eliminate species A by competition, in the heterogeneous environment species B may be eliminated from its own preferred habitat. For, if there is sufficient dispersal by species A, it may maintain, partly by immigration, such a high population in the marginal habitat that species B is forced to decrease. This process is probably very important in considering the environmental distributions of birds and implies that small areas of habitat typical for one species may not contain that species.

MacArthur lays out the theory of Sources and Sinks 23 years before Pulliam and Danielson (1991), including its implications for community ecology! In the spirit of strong inference, a second viable hypothesis is fleshed out, and revisited late in the paper.

MacArthur concludes with a discussion of methodology. While acknowledging that experiments manipulating proposed limiting factors are the ideal (and feasible with, say, nest boxes), manipulating

food supply for an insectivorous bird in a 20 m spruce tree is difficult. Instead, in a passage that, one suspects, has been read aloud with some eye-rolling in graduate seminars worldwide

The most feasible approach...is to compare the bird populations in two regions which differ in the abundance of the factor to be considered...The present study of the factors limiting warblers was...slightly less accurate than the first method, but permits studying more factors and requires less time.

We then move on to the data. Consistent with the preceding section, MacArthur focuses first on evidence for intraspecific density dependence. He finds published local censuses for three of his target species, Black-throated Green, Bay-breasted, and Blackburnian, and proposes that patterns of increases and decreases should be staggered if the populations are regulated by negative density dependence. Sure enough, populations of each tend to decrease following an increase, and vice versa. He then presents stronger evidence, in his view, for the two remaining warblers. Both Cape May and Myrtle Warblers increase during spruce budworm outbreaks, suggesting both the phenomenon of density dependence, and the likely limiting factor.

The next section, entitled “General Ecology” spans 10 pages. MacArthur musters a variety of evidence of variable quality from two summers of fieldwork, a winter trip to Costa Rica, and a search of the literature, museum, and agricultural records. All through this compendium is a dedicated effort to put numbers on the field observations compiled by his ornithological forebears. The famous “Christmas tree” diagrams that wound up in so many textbooks divided trees into height and branch categories and tallied the number of seconds and individual observations of each species in the 16 possible zones. When folks would later gripe that these trees were generated from a total of 27 to 80 minutes of continuous observation, MacArthur would reply that the data on the number of observations told largely the same story. Foraging behaviors were quantified (intervals between flights, components of motion—radial, tangential, vertical) and compared. Differences were calculated with simple statistics, and conclusions buttressed with previous descriptive studies. MacArthur took calipers to bird skins and combed diet records. He quantified nest height distribution (a topic to be taken up later, in an elegant series of experiments, by Tom Martin [Martin 1996]), nesting dates, clutch size. A trip to wintering grounds in Costa Rica was largely a bust; the trees were not comparable, and he only found one of his target species. He nonetheless compiled his observations ($n = 1\text{--}200$) of nine species to make the case that their feeding activities mirrored those on the breeding grounds (and thus were genetically determined and not plastic).

In a short discussion, MacArthur concludes that the mechanisms keeping the five species in these forests could result from five populations limited by differing resources, the same resources in different habitats, or the same resources at different times. The act of quantifying many of the niche parameters emphasized the “statistical” nature of their differences: species likely impacted each other to some

degree through diet overlap. Three *Dendroica*, the Blackburnian, Black-throated Green, and Bay-breasted, showed negative density dependence within local habitats, and reduced diet overlap through differences in where and how they fed. These were candidates for niche differentiation. The Cape May, a rarer and less predictable member of the community, could recruit to and ramp up reproduction during periodic budworm outbreaks. Its persistence in off-years, he conjectured, resulted from this periodic subsidy. (Between outbreaks, Cape May Warblers were in the process of being competitively excluded.) The notion that a warbler was a weedy “fugitive” species no doubt pleased Hutchinson, whose note, “Copepodology for the ornithologist” introduced the term (Hutchinson 1951).

The final warbler, the Myrtle, foraged from the forest floor to the treetops, had large territories, a broad range, and low abundance. It failed to clearly fit either of the two hypotheses. It was, MacArthur argued, a “marginal species.” This species was indeed marginalized—briefly mentioned in a short paragraph tucked between the others, with no clear logic for how such a tactic could persist. (The fact that the Myrtle invested in energetically expensive foraging behavior suggests that it may have been a “skimmer,” finding and harvesting dense patches of insects before the slower, more methodical, and energy-conserving “gleaning” species (Brown 1989). If so, Myrtles should on average leave enough food behind to still be profitable for the others, and have a basal higher metabolic rate than its competitors.)

The paper ends on a confident note.

There are differences of feeding position, behavior, and nesting date which reduce competition. These, combined with slight differences in habitat preferences and perhaps a tendency for territoriality to have a stronger regulating effect upon the same species than upon others, permit the coexistence of species.

None of the evidence compiled by MacArthur is necessary and sufficient to show any warbler species can increase when competitors are near carrying capacity. Instead, the paper reads more like a lawyerly compendium of circumstantial evidence, much of it quantitative and innovative, but hardly a “slam dunk.” In a posthumous homage, Steven Fretwell (1975) would say

[Weak tests] are insubstantial data contributions in response to a theoretical prediction, confirming the prediction but only raising the plausibility of the theory a modest amount. ... 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.

In the end, MacArthur seemed to believe that one way of doing science was to create provocative mixtures of theory and data that while in no way definitive, were nevertheless interesting. If the ideas were novel and clever enough, and the data suggested they were plausible, he would not be too

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concerned about typos (there are at least two in the paper), nor would he hedge too much (he uses the word “clearly” twice and “easily” three times). Throw it out there, and if other folks ran with it and tested it further, great. Of course, to pull this off in academia, the ideas have to be darn interesting, the presentation darn compelling, and the data, such as it was, darn suggestive. In virtually all of his work, I think MacArthur pulled it off.

What followed

A number of his colleagues report that MacArthur didn’t take the warbler paper that seriously. He, after all, continued to work profitably on a stunning variety of problems (Pianka and Horn 2005), and was thus not reticent about downplaying his earlier papers (MacArthur 1966). When he did return to the warbler paper, in a chapter on niche theory (MacArthur 1968), he refined and revisited some themes. First, in a way folks don’t do much anymore, he discussed his philosophy of science. He pointed out that Gause’s conjecture was on the face of it untestable. It was impossible to completely define the axes of the multidimensional niche, let alone calibrate them, and the problem of spatial scale and transport of resources made the whole notion of falsification impossible. Echoing Lakatos (1978), he suggested such theory should be viewed “pragmatically”; as long as it could be used to generate more circumscribed hypotheses that were themselves testable, it was useful. He then proceeded to plug his warbler data into a matrix algebra version of Volterra’s competition equations. He seemed pleased that a new and unexpected prediction arose: that increases in the density of Blackburnian Warblers would enhance the invasibility of the Bay-breasted. The former, in a population sense, were an indirect resource. In the pantheon of MacArthur quotes, what followed remains my favorite.

There are a great many testable predictions hidden in the equations.

Meanwhile Ph.D theses accumulated that emulated the warbler paper. Too often, however, the goal of the studies became the search for niche axes (they were out there somewhere) upon which species were staggered, thus allowing coexistence. Alternate hypotheses were few and far between, as were the experiments that MacArthur admitted took more time. The data that MacArthur himself insisted were most important, evidence that the observed differences among species allowed each population to increase when rare, were often absent. It appeared that species differences, albeit rigorously quantified, were enough to keep Gause firmly on his pedestal.

Needless to say, we know this didn’t last. Few had MacArthur’s ability to weave “one long argument” from a combination of novel theory, naturalist’s skills, writing, and moxie. (A large number of his most important papers were communicated in PNAS, many others in books and book chapters.) A correction was coming. Nicholas Gotelli (1999) described the three criticisms underlying the reappraisal of the “MacArthurian Paradigm”: the theory was wrong, the patterns weren’t there, and the evidence was weak and nonexperimental. The first is almost inevitably true for most theory (although optimal foraging and

island biogeography are still alive and kicking). The second resulted in a useful, and, in hindsight, highly entertaining, paroxysm as ecologists confronted the definition of random and null. (As systematics was simultaneously undergoing its own turmoil in the battle between cladistics, phenetics, and “traditional taxonomy,” the early 80s was a fun time for journal clubs.) The last has perhaps had the most profound impact, with field experiments continuing as the gold standard on NSF panels.

On the warbler front, Tom Martin’s studies of warbler communities have placed MacArthur’s niche differences in a different light. Using intensive field experiments, Martin suggests that frequency-dependent nest predation, not foraging overlap, may allow populations to increase when rare (Martin 1993, 1996). For at least some warblers, it wasn’t where they foraged that kept them in the community, it was where they nested relative to other species.

Why students should know MacArthur (1958)

The warbler paper serves at least two purposes in my undergrad classes. At university, students are taught the diversity of Phyla, but few come to my classes with a concept of species diversity. On the pre-test for Principles of Ecology, I ask my new students to list 10 species. Many think it’s a trick question. Most begin to falter after “humans, dog, cat, *E. coli*, rats, cows, horses...”. The warbler paper is a lovely tonic, in this respect. Once a student knows she can walk into an Oklahoma wood lot and see 20 species of birds, 15 of grasshoppers, and 20 or so of ants, the next question, often unprodded, is “what do they all do?”

Second, the warbler paper is a great story in the history of ecology. Undergraduates too often are taught science as a modern language—a list of vocabulary to be memorized, with a little added grammar. But science is first and foremost a process of understanding how the world works. Unfortunately, the demands of curriculum committees and the constituencies they serve nowadays encourage teaching a list of things we know, but not how we came, provisionally, to know them. What MacArthur helped bring to ecology, a conceptual approach using hypotheses to quantify, organize, and illuminate natural history, is what science education so often lacks. The arguments MacArthur’s work engendered, and the way they changed ecology, illustrate science as a process, not an encyclopedia.

Lawton (1991) quips “One of the problems with ecology is that there is an awful lot to read..” This is doubly so for graduate students nowadays, who drown too easily in a sea of downloadable PDF’s (when I started out, the number of quarters I could spare was the rate-limiting step). Grad school is a time to achieve scholarly breadth while creating one’s own intellectual niche. It is little wonder that grad students tend to scrimp on history. So my community ecology course begins with the warbler paper, Platt’s “Strong inference” (Platt 1964), and Jared Diamond’s wonderful “Overview: laboratory experiments, field experiments, and natural experiments” (Diamond 1986). Again, it is difficult to teach the process of science without teaching its history.

To spread, a scientific meme *should* be correct. But it *has* to be infectious. The way the warbler paper is constructed—compelling hypotheses (with lots of insights simply tossed out there) and quantitative data presented in tasty graphs—make it a fun read. (John Lawton [1991] caught one of these insights: “[MacArthur] recognizes that if there are time lags in regulatory processes, high intrinsic rates of increase will be destabilizing—the seeds of chaos in 1958!”) MacArthur eschewed a formal Methods section. After an introduction laying out the theory, the warbler paper unfolds like a clever story (...and after I looked at this, I tried this, and darned if I didn’t discover this...). That, I think, is a feature that characterizes his best work. The uniqueness of Robert MacArthur, and the loss of his early death, could perhaps be summed up thusly: he was always surprising us.

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