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My complete works and more*

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PREFACE

As we approach our last quarter of a century, some of us who might by some extension of the word be called writers may be swept away by a desire to summarize. This is my shot at writing a summary.

By what standard am I a writer? When I was a little boy in the East Bronx, people would point with great respect to rather ragged men, often with flapping overcoats and scarred shoes and usually with cracked plastic briefcases, and say *Ehr ist epes a schreiber!* (He is really a writer!) [I don't quite meet the physical picture. My shoes and briefcase are real leather.]

I decided a half-century later that one book did not a *schreiber* make – everyone has one book in them. Two books is getting closer. Three books defined writer status. Four books or one bestseller was the mark of a hack or a sell-out!

I have written three books, two of which are in print. The one that is out of print contributed to my academic advancement nicely. None were bestsellers. This paper consists of reports of events, people, and conversations that I feel taught me important things. I will not attempt to organize them into a formal autobiography. Autobiographies by persons whose works and thoughts are famous can be fascinating, but usually are not. Run-of-the-mill septagenarians have lived through exciting decades without doing or learning much of general interest. Knowledge does not necessarily provide wisdom, nor does it enforce correct beliefs. Wisdom gained from experience depends as strongly on the person as on the experience itself.

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* My title is borrowed from Sir Max Beerbohm, an Edwardian dandy born in 1872. He published the *Complete Works of Max Beerbohm* at the age of 24 followed two years later by the *Complete Works of Max Beerbohm and More*. He is perhaps the world's greatest minor author and is one of my heroes.

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Most of my writing has been about ecology – the science that starts with natural history and ends with large-scale atmospheric problems and sometimes extremely sophisticated mathematics and biochemistry.

INTRODUCTION

At the beginning of my scientific life, ecology was a small, underfunded corner of biology. Ecologists were motivated by a fascination with organisms, which they shared with few other people. The British humorist Stephen Potter wrote in 1952 that insisting on discussing 'oikology' [*sic*] was a highly recommended way of boring a girlfriend enough for her to end the relationship (Potter, 1952).

Modern ecology is important and complex. In the introduction to my 1961 book *Growth and Regulation of Animal Populations*, I briefly noted that atmospheric gases were in the process of changing as a result of human activity and that this would produce global warming. This was not my original idea. It was simply a fact known to ecologists. Like most facts of ecology at that time, it did not make a ripple.

Ecology has been part of a great transformation of human thought. It is now a focus of major, and very stylish, attention. Never again will it automatically appear boring to adolescent girlfriends. Never again will it need to be explained that humans and nature are connected by more than our intellectual curiosity.

This is not entirely because of new discoveries. In its most basic form, ecology was around before humans evolved. For millennia, we have expected animals to behave as if they know the properties of other animals. For example, animals of an appropriate size range have been expected to 'know' that humans are to be feared, as can be demonstrated by trying to catch swimming fish or frogs with your bare hands. Tiny animals like mosquitoes or very large ones like great white sharks may not share this fear.

Fear of humans is so prevalent that the exceptions gain attention. Sailors and explorers commented on the fearlessness of various island birds. The phenomenon of fearless birds is less common than it once was, in part, because birds – like dodos (*Didus ineptus*) and great auks (*Pinguiness impenis*) – that were fearless have been eaten[1].

Information about natural history is not built into each of us. It must be discovered or learned. Serious attempts to crystallize the study of natural history into a formal science of ecology were twentieth-century phenomena. My 60-year career witnessed many of these attempts.

The first university Ecology and Evolution Program was established at Stony Brook in the late 1960s. There are now hundreds of them, but the attempt to establish a new rigorous science has been only partially successful.

I will present some of the questions that have occupied me since 1947, when I decided to be an ecologist, together with the logical sequences that connected them. I will also sketch, when possible, partial answers to these questions.

Most of the other papers in this special issue of *Evolutionary Ecology Research* are the work of my students and an immediate circle of friends. *Daphnia*, dinoflagellates, hydra, corals, fish, friends, teachers, students, and some other people will be among the organisms discussed.

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[1] Being eaten by people was only one of their problems. The fearless birds were island dwellers and their first contact with people coincided with their first contacts with people's companions: rats, cats, snakes, and dogs.

I followed a sequence of ideas. My students and friends have each followed their own sequence. We each travelled on our separate courses, but occasionally our ideas have touched and these occasions have sometimes been marked by new joint insights. These moments of touching are like travellers sharing landmarks, at least for a while. I will be concerned with these junctions.

Here is a possible analogy: While sailing my 22-foot sloop at night in Long Island Sound, I used to watch for the lighthouses and their various white, red, blue or green signals. Each signal was recognizable and cherished. If I could see two light signals at once I could even triangulate my position on a chart.

The shores of Long Island Sound are now lined with villages, each with its various lights. As more and more houses and stores are built on the shore, suburban sailors face a worsening problem. Which of the lights are navigational aids and which are unrelated to finding my course? The navigation lights do have a pattern of occultation, but when they are embedded in all the other lights, careful observation is required to know which ones to steer by and which are for supermarkets.

In a similar sense, sailing through the sea of scientific literature, we are surrounded by presumably illuminating papers. But it is by no means obvious which of them are meant to be our guides and which ones are markers for an entirely different course or purpose. Without a guide, it is hard to distinguish intellectually significant lights from advertising displays.

Just as lights appear on the shore for reasons quite unrelated to the needs of sailors, so papers may be written and published for reasons that have very little to do with scientific information. Articles may be counted and weighed and used as currency for academic business. In this paper, I will try to explain what I thought I was shedding light on and which lights I was following. This is a description of growth within a science; some of the facts and ideas that have changed the science of ecology during the last 60 years.

The research that I will discuss grew from questions of different grades of generality, such as 'How can hydra move about when they lack organs entirely?' and 'Why is normal sea water, sometimes and in certain places, replaced by a "red tide"?' And 'Can populations fluctuate if the environment is constant?'

Some questions are broader. Four of these broader questions, and their very brief answers, are:

- Is ecological efficiency real and is it in any way maximized? It is real and meaningless.
- Is anything maximized in evolution other than persistence itself? Not really, but taking that question seriously leads to interesting conclusions about optimality.
- Is the evolution of humanity unique? Yes, but watch out for dangerous just so stories.
- Is ecological theory useful and is there a unified, useful, mathematical theory of ecology? I have concluded that there are useful small theories in ecology but not a single big general theory.

Some other questions are too broad for specific research projects and functioned more as foci of interest.

Many of the particular problems that concerned me came from dissatisfaction with accepted teachings. Had I agreed with what I had been taught there would have been no point in asking questions.

Sometimes I chose research problems for their presumed importance, but often I was attracted by their beauty. My research and that of most of my friends is not a story of triumph but rather of fascination by nature.

Often, my attention turned away from a problem before its solution was complete – either because I could go no further with it, intellectually or technically, or because funds dried up. Sometimes I had to turn my attention to problems of my health or that of my family. Occasionally, I abandoned a problem simply because something more exciting crossed my path. After my attention was drawn elsewhere, most of the problems I abandoned continued to be studied by students and friends.

My work and that of some of my friends and students will be presented in a much abbreviated form, as if parts of my autobiography. I will also attempt to make clear the sequence of intellectual steps that we made. It will be evident that these steps were mostly small and, in retrospect, some were obvious. But occasionally they seriously modified how we think about nature.

CHILDHOOD

I was born in 1928. I never faced the desperation of job seeking during the Depression and I was too young for military service in the Second World War. But shadows of the Great Depression and the Great War coloured my life.

My childhood was surrounded by New York City, especially the East Bronx. The museums, the Bronx Zoo, and the Bronx High School of Science were important to me, along with interesting relatives and neighbours. These were elements of my ‘village’[2].

My autodidact grandfather had read about Darwinian evolution and coral reefs and many other aspects of science in Yiddish translations. To introduce me to science before I attended school, my grandfather gave me iron filings, magnets, and a compass. He also assembled for me a Cartesian diver and we had a long discussion about Archimedes and specific gravity[3].

My concern with ecology, a decade before I knew the word, began as an interest in animals. I saw them in the zoo and in Crotona Park[4]. I saw woodland, stream and farm animals during summers in the ‘country’ and while exploring the rocky tide pools of the artists’ summer colony of Rockport on Cape Ann, Massachusetts.

At age 9, in a four-room Bronx apartment, which for a while also housed my father’s sculpture studio, I kept a canary, rabbit, tortoise, horned toad, an aquarium with newts and baby turtles, and another aquarium of tropical fish. In those days, 8- and 9-year-old children could wander around New York by subway without their parents. I was fascinated by the American Museum of Natural History, especially the dioramas and marvellous glass protozoan models.

I also had a toy Japanese microscope and some stinking infusions of lettuce leaves in tap water. They were full of rotifers and ciliates that were, and are, absolutely amazing to me.

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[2] A general idea of my Bronx in the 1930s is available in *The World Of Our Fathers* by Irving Howe (1976).

[3] My father and I discussed theories and history of art but these nursery conversations did not lead to an educational programme.

[4] Crotona Park was a wonderful playground in those days. It became a drug addicts’ centre and I have been afraid even to enter it for 30 years.

This opened the world of Leeuwenhoek and taught me that the complexity and diversity of organisms could be examined in miniature.

Sometime around 1939 I found Kudo's *Handbook of Protozoology* (Kudo, 1931) in the public library. At age 11, I dreamt of being a protozoan taxonomist, which unfortunately never worked out.

EARLY ADOLESCENCE: HIGH SCHOOL AND COLLEGE

When I was 12 years old, my dreams of being a professional scientist were encouraged at the Bronx High School of Science. Almost everyone there was working on something that sounded abstruse and required a white coat or collecting gear. The students spoke of themselves as 'we scientists'. The sense of competition was as acute as any that I ever found later on.

I was a member of the 'protozoa squad', a low-tech, mainly unsupervised, and very small group of students, who maintained the live protozoans used in teaching. I had living cultures of *Spirostomum*, *Blepharisma*, *Stentor*, *Paramecium*, *Arcella*, *Dileptus*, *Didinium*, *Ameba chaos*, and *Ameba proteus*. (The names have almost certainly changed.) In my later career, I never succeeded in getting as good a live collection of any group of animals and never worked on protozoans after high school, although later I did a little on dinoflagellates and zooxanthellae.

The Bronx High School of Science, like science itself, was not yet co-ed. So I was mildly active at age 15 in the Young Communist League and a synagogue youth group in the fruitless hope of making contact with girls.

My father was eventually recognized as an important sculptor, illustrator, and children's author but, during my childhood and adolescence, money was a chronic problem. Outside of school I delivered groceries for tips. This interfered with my schoolwork.

At almost 16, I went to Bethany College, West Virginia, the mother school of the Disciples of Christ Church. My choice was not deliberately ecumenical. It was dictated by not having any money, not having very good grades, and wanting to get out of a big city. It did focus my attention on organized and disorganized religion and I also met my first Republicans.

I very much enjoyed Bethany. It had a beautiful setting in woody hills. The faculty was limited and, I suspect, lazy. This meant that many of my 'courses' consisted of what is now called 'independent study'. In the absence of a botanist on the faculty, I learned botany from an old edition of *Gray's Manual* and from the West Virginia woods.

When it became clear that I intended to go to graduate school, and knew essentially nothing about the anatomy of birds, the Dean (B.R. Weimer) took me to his backyard, chopped the head off one of his chickens and handed me the headless body, telling me to do its anatomy as if it were a new species. Drawings were to be in India ink.

By age 19, I had graduated and was working as a technician at the Sloan Kettering Cancer Research Institution.

LATE ADOLESCENCE: GRADUATE SCHOOL

I was admitted to Yale Graduate School because of high GRE scores and the idiosyncratic admission standards of G.E. Hutchinson, the director of graduate studies for the Zoology Department. Hutchinson believed that he could recognize scientific talent from facial appearance in photographs.

Hutchinson's delight in learning new and curious things and theories permanently altered my life. His obsession with the possibility of formal ecological theory has influenced all my work. I followed him about for many years (Slobodkin, 1993; Slobodkin and Slack, 1999). He believed, and I still do, that descriptive natural history is the basis for ecological theory, but that natural history alone, without attempts at generalization, condemns us to a fascinating but unfortunately endless task, rather than increasing our ability to understand new problems.

Hutchinson taught a seminar course strongly based on Gause (Gause, 1934) and Lotka (Lotka, 1925, 1934). He taught that the Verhulst-Pearl logistic, or sigmoid, growth equation was how populations grew, coming to equilibrium and staying there unless environmental conditions changed. As a new graduate student, I believed all published scientific results and all I heard in lectures, an opinion I have since revised.

In 1947, Hutchinson reported in a seminar that David Pratt had shown that populations of *Daphnia magna* fluctuated in a constant environment (Pratt, 1943). I was convinced that Pratt had to have been mistaken. Pratt had maintained his *Daphnia* on a dilution of 'green aquarium water'. Initially, I felt that this essentially uncontrolled food supply might be the source of the oscillations.

My first serious experiments were designed to refute Pratt. After 2 years I concluded he was correct.

I cultured *Chlamydymonas*, following directions from the eminent algologist, Ralph Lewin, at that time a fellow student. I measured algal concentration, roughly, with a colorimeter. I then added a dilution of the algal suspension to a fixed quantity of pond water giving a rough control of the quantity of food.

Due to my lack of funds and to their convenient size and shape, I grew my *Daphnia* in used baby food bottles. I did not use *Daphnia magna* for several reasons. I wanted to make complete counts of my populations of *Daphnia*, not merely to sample them. To do that I required a small *Daphnia* that could be transferred by medicine droppers during the count. Also, I intended eventually to grow two species of *Daphnia* together in competition – mimicking the work of Gause (1934) on inter-specific competition – and therefore I wanted a *Daphnia* that I could tell from other species.

I used *Daphnia obtusa*, a pulicoid *Daphnia* from Lago Maggiore in Italy[5]. According to the literature, *Daphnia obtusa* did not have a tail spine but did have three spines on the interior face of each valve. I hoped that this would distinguish it from other species in mixed culture.

The hope evaporated. The supposed absence of tail spines in *D. obtusa* only occurred under conditions of very slow growth and the spines on the valves were almost invisible when sorting live animals.

As often happened, my plans for this project were much larger than what I actually accomplished. I have learned that this is typical for my experimental plans. I got side-tracked by single-species populations and did not grow two species together in the same container until much later (Slobodkin, 1964a).

By counting laboratory populations of *Daphnia* several times a week for over 2 years, I established that they did not follow the logistic curve. Oscillations in constant environments are real and can be due to age structure effects under constant limited food conditions.

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[5] The *D. obtusa* came from a small pond in the garden of the Istituto Idrobiologica Marco di Marchi in Pallanza Verbena, courtesy of Livia Pirrochi-Tonolli.

Temperature and other chemical and physical effects can modulate population dynamics. *Daphnia* compete for food but do not directly crowd each other in any significant way (Slobodkin, 1954).

What seemed significant to me about these experiments, aside from information about the biology of cladocerans, was the following:

1. They were done in the laboratory and were clearly 'unnatural' but they demonstrated that being unnatural had compensations. Experimental conditions do not precisely mimic nature. To attempt to mimic nature in an ecological experiment is probably impossible, but to extend beyond nature is sometimes expedient and informative. Experimental conditions can exceed the range of natural conditions. That makes nature a subcategory of the domain of the conclusions from correctly designed experiments. Results that hold well beyond the conditions found in nature will, in particular, hold for nature.
2. Population size in *Daphnia* depends linearly on food supply at crowding levels ten times greater than have ever been found in nature. Therefore, no 'crowding' effects occur in *Daphnia* in nature. Up until then, crowding, without further analysis, had often been used as an explanation of population-level phenomena (Chapman, 1931).
3. My experiments were deliberate repetitions of previous experiments. At that time, ecological studies usually stretched into new areas and the idea that it was worth repeating an experiment was novel. Some people could not understand why I wanted to examine single-species population growth after single-species populations had been so carefully studied in flour beetles (Park, 1948; Park and Frank, 1948).
4. I demonstrated that models of populations must be concerned with more than simple enumeration. The age, genetics, and physiological condition of the animals are all important (Slobodkin, 1953b; Łomnicki, 1988). This is now generally accepted practice in conservation biology (Ferson and Burgman, 2000).
5. Averaging census data from 'replicate' populations is illegitimate, except under steady-state conditions. Each population, as each individual in the population, has an individual history. Populations should be treated as entities in their own right. What had been, and often still is, the practice of averaging data from different populations seems to assume that the average was providing in some sense a more accurate number than the census of a single population. This is somewhat similar to attempting to determine the correct time by averaging the times on a series of differing clocks.
6. While the very early history of any population may follow what superficially appears to be a sigmoid curve, if the population is followed long enough it will usually be apparent that the Verhulst-Pearl logistic is not being followed. This conclusion came in the context of a general belief to the contrary. The most important text in population biology (Allee *et al.*, 1949) assumed that all populations grew according to the logistic curve and that any deviation from that curve was an artifact.

I thought my attempts to refute the use of the logistic should have generated at least anger. There was no anger. I felt that this meant most ecologists had not seriously considered the questions. Because of the curious lack of response to my concern with the logistic equation, I took on as part of my scientific goal to destroy empty theories in ecology (Slobodkin, 2001).

I felt I had destroyed the logistic equation, but despite my opinion, almost any current theoretical ecology book or journal will contain new examples of theories in which the building blocks are logistic equations – as if many invalid equations, fitted together, somehow gain validity in the process.

The primary argument for the continued use of logistic equations is that they are simple and convenient[6]. In terms of explaining the world, angels are equally convenient and perhaps prettier, if not simpler.

G.E. Hutchinson, water fleas, and the logistic equation were foci of my 4 years in the Yale Graduate School. But these were not the sole foci. At the Yale Hillel in 1951, I met Tamara Jonas, whom I married one year after getting my degree. We are still together after 57 years.

POST-ADOLESCENCE: RED TIDES

After completing my PhD in 1951, at age almost 23 and with no marine experience, I was appointed Chief of Red Tide investigations for the United States Fish and Wildlife Service at the laboratory in Sarasota, Florida.

At the time, the cause of red tide blooms was sought solely in phosphorus and nitrogen concentrations. Unfortunately, the correlation between outbreaks and nutrient contamination was not very good. There were locations with normally low nutrient concentrations that broke out overnight into red tides, and locations with high nutrient concentrations that had no red tides.

After approximately 2 years I developed a theory of red tides that called attention to the fact that water mass structure was as vital to bloom prediction as is water chemistry (Slobodkin, 1953a). This theory denied that endless plankton tows and chemical analyses were the only research procedure for studying blooms. It was a simple change that is now generally accepted.

The great oceanographer Henry Stommel[7] listened to my description of red tides and introduced me to a mathematician, Henry Kierstead. A general mathematical model relating water mass size, diffusion rate, and reproductive rate of phytoplankters was developed (Kierstead and Slobodkin, 1953). This model was built on ideas about minimum mass of explosive material in atom bombs. In too small a water mass, diffusion at the borders overcomes reproduction of the dinoflagellates inside the mass so that an increase in their concentration is impossible.

Any set of physical and chemical conditions will favour one algal species over all others. Which species blooms depends on nutrient conditions, salinity, and temperature. Different red tide organisms prefer different conditions. Some like higher and some slightly lower temperatures, slightly different salinities, and many require specific micro-chemical properties. Some red tides on the Florida west coast required vitamin B12 (Hutner *et al.*, 1954). But that a bloom will occur at all depends on water mass stability. Relative constancy of water mass condition is necessary if any plankton bloom is to occur.

Potential red tide water was normally found in the bayous and embayments of the west coast of Florida. A significant red tide required this water to retain its identity long enough for the development of a bloom.

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[6] For example, despite all of the above even I will use logistic equations in some theories.

[7] Stommel also introduced me to Robert MacArthur. I in turn introduced MacArthur to Hutchinson. Their collaboration was basic to ecological theory, although not all its products were correct.

Decades later, I noted that in the Great South Bay of Long Island, the ‘brown tides’ depended on the stability of more, rather than less, saline water but the general principle was the same (Slobodkin, 1989). If conditions in the water change too rapidly, no single species can continue to increase at an inordinate rate.

The fundamental fact of discrete water masses being associated with red tides has become basic to understanding red tides. Conversely, we can infer the existence of discrete water mass and relatively low mixing from the occurrence of any red tide.

I am delighted that our simple mathematical model of 1953 was used by later theoreticians in very elegant ways. It was the starting place for a general theory of population growth in diffusive systems by Okubo (1980).

My Fish and Wildlife Service supervisors were furious at my claiming to have solved the ‘Mystery of the Red Tide’. They had an institutional commitment to working on the ‘Mystery of Red Tide’, but not to its solution. The ‘Mystery’ was important. A mystery solved was an investigation ended, requiring actual thought, rather than endless repetition of some set of procedures. Endless repetition of particular favourite procedures is in one sense the scientific analogue of painting by numbers. From the standpoint of institutional maintenance, a busy programme of endless repetition may be a goal. So long as there was ‘Mystery’ they could defend the size of their appropriation.

The only way I could get my two red tide papers published was to quit the civil service and take my manuscripts with me.

Some still cling to the ‘Mystery’. Dr. Pierce of the Mote Laboratory in Sarasota, in denying the usefulness of our theory, stated in a Sarasota newspaper in 2006, that ‘relying on suppositions made in the late 1940s and early 1950s is just not good science’. Simply discarding scientific theory because of its age, as if it were spoiled milk, can force us to repeat the same investigation endlessly. A theory may be corrected or modified by later research, but not discarded for mere age. Calculus is centuries old and geometry is thousands of years older than that. The applied science of animal husbandry is surely ten times older than that.

Science progresses by preserving valid assertions, while perhaps modifying them or adding to them as a result of further investigations. For example, if I were studying red tides today, I would have considered dinoflagellate spores, which reduce the time needed for water mass stability before a bloom (Imai and Itakura, 1999).

I’ve looked so far at just the first few years of my career. I must avoid letting my autobiography take longer than my life. For the remainder of this account, I will try harder to omit details and simply focus on what questions were asked and why, and what answers emerged and what was wrong or right about them.

MY HAPPY RETURN TO UNIVERSITY

After quitting the Fish and Wildlife Service, I returned with my new wife to New Haven where I was supported as a research associate for around 6 months[8]. In 1954, I was hired by the Zoology Department of the University of Michigan at Ann Arbor. I taught undergraduates but was free to choose my own research questions and to work at my own pace.

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[8] I don’t know where the money came from. I think it was from Carol Haskins.

While I was in the civil service, I had felt the shadow of more than a hundred million people looking over my shoulder and asking, ‘What have you done today?’ At universities, that question did not arise, and if it had, I could have answered, ‘I have taught pre-meds!’ I also had a chance to teach more advanced students.

To help in teaching graduate ecology and to clarify the content of Hutchinson’s seminar in my own mind, I wrote a small book, *Growth and Regulation of Animal Populations*, a kind of primer for ecological theory (Slobodkin, 1961). It stayed in print for more than 20 years and was then reprinted (Slobodkin, 1980). During those years, it served as an elementary text for first-year graduate students in the use of logistic equations!

HYDRA AND CORALS

I began studying hydra to compare them with *Daphnia* in the early 1960s. But having rearranged my lab for the convenience of hydra, we studied hydra biology and its implications for the next several decades. These studies ranged from the generally descriptive (Slobodkin and Bossert, 2001) through collaborations with mathematicians and physiologists (Slobodkin *et al.*, 1991) to studies of population dynamics in hydra – which is particularly fascinating because feeding rate and body size and bud size and temperature all interact (Hecker and Slobodkin, 1976).

Adam Łomnicki of Krakow, a senior scientist visitor to the laboratory, became fascinated by the motility of hydra in the essential absence of organs of motility. Hydra simply let go of their substrate and float to where food may be found, and then sink and attach themselves to the new substrate (Łomnicki and Slobodkin, 1966). Floating occurs in response to crowding and starvation and has the effect of concentrating hydra in the food-rich sections of lakes. Tom Griffing and Conrad Istock used diving gear in a small Michigan lake to study populations of hydra in nature (Griffing, 1965). This was one of the first times that populations of hydra were examined in such a direct way. It demonstrated the movements in time and space of these supposedly sedentary animals. Griffing actually left academia to start a business in water purity management, demonstrating practical applications that might grow out of an initial research concern.

Istock was extremely active in many fields, including the biology of water beetles, the DNA of bacteria in nature, the peace activities of the Association of Atomic Scientists, and the political controversy involving the siting of an astronomical observatory at the University of Arizona, where he was head of the Ecology and Evolutionary Biology Department.

Students picked out areas for doctoral dissertations using hydra. For example, Kenneth Dunn became fascinated by cellular and sub-cellular fluorescence microscopy of the algal symbionts in green hydra (Dunn, 1987). He left ecology and is now Scientific Director of the Indiana Center for Biological Microscopy at the medical school of the University of Indiana. Patricia Bossert did doctoral research on hydra (Bossert, 1986) and continues to study hydra as a model organism in many contexts – particularly as the focus of high school biology teaching.

Studying hydra, I developed an affection for coelenterates (Slobodkin and Bossert, 2001). Coral reefs are gardens of beautiful coelenterates. One of the most beautiful coral reefs was on the northern tip of the Red Sea in Eilat, Israel[9].

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[9] Much of the reef has since been severely damaged.

As an American Jew, I was fascinated by Israel, its language, and its good and bad politics. I was also concerned with my own education and that of my children. Specifically, I felt that the Hebrew language should be available to us. Also, my father-in-law and his family and my brother are Israelis. I therefore spent two sabbaticals in Israel. I taught graduate ecology courses at Hebrew University, Tel Aviv University and Ben Gurion University of the Negev, and I joined with Israeli marine scientists working on the Eilat coral reef.

In Israel I met Uzzi Ritte, now Professor of genetics at the Hebrew University, my last doctoral student at Michigan. On the second sabbatical, I met Yossi Loya, my first doctoral student in Ecology and Evolution at Stony Brook. Yossi is now a pre-eminent figure of coral reef research on a global scale.

Studies in Israel by Phillip Dustan, Joel Sohn, and Sumner Richman were supported by Smithsonian Institution International funds growing out of my time in Israel.

Dustan continues to study corals, among other things. He has been curiously effective at finding himself on expeditions all over the world. In particular, he has been closely associated with the work of Jacques Cousteau. We have never actually published together but there has been an ongoing consultation for the past three decades

One result of work on the Eilat reef is called the Loya-Slobodkin Line Transect Method of measuring reef diversity (Loya and Slobodkin, 1971). This is now sometimes used in place of complete censusing of quadrats (Connell, 1978). As might have been expected, the diversity of species was highest where crowding was not excessive.

This expectation was based on the old competition theory of Gause, which in turn was based on logistic equations that I had discarded! Once again, this demonstrates the uncomfortable fact that valid conclusions can emerge from erroneous theories. I believe this is a result of weakness of formal theory in ecology, which I intend to discuss elsewhere. Perhaps it matters for the philosophy of science, which is not my specialty.

The study of Israeli ecology, like that of most ecology concerned with geo-political units, is intertwined with politics and history. Recall the importance of state birds and flowers and national birds to nationalist movements in almost all countries. Ecological education can be used to develop a concept of 'nature and homeland'[10]. Yossi Loya and I tried to briefly explain the role of ecology in the history of modern Israel (Slobodkin and Loya, 1981).

One curious feature of ecology in Israel is the Israeli attitude to wildflowers. When my Israeli-born grandson was a little boy, around three, I picked a single violet blossom for him in a Westchester park and thereby horrified both him and his mother.

ENERGY IN ECOLOGY

A basic role for ecology has always been learning how to exploit or preserve natural systems so as to get maximum yield without destroying the resource. The yield from a system might be tons of fish, board feet of lumber, number of pearls, pounds of flesh or thousands of dollars. Was there a possibility of a single theory to cover all exploitation situations? To develop a general theory seemed to require some common descriptor.

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[10] Consider *Natur und Heimat* in German, *Teva v'Aretz* in Hebrew, and the litany of Boy Scout mottoes in English. These are often vestiges of European Romanticism and nationalism and may have dangerous associations. What is almost a cult of nature in Japan cannot be blamed on European nationalism.

Simple enumeration would not do without drastic correction terms. Consider how many mosquitoes are required to have the quantitative effects of one elephant!

It seemed possible that ‘biomass’ – the weight of living material – might serve as a common currency. Unfortunately, the meaning of biomass is ambiguous. A tree may weigh tons, but its living tissue would be only leaves and cambium and not include the lumber of the trunk. Coelenterates include marine jellyfish metres across, but the bulk of their tissue is water. Even their dried tissue is more than 95% salt (Slobodkin, 1962).

The idea of biomass as a universal unit quickly succumbed to what seemed a better idea – energy content. In fact, biomass was a stand-in for energy from the beginning. Lotka (1925), Hutchinson (1948), Lindeman (1942), and others considered that the multi-species assemblages referred to as ‘communities’ could, in some sense, be considered as thermodynamic systems transforming solar energy into chemical energy and then dispensing this to all of the community members to eventually all be dispelled as heat. ‘Ecological efficiency’ was defined by Lindeman as the fraction of the energy consumed by a population or trophic level that was consumed by the next higher trophic level. This image even generated the hope that the results of thermodynamics could be directly extended to ecological systems, with entropy represented as organizational disorder in some sense (Odum, 1971; Ulanowicz and Hannon, 1987).

Unfortunately, the correspondence with thermodynamic theory does not hold. Classic thermodynamics refers to closed systems in transit between equilibrium conditions and usually focuses on non-feedback systems. Living organisms are open systems that for brief periods might be approximately at steady state but are never at thermodynamic equilibrium. Despite this failure to provide theoretically valid ecological extensions of thermodynamics into ecological theory, except in a very limited sense (Battley, 2003), energy remains of interest.

My first PhD student, Sumner Richman, and I, using a micro-bomb calorimeter (disposed of by the US Navy’s solid-fuel rocket programme) measured the energy released by burning dried, whole, small organisms (Slobodkin and Richman, 1961). This provided a set of conversion values that could be used in observational and experimental studies. It also attracted others to make similar measurements (Paine, 1964; Paine and Vadas, 1969).

Richman used direct bomb calorimetry to study energy transfer in individual *Daphnia* (Richman, 1958). Ecological efficiency sustainable by *Daphnia* populations in laboratory population experiments (Slobodkin, 1962) more or less corresponded with the range of values considered by Lindeman (1942) for trophic levels in lakes. This was surprising.

If ecological efficiency was free to vary, how come the values for *Daphnia* populations were so similar to those for entire trophic levels? Would entirely different systems have had the same range of values?

I therefore repeated the studies using hydra populations feeding on *Artemia* nauplii, organisms as far as possible from *Daphnia* but still amenable to laboratory experiments. The maximum sustainable ecological efficiency values were approximately the same for hydra populations as for *Daphnia* populations (Slobodkin, 1964a).

Was ecological efficiency an evolved constant? I suggested the tentative hypothesis that ecological efficiency had been maximized by evolution at around 10% (Slobodkin, 1962). This incorrect conclusion was widely accepted and is still used, despite Turner’s excellent rebuttal (Turner, 1970) and my retraction (Slobodkin, 1972).

I now believe the reason for the apparent agreement between different studies was the general sloppiness of the numbers. Also, it is possible that after several papers had appeared with approximately the same results, later investigators did not quite trust deviant values and therefore modified conversion constants until the results fit.

The most important theoretical reason for rejecting the idea that ecological efficiency is an evolved constant is that natural selection would have had to act in a coordinated way on three trophic levels. This would be carrying group selection beyond all rational limits (Slobodkin, 2007).

From experimental predation studies on laboratory populations, I also derived a widely unused concept I called 'population efficiency'. This is explicitly defined in terms of age-structured populations and is the number to be maximized by appropriate choice of kind of prey. It will give maximum yield with minimum damage to the prey population (Slobodkin, 1962, 1968).

When there was too small a response to the idea of population efficiency, I rewrote and republished it using different terminology. Referring to it in terms of 'How to be a predator?' seemed most effective (Slobodkin, 1968).

To reinforce an idea by repetition is not always a sign of weakness or cowardice. If they didn't get it at first, say it some other way and perhaps it will break through. It may be worse to develop an easily misunderstood conclusion and leave it dangerously afloat in the information stream, like a log in a waterway.

The remainder of this account is only approximately in chronological order. As time went on the straightforward linear sequence of research dealing with one problem at a time became more complicated. I found that I had around half a dozen problems at the same time. I moved from one to another advancing a bit on each. The intellectual threads nevertheless seem clear.

HSS AND OTHER CONVERSATIONS

At Yale there had been weekly teas at the office of Professor Alexander Petrunkevitch, the last student of August Weissman. Perhaps the greatest pleasure at reasonably good universities is the presence of serious colleagues who permit serious informal conversations. At good universities, a constant stream of coffee, tea or other beverage is available[11].

At Michigan, Nelson Hairston Sr., Fred E. Smith, and I argued over bag lunches for fifteen years. I was obviously the junior on the team but they were very patient and polite. One result of these Michigan conversations was the general model of a green world, sometimes called 'HSS' (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967).

Andrewartha and Birch had published a massive book in 1954 stating that population size is controlled by random physical and meteorological events and that change in population size was basically a random walk. We were convinced that it was very unlikely that, at least to some degree, biological processes did not control abundances in nature. Our conviction was based on the following observations:

- Herbivores usually do not completely consume green vegetation but almost any leaf shows signs of being partially eaten. This suggests that something limits many herbivores other than energy.

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[11] The British and Israeli emphasis on tea and Italian coffee in some location other than one's office is important. When I taught at the Imperial University of Tsukuba, Japan, young faculty members gathered and drank alcoholic beverages, sitting on the floor of a neighbourhood bar. I was told that these informal conversations were needed so that decisions could be made.

- We knew that detritus and litter left over from herbivores is mainly consumed by detritivores, with very little left over. Therefore, detritivores, in general, are energy limited.
- If the local world is not green and trees are actually denuded of leaves, it is usually the case that an exotic herbivore has done the eating. It is unlikely that exotic herbivores are better adapted to local physical conditions than are local herbivores.

We inferred that it was not local physical conditions that usually prevent herbivores from becoming so numerous as to pressure their food supply. We suggested that predators usually control local herbivores but might not be able to attack exotic herbivores. The herbivores are usually expected to be well fed and carnivores are usually expected to be hungry.

There are caveats. For example, many herbivores can eat only young vegetation. And, in Australia, local rains are important and actually are almost random. Also, the green world is accompanied by brown soils whose occurrence hinges on the chemistry of decomposition (Allison, 2006). It is also true that the precise chemistry of particular compounds will make a difference in how they act in an ecological system (Slobodkin and Lerdau, 2006).

But the conclusion that ecology is not a random walk still holds. Biological interactions matter.

Our paper was built on general observations, was 1500 words long, and presented no new data! It is a 'citation classic'.

OTHER FRUITFUL CONVERSATIONS

In addition to specific empirical problems, and the important papers with Smith and Hairston, there were other ideas that grew out of conversations with colleagues and students. These conversations were very much the crossing of paths.

For example, Fred Smith noted the inverse correlation between size and maximum rate of population increase in a wide range of organisms (Smith, 1954). This relationship has often been rediscovered and republished, almost never with reference to Smith or to any evolutionary mechanism. Smith explained the relationship by considering that small organisms live in more fragile and temporary worlds than large ones. They must be spending more time growing rapidly to refill recently disturbed habitat that at least temporarily has abundant resources. I discussed Smith's insight with Dan Dykhuizen and with students.

Dykhuizen's student, I.N. Wang, came up with an important original consequence. If a population is not increasing, there perhaps is selection for those individuals who can survive starvation, but when resources are always abundant there is always selection for rapid increase. One way of achieving rapid increase is to be smaller. This was of interest because, if it is taken at face value, small size must be correlated with higher rates of potential increase even in the smallest of organisms. Larger bacteriophages should have higher increase rates than small ones, and they do (Wang *et al.*, 1996).

In the small field of ecology there were all manner of interconnections, at times functioning like an extended family. For example, Bob Black was an undergraduate at Lawrence University in Appleton, Wisconsin with Sumner Richman, my first PhD student at Ann Arbor. Bob became my PhD student at Stony Brook. He was working on a field study of interspecific competition and micro-evolution in cladocerans, which required field facilities and ultimately genetic analyses that were beyond the accommodations of my laboratory in Stony Brook.

We arranged that he would do most of his research at the University of Washington in Seattle under the wing of W.T. Edmondson. Note that Tommy Edmondson was one of the earliest PhD students of G.E. Hutchinson, and that a graduate student with Edmondson at that time was Nelson Hairston, Jr., the son of my colleague Nelson Hairston, Sr. John Brooks at Yale demonstrated that some *Daphnia* change their anatomy in natural situations as a result of differences in temperature, and most curiously, differences in water turbulence (Brooks, 1946). Brooks supervised much of my thesis work; he was a former PhD student of Hutchinson. The small cladoceran *Bosmina* in Lake Washington changes its appearance during the course of the year. Until Black's work it was not clear if this was a shift in genetics, species being collected, or a shift in selective pressures to predators or to cyclomorphosis.

Black demonstrated both local genetic differences and species abundance changes (Black, 1980). By the time of Black's thesis, the word 'cyclomorphosis' had lost enough of its meaning so that Bob and I wrote a paper clarifying the definition of the term (Black and Slobodkin, 1987). Part of the motivation for this rather popular paper was that we both wanted to have some joint publication.

Sean Craig had found polyembryony in barnacles in the course of his thesis research at Stony Brook. He was not my student but we spoke in the coffee room. Polyembryony is relatively rare. It involves an embryonic life stage reproducing another embryonic life stage rather than waiting for maturity to reproduce. For example, the redia larvae of some trematodes sometimes asexually produce more redia without maturing further.

Several others joined in the conversation culminating in the suggestion that polyembryony is found only when a parent is unable to realize what the larvae must accommodate to. Should conditions improve after the first set of embryos has started to develop, those embryos have the ability to reproduce so that the number of young is increased – presumably to something near what the parents would have done if they had known about the improved conditions initially. It sounds a bit complicated as I write it, but it is more clearly explained in our publication (Craig *et al.*, 1997).

There were many other conversations that mattered. In fact, drinking coffee was one of my major study tools. But this is not encyclopaedic and the other conversations will live in memories.

SPECIES DIVERSITY

So far I have been concerned with sequences of questions and answers that have been reasonably linear and discrete. Each of these sequences could be thought of as one path of ecological thinking through time. Some of them, questions or answers, like HSS and its progeny, are too rich in consequences to permit me to see easily the pattern of person-to-person transmission and response. Only the vaguest semblances of linear sequences can be discerned. The analogy of the suburban sailor in the night may disappear in a flood of light even with relatively modest advances.

Perhaps the paramount, all-embracing, recurrent questions of the past half century have related to species diversity.

It is apparent that the number of species that can be seen varies from place to place on the earth's surface. The first European explorers were amazed by the rich diversity of tropical vegetation and even today divers who see the diversity of some coral reefs are overwhelmed (Loya and Klein, 1994). Why are there eight or ten kinds of trees per acre in some forests and hundreds of kinds in some other forest?

We take it as axiomatic that different species cannot persist in the same ecological niche. Why haven't tropical forest epiphytes accepted this axiom – or have they? In general, the places that seemed salubrious for life showed maximum diversity, true, but this doesn't form a complete theory of diversity and in fact is not always valid.

Hutchinson partially crystallized the problem with his classic paper in which he invoked a mythical Santa Rosalia as patroness of diversity (Hutchinson, 1959). This dodged commitment to mechanism but ignited concern for the question. Why are there so many kinds of organisms in some places, all doing approximately the same things, and so few kinds in other places?

Among the circumstances that enhance the number of species in a region is geometric complexity, the presence of predators preventing the elimination of populations by competition (Slobodkin, 1964a; Paine, 1966), the absence of predators permitting persistence of prey species, the occurrence of destructive events preventing competition from going to completion (Connell 1978), and the absence of destructive events permitting local evolution (Janzen, 1967).

The number of papers focused on species diversity is enormous but there is no single theoretical framework that can be called a theory of diversity. At best it can be shown that in some set of circumstances species diversity will either be higher or lower than in some other set of circumstances.

It is relatively easy to compare two locations and assign a cause or at least a plausible correlate, for the greater diversity of one rather than the other. For example, sections of the Eilat coral reef that have resident cleaning wrasses have higher fish diversity. One may then speculate as to causes. Are there more kinds of fishes at these locations because there are cleaning wrasses in residence or do the cleaning wrasses take up residence where the number of fish species is greater (Slobodkin and Fishelson, 1974)?

In a laboratory study, we demonstrated that populations of brown and green hydra can co-exist if either there is very heavy predation on the green hydra or if they are maintained in dim light, minimizing the competitive advantage that green hydra have because of the photosynthetic activity of their symbionts.

Paine showed that predation encourages diversity among the sedentary animals in tide pools and has promoted the importance of predation in diversity.

THE DEEP SEA

Perhaps my most interesting conversation about diversity was with the late Howard Sanders, the marine biologist who studied the bottom fauna of Block Island Sound, one of the most studied parts of the sea floor. There he discovered the Cephalocarida, a whole new class of Crustacea that had been looked at by many and really seen by no-one until Sanders picked it out of a bottom sample (Sanders, 1955).

From 1872 to 1876, *H.M.S. Challenger* explored the fauna of the deep sea floor, using rough collecting methods, like tangles of rope dragged over the sea floor and deep quick grabs of bottom mud and nets. While this was one of the great explorations of biology, it wasn't until the work of Sanders and his associates that the diversity of deep sea life was discovered (Sanders, 1968). Howie, a fellow student at Yale, invented what he called 'the epibenthic sled', which carefully and slowly peeled back and collected the top few centimetres of the sea bottom. This gentler sea bottom collecting device demonstrated that the variety and abundance of deep sea infauna were considerably greater than had previously been revealed. They found that the diversity of species in different parts of the ocean varied and was several times greater than had been recorded.

These new deep sea explorations demonstrated that thoroughly dark, cold, energy-poor environments could also have high species diversity. In conversation, Sanders and I came up with the idea that an environment that is disturbed at just the right rate will develop high diversity, in part because the various processes of competition and predation could not go to completion if the environment varied enough (Slobodkin and Sanders, 1969). This was independently suggested by Joe Connell of Santa Barbara as the 'intermediate disturbance hypothesis' (Connell, 1978). That coral reefs show their highest local diversity in those parts of the reef in which the space is not quite covered with living organisms is an example of the intermediate disturbance hypothesis in action (Loya and Slobodkin, 1971).

Somehow, the geometric projection of the ecological niches of species evolved to co-exist is 'narrower' than that of species evolved in the absence of similar competing populations. Connell was referring to the time-scale of ecological events, while Sanders and Janzen were thinking in evolutionary time. Evolutionarily, environmental differences and changes are of greater significance in places where change is small and infrequent (Janzen, 1967). It is of interest that the same mechanisms that produce high species diversity in the cold, dark, starving world of the sea bottom also seem to work in the terrestrial tropics.

STRATEGY OF EVOLUTION

In the early 1960s, game theory was proving to be useful in many fields of biology, sociology, and economics (Rapoport, 1960; Neumann and Morgenstern, 2007). Does game theory apply to evolution?

Game theory in fact effectively described aspects of the evolution of many 'components of fitness'. The payoff from a formal game is usually thought of as something that the winning player gained more of than did the losing player. Usually payoff can be thought of in terms of money, but obviously organisms do not have money. Is there anything else that fits into a theory of games in evolution in the same way as money fits into the theory of games of the economists? 'Fitness' seemed right but this forced a careful examination of what was meant by 'fitness'

Components of fitness are properties of organisms with genetic correlates that, under specified circumstances, can lead to a greater probability of survival than alternative properties. Components of fitness include survival, reproduction, and immunity to predation or disease.

Typically, the components of fitness are measured numerically – for example, higher birth rates, greater longevity, higher capacity to survive particular environmental insults. Fitness itself, in its entirety, can be defined only in terms of persistence.

Note that most properties of most organisms do not change as fast as expected under natural selection. This suggests the presence of some kind of inertial resistance. The point was emphasized in Lerner's concept of 'genetic homeostasis' (Lerner, 1954). I believe that for any given component of fitness in any particular organism, one may imagine a set of environmental circumstances in which increase in that component of fitness is not selected for! So, for any component of fitness, there are circumstances in which there would seem to be an 'optimal strategy of evolution'.

Most discussions of fitness and evolutionary success are ultimately numerical. Most assertions about ecology are verbal descriptions. Why should we care about numbers?

The unique importance attached to numbers depends on three things. Two of these are quite clear:

- Precise theoretical models are more easily constructed with numbers than with words.
- They permit translations between areas of interest – for example, abundance of fish and abundance of lumber can both be translated into an amount of dollars.

Some time around 1963, I realized that the two most basic assumptions of most of quantitative evolutionary and ecological theory were intimately related to capitalism: the assumptions that increase is good, decrease is bad and that more is better than less (Slobodkin, 1964b).

We talk about evolution on many levels. We can describe in remarkable detail comparative anatomy, comparative behaviour, and nucleic acids sequences of living and some fossil organisms. From these we can prepare amazingly detailed phylogenies. There may be dispute about details and there may be missing data, but there is usually broad agreement about the results based on data in hand.

Analysis of the evolutionary past has become an exact science, amazingly different from the speculative discourse of twenty or thirty years ago. By contrast, predictive evolutionary and ecological assertions are much less certain. The goal of a predictive theory is to describe which of the possible paths into the future a particular system will travel. Central to this uncertainty is the fact that the evolutionary process, like all historical processes, admits of myriad possible future scenarios based on initial conditions ranging from climatic to genetic and finally a cloud of possible 'butterfly effects'. Nevertheless, smaller scale attempts at prognostication are made to predict both evolutionary and human history.

News media constantly predict the future of politics, military engagements, and elections. Most of these predications are in the form of hypothetical and uncertain narratives but some of the most widely respected are presented as numbers. Of paramount importance are the numbers that emerge from economic models. The central focus of economic models is money, or things that are presumably translatable into money.

Economic theory is developed by use of contingent models – if the following conditions are met, the economy will have the following properties. This approach often provides a guide to more or less successful manipulation of the system (e.g. the alterations of interest rates to prevent inflation without excessively disturbing stock values). The classical theories of population genetics (Fisher, 1958; Haldane, 1990), and the enormous literature of population genetics that used them as starting points, were also based on quantitative analysis.

We make a tacit assumption that being numerous is a measure of evolutionary well-being, ignoring the fact that both rare and common species currently exist and in many cases rare species are historically older than common ones and that some extinct species were enormously numerous. 'There is safety in numbers!' as the passenger pigeon might have said to the whooping crane. Also in population growth, there is often a trade-off between abundance and physical condition.

Evolutionary success is more difficult to define. In fact, perhaps the best we can do is to define evolutionary success as the opposite of evolutionary failure and evolutionary failure is unequivocally defined as becoming extinct (i.e. having no descendants). Mere numbers are not all that is involved. Very common species can become extinct while very rare species may persist. Passenger pigeon extinction and Kirtland's warbler persistence are supporting examples.

Larger numbers are an indicator of increased probability of survival if, and only if, random events actually are important in determining whether a lineage will survive. Generally, when random events are of high importance, population size and high rate of increase are of highest value. High abundance and high reproductive rate are of value in highly variable environments. Random events can more easily wipe out a small population than a large one.

The components of a formal game are players, strategy, and payoff. Strategy varies with circumstances. In his elegant book *Homo Ludens*, Johan Huizinga[12], a pioneer Dutch cultural historian, described games in a full context (Huizinga, 1938). Specifically, he made it clear that in addition to the components of the game-theoreticians' games, real games always have a playing field of some kind, a place where the rules of the game are the only rules that apply. He also said that winnings from games have usefulness away from the playing field. The winner can walk away from the table with his winnings in his pocket.

In nature, organisms and winnings can never leave the playing field, nor is there any place in which 'winnings' can be safely stored. This suggested the metaphor of an existential game – a game in which the best to hope for was the capacity to continue to play.

All organisms confront the moves of the environment as best they can, ultimately losing and dying, both as individuals and as populations. All populations that are not yet extinct have, so far, successfully played the environment to a draw. I concluded that optimal evolutionary strategy is to change just enough to meet problems, and that big, sudden changes are dangerous (Slobodkin, 1964b).

This idea caught on, although not as broadly as I felt it deserved. Therefore, I rewrote it in collaboration with a real game theorist, my late friend Anatol Rapoport (Slobodkin and Rapoport, 1974). We concluded that an optimal evolutionary strategy is to change just enough to meet problems and that more dangerous environmental changes should claim more attention and resources than less dangerous ones. If there is a massive perturbation, failure to respond massively is extremely dangerous.

If the argument of the existential game is of value, it ought to be the case that organisms should act as if they are making judgements about what is or is not an important perturbation. For example, small perturbations should be responded to by small responses of the organisms.

This suggests an inverse relation between the speed of a response and its utilization of resources or at least its degree of interference with other activities in a specific environment characterized by a particular set of possible perturbations.

Perhaps the most important conclusion of speculation about evolutionary strategy is that evolution generally occurs only in response to perturbation and has no momentum of its own, with the stipulation that new mutations may arise, providing novel solutions and novel problems. It is this new genetic material that permits evolution to continue even if no environmental change is involved. Likely evolutionary futures are highly restricted by the properties of the evolutionary present and the conservatism of the evolutionary process. There are no trends in evolution other than an ongoing, unchanging

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[12] Unlike so many of the iconic intellectuals of the 1940s, Huizinga did not collaborate with the Nazis but died in his third year of imprisonment in 1943.

evolutionary tendency to do nothing and, if anything does occur, to do something in the smallest possible steps.

There are even some social implications. Perhaps the simplest and most important of these is that there is no way to infer from the inevitability of biological evolution that there is inevitability to any particular historical event (Slobodkin, 1977, 1978b). Note that this contravenes a temptation to push evolutionary theory beyond its legitimate borders.

Studies of human behaviour are the deep and muddy waters of biology. Even racism and anti-Semitism can intrude. Some of the material written on this subject is intellectually sound and fascinating (Cantor and Swerdlitz, 2006). More often it is just a series of stock platitudes of philosophy and misuse of history, with a thin shell of evolutionary vocabulary on top. Sometimes these are thinly disguised beery adolescent dormitory debates with an anti-Semitic slant (MacDonald, 1994; Hartung, 1995). I have been reluctant to become involved but I have asserted that human decision makers cannot rely on evolutionary events or theories to provide them with rectitude, explanations or sanctity (Slobodkin, 1977, 1978a, 1978b). Note that this point conflicts with psychobiological theories and sociobiology (Wilson, 1975; Sober and Wilson, 1998).

The recipe for producing explanations of this sort is to begin with a loose stereotypic characterization of some nameable group of people. Then add a sprinkling of quasi-historic facts. Often this involves a loose reading of history, taking some idea that may have been important at one time and acting as if it has been central to all of the history of the group. Most pernicious is to assume that the behaviour of the group members has been unchanging over some long period – usually centuries, but sometimes, if there is some literary excuse, this assumption may be extended to assertions about how these people have behaved, believed, and lived over as long as three millennia. Now add the undemonstrated false assumption that this has had a selective effect on the group's genes. Almost any group that has been even mildly endogamous will show some genetic distinctness.

Finally, one assigns some destructive, or at least unsavoury, property to the characters in the story one has constructed. 'Jews are good at finance'; 'Germans are brutal'; 'Russians are soulful, Armenians complicated'. And we are back where we started, at a baseless prejudice, but now it has supposedly been scientifically demonstrated. None of this corresponds to valid science.

Obviously, there is more to say about this, for example the curious position of the highly influential evolutionary theorist William Hamilton, and the curious relation between the Society for Evolutionary Psychology and overtly anti-Semitic authors like MacDonald (1994) and racist hate groups.

I recommend consideration of detailed description rather than this type of dangerous simplification. As a Jew, I have a personal concern that those who discuss the evolution of Jews read at least a pound of the history and sociology, like that found in the excellent three-pound treatise on recent Jewish American history (Howe, 1976), and also a good collection of scientific studies of Jews, like that by Cantor and Swerdlitz (2006).

Further detail would not be appropriate in this paper, which I am trying to keep as short as I can.

SELF-IMAGE

My concern for the evolutionary role of self-image began with my realization of the obvious fact that words are puffs of air that are harmless in and of themselves, but people may respond as much or more to loaded words than to actual external events. If small responses to environmental disturbances are generally preferable to excessive large responses, how can the capacity for large, sudden responses to relatively minor stimuli by humans have evolved? Why does an insulting word sometimes result in a fight to the death?[13]

I invoked the idea that humans, and at least our nearest primate relatives, have self-images that are powerful factors in determining their actions. The capacity to generate non-hereditary self-images broadens the scope of possible futures resulting from social, historical or environmental perturbation and weakens the expected role of genetic determinism in the study of human behaviour (Slobodkin, 1978a).

Organisms' estimates of the importance of a perturbation may be made in terms of their self-images, without necessary reference to immediate actual physical danger. To some degree, self-image is learned.

RESEARCH BY MY STUDENTS

My teacher, Evelyn Hutchinson, tacked to his wall a magazine page of mottoes. I found the most important one to be, 'Never try to discourage a student for you will certainly succeed'.

Many of my students were so independent that I cannot claim to have taught them how to work. With several students my relation was that of an appreciative spectator and advocate rather than a teacher of biology.

At Michigan, Hairston, Smith, and I taught a 'non-majors' freshman course that the very wise chairman at Michigan, Dugald Brown, gave to us to play with. One fall, my house in Ann Arbor became infested with box-elder bugs. We felt bound to use them and Smith designed a laboratory demonstration that bugs had memory. He set a modelling clay maze consisting of a set of choice points into a pan of water. The bugs could either turn left or right. In fact, they alternated, approximating as close as possible a straight line towards the light.

Hugh Dingle, our TA and a very independent student, manipulated the length of the runway between choice points and also stopped the bugs for an interval until they 'forgot' which choice they had most recently made. The box-elder bugs served as a starting point for his PhD dissertation (Dingle, 1961). He later extended his concerns into a broad variety of organisms and questions (Dingle, 1996).

Some of my students were in graduate school at the same time and taught each other while I watched.

Doug Futuyma and Rob Colwell started their very distinguished careers together at Michigan. I was working on hydra when they were in graduate school. Both of them were terrestrial ecologists.

Very original graduate students are frequently subject to threat from faculty members who are more classical in training and orientation. For these students, I have tried to be a protector against coercion and misguided criticism and against some of the nastier aspects of academic politics. For example, Doug dressed in a mildly 'hippie' mode, which upset some of the Michigan faculty. At his thesis defence, I deliberately wore beads[14]

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[13] Note Groucho Marx's response to the word 'Upstart!' in the 1933 film *Duck Soup*. (Risking war between Sylvania and Fredonia, he slapped the Ambassador who spoke it.)

[14] My beads were three Sassanid seal stones purchased in Israel.

and a dashiki cloth scarf to focus the unhappiness of the faculty on me and away from Doug.

Scott Ferson and Rosina Bierbaum were each enormously self-sufficient. Both of them had chosen what they wanted to do before they arrived at Stony Brook. On only one occasion did they collaborate.

Rosina was working on pea crabs that live in the gill chambers of pelecypod molluscs[15]. These small crabs supposedly did no harm to their hosts. Rosina asked why some pea crabs parasitized only one or two species of pelecypod while others could infect a multitude of species. She found that the ability to tolerate drying during low tides was reduced in infected blue mussels. Also, there were subtle shell shape differences between infected and uninfected mussels, revealed by new statistical tests developed in collaboration with Scott Ferson (Bierbaum and Ferson, 1986).

Rosina took a leave to work for the Office of Technology Assessment of the US Congress. She was so good at this job that when she came back to Stony Brook to finish her graduate work the people in Washington provided her with technical assistance to hurry her return.

The OTA was a brilliantly conceived agency providing carefully researched answers to any and all questions raised by legislators. It was destroyed at the instigation of Newt Gingrich in his second year in Congress on grounds that it gave inferior information and was too slow giving answers. Apparently superior information is gained from less expert personnel and more rapid turnaround time!

Rosina's work in Washington interfered with her research. She was almost kicked out of graduate school because it took her 10 years to complete her thesis, which was against the rules by several years and she never got beyond the common pea crab and the blue mussel.

She worked in several capacities including as a senior adviser to the Clinton administration. She continued in Washington, focusing on climate change before it became a mantra. She is now Dean of the University of Michigan School of Natural Resources.

Scott Ferson did his thesis on the dimensionality of the border between two plant associations (Ferson, 1988). I did understand it briefly. If I tried to explain it now I would need a major review of some difficult math. It was sufficiently abstruse that there were real questions in our faculty meetings as to its applicability to anything 'real'. I threatened a minor tantrum, which decided the issue favourably. In his more recent career, he has been lucid and devastating in his reconstruction of statistical methods for very practical business and government people and has written several clear books on risk analysis, conservation, and more (Ferson *et al.*, 1989; Ferson and Burgman, 2000).

Sometimes the collaboration between students was very practical. Conrad Istock went diving in small ponds to aid Tom Griffing in his collection and observations on hydra.

Glen Lopez at Stony Brook has used field and laboratory studies to deal with many problems. Among these he showed that animals, which certainly cannot digest most detritus, nevertheless contribute to its decomposition by triturating it, making more surfaces available to bacteria and moulds, and also by apparently eating the bacteria off the particles in a fashion reminiscent of consuming corn on the cob, but the 'cobs' can then act

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[15] Almost 100 years ago, when my father was running the elevator for guests like Diamond Jim Brady and Lillian Russell at the Ten Eyck Hotel in Albany, New York, these were considered special treats when found in platefuls of raw oysters. They were eaten alive while crawling over back teeth. Note that this kind of information often tries to crawl into my account and must be seriously resisted.

as new substrate. In fact, Glenn has done much more than that and my role in his life was just perhaps as a starter – but perhaps not even that. Hecker, Lopez, Loya, and Dustan became full-fledged biological oceanographers, a specialty I have envied but never attained.

SIMPLICITY

This section relates to one of my excursions beyond ecology. Inquiring into 'simplicity' was clearly beyond the borders of my scientific authority, although it was suggested to me by research and continues my broad programme of questioning whatever seems to be incomprehensible[16]. It would have been difficult and dangerous for any graduate student to follow. As a matter of fact none did.

Recall that I decided to study hydra because they were 'simple'. As the decades passed, it finally penetrated my consciousness that the meaning of 'simple' varies with context and that I was extremely uncertain as to what the word 'simple' meant. The meaning of simplicity is not obvious. The more I thought about simplicity and complexity, the less I understood. I discussed these problems initially in a presidential address to the American Society of Naturalists (Slobodkin, 1986).

What does it mean to say that an organism, or anything else, for example a painting or a song, is simple as opposed to complex? What is the role of extreme simplicity, of minimalism? In art, minimalism can be built only on complex predecessors, growing from rejection of complexity. On the other hand, complexity often evolved out of simplicity. Although some philosophers are concerned with this issue, I was not concerned with philosophical analyses, which, ironically, usually begin by simplifying the problem. I could not provide any definitive analysis of simplicity and complexity but I could provide an abundance of examples to encourage further questions.

Most of the philosophical analyses of simplicity start with redefining the question in such a way as to eliminate some of its most interesting aspects. For example, they often ignore ethical elements in the problem. They simply accept that simplicity is virtuous and will be rewarded, while complexity is somehow evil and that deliberate complexity probably deserves to be the object of sumptuary legislation.

In the history of organisms, apparently simple ancestors have sometimes given rise to complex descendants and the converse. While hydras are considered a prototype of morphological simplicity among metazoans, their cellular structure is complex. Mammals are usually considered to be more complex than hydra but each mammalian cell is by most standards simpler than most types of hydra cell.

In 1992, I had the good luck to have an extended sabbatical while I was worried by these issues. I wrote a book, *Simplicity and Complexity in Games of the Intellect* (Slobodkin, 1992), hoping to clarify my understanding of simplicity and complexity, the way *Growth and Regulation of Animal Populations* (Slobodkin, 1980) clarified my thinking about classical population dynamics. I was supported by the Woodrow Wilson Institute, the Italian National Research Council, and the Imperial University of Tsukuba. This is the only 'research' I have done that did not have an immediate relation to colleagues or students.

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[16] 'Science' in this sense consists of the intellectual areas in which my academic status lends *gravitas* to my pronouncements.

I liked the book, as do some others, but it did not sell well. It was excessively interdisciplinary. It is one of my favourites but no-one actually needs a book that is not part of a defined field of interest.

IN CONCLUSION: WHAT ARE THE LIMITS TO ECOLOGY?

Clearly, ecology can be done on many levels, ranging from interrelations between microbes to those between oceans and nations. Occasionally, ecology has even altered everyday language. An early example came from the observations on pecking order in chickens and dominance in wolves and dogs (Allee *et al.*, 1949). People speak of themselves and others as high or low in the pecking order[17] or as being alpha or beta males.

To feed low on the food chain had the original sense of herbivores or detritivores, but popular usage has fixated on the word 'low' in its sense of inferior, suspect or immoral. To say that someone feeds low on the food chain originally inferred a vegetarian diet but now connotes that they are in some sense 'inferior'.

There is a danger that scientific momentum can become lost and, in the stagnation, a generally accepted set of procedures may be canonized. Papers may be judged by the apparent elegance of their statistics and sophistication of their procedures and by how closely they approach some previous work. This is somewhat analogous to the emphasis on 'finish' in evaluating nineteenth-century painting. It becomes a particularly attractive approach in the context of having to award funding.

Ecology was a very small field. Sometime around 1961, MacArthur said, quite seriously, that there were only a dozen ecologists. It was not true when he said it, and is considerably less true now. Nevertheless, when compared with most sub-areas of biology, ecology does remain a relatively small field. Ecologists are measured in thousands rather than the tens of thousands of biochemists or physiologists.

I have been most fortunate in my students, colleagues, and friends. Some are acknowledged leaders. Some function on a more local scale. With a very few exceptions, who I have not mentioned and will not mention now, I feel proud of them or at least proud of not destroying them. Students are fragile.

Some of the specific questions that have focused my attention have been discussed. There are, underlying these, a set of implicit questions and possible answers that may be important:

- Is ecological theory useful? Yes.
- Is there a unified mathematical theory of ecology? No, but there can be very useful, small, null models.
- Is ecological efficiency real and is it in any way maximized? It is real and meaningless.
- Is anything maximized in evolution other than persistence itself? No, but local circumstances may permit the use of maximization or optimization for specific properties.
- Is the evolution of humanity unique? Yes, but watch out for dangerous just so stories.

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[17] I have been told that W.C. Allee, a famous early ecologist, while in charge of department meetings at the University of Chicago, would hand out memos saying that they should be 'passed down the pecking order'.

A usual pattern for the conclusion of collections of papers is a kind of soft euphoric fading into the sunset. I feel that I have been lucky in various ways and have also failed in various ways. I do claim that what ecologists have done – and I, my students, and my friends were active participants in the process – is to change humanity's sense of itself as an inhabitant of the planet. In the last 60 years, there has been a massive alteration of the human attitude towards nature. On 7 June 2007, two billion people around the world watched celebrities loudly supporting ecology! When partisans number in the billions, we are not talking about eccentric tree huggers.

Were ecologists necessary for this alteration in attitude?

Recall the old story about the fly on the chariot that looked back and said, 'See how much dust I have raised'. Of course, political leaders and other celebrities are the most conspicuous faces and sounds of the great ecological revolution. But it was our chariot in the first place and we had best be prepared to take the reins as necessary!

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