Aldo Leopold and the Ecological Conscience

Edited by **Richard L. Knight**
Suzanne Riedel

Chapter 4

Then and Now

JAMES A. ESTES

To be entirely honest, Aldo Leopold was unknown to me in 1967 when I began graduate study in wildlife biology at Washington State University. I entered graduate school with a traditional education in zoology, which did not emphasize conservation, natural resource management, nor, for that matter, even ecology. Frankly, I can't remember what it was that drew me to the natural sciences other than perhaps a fondness for nature and an aversion to normal day-to-day work activities. I first learned of Aldo Leopold from Professor Irvin Buss, one of Leopold's last doctoral students at the University of Wisconsin. *A Sand County Almanac* was recommended reading in Professor Buss's wildlife ecology course, which I took during my first semester. The course itself probably left little of substance in my worldview, but my first reading of *A Sand County Almanac* struck an emotional chord that I will carry to my grave. From the initial sentence of the foreword, I counted myself among those who could not live without things that are wild and free. Although biology was a topic of boundless wonder for me in those days, I knew then that my quest was for a life that offered intellectual fulfillment in places that were wild and free. In looking back now, the poetic force of Leopold's words influenced both the way I

think about nature and my approach to science. This essay is a reflection on those influences.

Leopold's Visions of Nature

A Sand County Almanac has touched the human soul in various ways. For some, the power of Leopold's writing lies in its poetic quality—his magical ability to capture in words the emotions that most of us only feel when we hear a wolf howl or see the spectacle of sun and clouds at twilight. For others, this power comes from the philosophical revelation of his land ethic—a neo-Malthusian realization that humans must learn to value land as the cradle of existence rather than as the economic commodity of further growth and development. For a smaller number of professional ecologists, Aldo Leopold's force lies in his remarkable grasp of nature's fabric. I have read *A Sand County Almanac* on various occasions over the past thirty-four years, usually in an effort to revitalize my own spirit. But in refreshing my memory of the details as I prepared to write this essay, I was astonished to discover that Leopold had observed and clearly understood the ecological relationships among wolves, ungulates, and vegetation more than fifty years ago—that the systematic elimination of wolves from North America meant too many ungulates and overgrazed rangelands. I really can't imagine how this important realization escaped me, as it apparently has escaped so many others who also should know better.

The roots of this general idea—that herbivores are limited by predators, thus releasing plants from regulation by herbivory—are commonly attributed to Hairston, Smith, and Slobodkin's Green World Hypothesis, published in 1960 and still a cornerstone in the conceptual arsenal of community ecology (Hairston et al. 1960). Food chain interactions of this sort have come to be known as trophic cascades (Carpenter and Kitchell 1993), and the degree to which populations are regulated by "top-down control" remains one of ecology's foremost topics of debate and inquiry, especially in terrestrial ecosystems (Pace et al. 1999; Polis et al. 2000). In the early 1990s, newly discovered evidence for a trophic cascade among wolves, moose, and balsam fir on Isle Royale in Lake Superior was viewed as so novel and important that it warranted publication in *Science* (McLaren and Peterson 1994).

But having lived through that time in history when wolves went from being abundant to rare, Aldo Leopold saw and understood the general process much earlier.

The conceptual significance of Leopold's allegory on wolves and deer escaped me in 1968, even though eight years already had passed since publication of the Green World Hypothesis, during which time the subject of top-down control in population regulation was an issue of active interest and debate (Murdoch 1966; Ehrlich and Birch 1967). My failure to make the connection probably stemmed from the fact that I had not yet seen enough of nature firsthand to solidify the ideas in what was then a contextually vacant mind. However, the fact that the centerpiece of my life's work on sea otters and kelp forests was to be founded on this very concept strikes me in retrospect as ironic, if not somewhat embarrassing.

Although I admit to being unmoved by the Green World Hypothesis during those early years and blind to the significance of Leopold's vision, a fascination with the larger temporal dimensions of nature was beginning to capture my lasting interest. Every person with even a modicum of sense has a clear grasp of what time is. But in the *Almanac*'s entry for February, the poetic chronicle of time that unfolded as Leopold's sawyer passed through the "good oak's" eighty annual rings made the interplay between time and nature come alive for me. Considerations of history and time were not new to biology. Time had long been a fundamental dimension in paleontology and evolutionary biology, but wildlife biologists and ecologists tended to collapse the relevant temporal dimensions in their thinking to scales that could be observed over the course of a human lifetime, usually much less time. This limited perspective of time probably stemmed in large part from a desire for methodological rigor in ecology and wildlife biology. Many practitioners of these disciplines believed then that the best science comes from controlled experiments, which necessarily limit the scale of time over which science can be done. But this approach also leaves many important questions unanswered and unanswerable. It also tends to lull us into a state of intellectual apathy when confronted with the potential importance of past events, such as the extinction of wolves in large parts of North America. Moreover, such an approach encourages us to view modern-day ecosystems as though they have always been more or less the way we now under-

stand them to be, even though we all know that isn't the case. I admit that this characterization of how many ecologists viewed the world is an oversimplification and perhaps even unfair, but one need not look far for examples of its overlying truth.

Why History Matters

History matters for the simple reason that it is the pathway to the present. This principle is well known in both human societies and the field of evolutionary biology, where fortuitous events have set the course for all that follows. Imagine just how different the track of human history might have been if the Mesopotamians had not lived in a region with such a large proportion of the world's potentially domesticable plants and animals. The resulting shift from a hunter-gatherer to an agricultural society permitted the accrual of wealth (largely in the form of food), in turn leading to the development of armies and European dominance in the course of world conquest (Diamond 1997). Imagine just how different life on earth would be today if a happenstance meteor had not collided with Earth some sixty-five million years ago, extinguishing most of the dinosaurs and setting the table for the Cenozoic radiation of birds and mammals. In neither case is it possible to predict the course of events had the original natural phenomenon not occurred. But without doubt, subsequent history would have been very different.

The fundamental importance of many other signal events in human history and evolutionary biology is widely known and broadly appreciated. However, the conceptual underpinnings of ecology have never placed an unequivocal premium on the nature of connections between past and present. Lewontin (1969) set the stage for thinking about this issue in his classic paper, "The Meaning of Stability," in which he recognized two fundamentally different ways that ecological systems might behave. Lewontin imagined that systems perturbed from equilibrium conditions are subject to "transition vectors"—forces that cause populations to change depending on their altered relationships with other species and the physical environment. For instance, an abundant population of deer reduced by overhunting or a hard winter would be expected to increase until it returned to its natural equilib-

rium state; the transition vector in this case would be the demographic differential between births and deaths, fueled by a surplus of food. But Lewontin also recognized that whether perturbed systems return to their initial state or some other state depends on whether the field of transition vectors is linear or nonlinear. If the transition vectors are linear, the system will always return to its initial state. However, if the transition vectors are nonlinear, a perturbed system may shift to alternate stable states, depending on the magnitude and direction of the perturbation. History is of no real consequence to globally stable systems because such systems predictably return to the same state following perturbations of all kinds, so long as no species is extinguished in the process. However, history is an essential dimension in understanding systems with multiple stable states because their current position always depends on where they came from. Although there now is reasonably good evidence for the existence of systems with multiple states in nature, ecologists remain undecided as to whether such behavior is the exception or the rule. Thus, even from this theoretical perspective, the importance of time and history in understanding ecosystem behavior is equivocal in the minds of many ecologists.

Some Examples

A growing number of examples point to the depth of understanding that historical data bring to wildlife biology, fisheries, and ecology. The foremost such example in my mind is in what Janzen and Martin (1982) have termed "neotropical anachronisms"—alleged misinterpretations by many tropical ecologists of the results of modern-day studies by failing to recognize important roles played by the recently extinct New World megafauna. Janzen and Martin's insightful theory was founded on a history of observations of these facts: numerous tropical trees produce large, sweet fruits that surround tough seeds, and, throughout much of the modern neotropics, these fruits fall to the ground below their parent trees where they rot or are eaten by various micro- and mesoherbivores. The dynamics of these fruit-herbivore interactions had been the subject of a rich ecological literature in which, in many cases, evolutionary consequences were stated or inferred. Janzen and Martin speculated that, in the past, these fruits were likely consumed and

their seeds dispersed by the gomphotheres and other large Pleistocene frugivores. Thus, they rarely, if ever, accumulated to rot or be consumed by the micro- and mesoherbivores until the New World megafauna was extinguished some ten to fifteen thousand years ago. They used changes in plant distribution and fruit-frugivore dynamics associated with the recent reintroduction of Pleistocene horses and other large mammalian herbivores to the New World tropics to make their point.

Similar stories are unfolding through the amalgamation of ecological and retrospective data to enrich our understanding of other contemporary ecosystems. For instance, Jackson et al. (2001) have concluded that coastal marine systems throughout the world now function in grossly different ways than they did in the recent past, in large part owning to the reduction or extinction of large consumers and other abundant species. For example, in the Chesapeake Bay, the removal of oyster reefs (estimated to have filtered a volume of seawater equivalent to the entire bay every three days!) has brought about dramatic changes in the marine food web, converting a system driven by benthic producers into one driven by phytoplankton. Benthic cores provide marine ecologists with evidence that the waters of the Chesapeake were clear before the oyster reefs were gone. Similarly, notes recorded by early Spanish explorers reveal that Caribbean sea grasses were short and sparse compared with what they are today. This difference is likely connected to the history of sea turtles and perhaps manatees, which consume sea grasses. These animals were spectacularly abundant several centuries ago but are rare today. In these and many other cases, the knowledge of history adds richness and relevance to the results of modern-day research in ecology, wildlife, and fisheries. These connections, for the most part, are yet to be discovered.

The Tree-Ring Prophecy

The aforementioned examples, although probably conceived by their creators with little or no influence from Aldo Leopold's words in *A Sand County Almanac*, nonetheless are indicative of the prophetic nature of his thinking. Nowhere is that prophetic insight more evident than in his prediction that "Some day some patient botanist will draw a frequency curve

of oak birth-years, and show that the curve humps every ten years, each hump originating from a low in the ten-year rabbit cycle" (Leopold 1987, 7). Indeed, tree rings have since been widely used by ecologists and geochronologists to unlock the broader sweep of nature's time, including the history of fire and rainfall and even the influence of predators. McLaren and Peterson (1994) used tree-ring analysis of the growth of balsam fir saplings on Isle Royale to chronicle evidence in support of their theory of top-down control by wolf predation on moose. Similarly, Ripple and Larsen (2000) reconstructed a frequency curve of aspen birth years from the record of annual rings in living trees to show that there has been virtually no recruitment in northern Yellowstone aspen forests since about 1920, the approximate year that wolves were extinguished from Wyoming to better the interests of ranchers and big-game hunters. To use Leopold's own words, these examples "attest the unity of the hodge-podge called history" (Leopold 1987, 16).

How many similar stories will emerge as future testimonies to Leopold's vision of time? Many, I suspect. Consider the potential significance of history to the understanding of a major human epidemic, Lyme disease. The ecology of Lyme disease is well known, at least in the northeastern United States (Jones et al. 1998). The disease is caused by a microbe contracted by humans through the bite of deer ticks. Deer ticks require two other species —white-footed mice and white-tailed deer—to complete their life cycle. If either of these species is rare, tick populations remain depressed and the threat of Lyme disease in humans is reduced. Oak mast events are the key to bringing sufficient numbers of deer and mice together in space and time because both species are attracted to acorns. Consequently, the threat of Lyme disease is greatest following oak mast events, which occur episodically in eastern deciduous forests. Now imagine how the events of history may have impinged on this situation. Oaks and chestnuts are natural competitors in forest ecosystems. Oak forests undoubtedly have become more abundant over the past century because of chestnut blight. White-tailed deer also have become more abundant in recent decades with the extinction of wolves, their main predator. Today, mast crops probably accumulate in larger numbers and remain on the ground longer than they did when passenger pigeons darkened the skies of the eastern United States. In fact, this now extinct

species appears to have been designed to key in on and exploit oak mast crops, traveling from area to area in immense numbers in search of these events. Might it be that the collective force of these events has lead to the Lyme disease epidemic?

Nature's Fabric

The fabric of nature is woven more by species interactions than by species themselves. But while species are reasonably easy to observe, species interactions are not. Witness the large number of species and the small number of species interactions that are presently known to science. The cryptic nature of species interactions stems from the fact that such interactions are typically only recognized following perturbations to one of the interactors. This is one of the principal reasons that ecologists do experiments—to clarify the nature and strength of species interactions. The experimental approach has indeed revolutionized ecology. The problem is that the amount of time needed to see an interaction varies greatly among species and ecosystems, in general scaling to generation time, thus explaining why so much of experimental ecology has focused on short-lived species and why so little is known about interactions among longer-lived species. Many species studied by traditional wildlife biologists are experimentally intractable.

A good deal of my professional life has been devoted to the study of interactions between sea otters and kelp forests, an experimentally intractable system but one in which history and time have served as essential methodological allies. I was introduced to sea otters and kelp forests at Amchitka Island in 1970, a time at which sea otters were abundant and had been for several decades following their recovery from near extinction by overhunting in the Pacific maritime fur trade. I remember studying the otters and diving in their kelp forest habitat for nearly a year with a mind toward somehow understanding the ecology of that system but with almost no idea of what to look for. I was aware that, in the past, otters had been eliminated from nearly all of the Aleutian Islands and were still absent from some of these, but my mind was so focused on bottom-up forcing that it never occurred to me that

a visit to one of the unoccupied islands might be of any interest. In 1971, I was fortunate to meet R. T. Paine, who had recently completed the first of his now classic studies of predation by sea stars in intertidal mussel beds. Bob encouraged me to think about how the otters might be influencing the kelp forests. With that kernel of inspiration, a reason to visit the unoccupied islands was clear and urgent.

So, together with fellow graduate student John Palmisano, I traveled to Shemya Island (then unoccupied by otters) later that summer for a look. Our first peak at the sea floor immediately provided one of the most exciting revelations of my professional life. While Amchitka supported a few small sea urchins and lush kelp forests, at Shemya, large and abundant sea urchins had grazed away the kelp forests. Knowing that sea otters consumed sea urchins, that sea urchins consumed kelp, and that sea otters had once been abundant at Shemya, we immediately surmised that sea otters played an essential role in maintaining the kelp forests (Estes and Palmisano 1974). Further investigations comparing areas where sea otters had recovered with those from which they remained absent confirmed this interaction, as have longitudinal studies of particular sites at which the otter numbers subsequently have increased or decreased. This same approach has revealed complex linkages between sea otters and numerous other species in the kelp forest ecosystem, thus contributing to our view of the sea otter as a keystone species. This experience taught me the role history could play in shedding light on natural processes that might otherwise be difficult or impossible to discern.

Concluding Remarks

My view of nature has been strongly influenced by the force of history, in part from what I have seen in my own work and in part from what I have learned from others. It is difficult for one to look back over a lifetime and really understand how such views come to be, although there are formative events that stand out. Aldo Leopold's chronicle of time as the sawyer's blade passed through eighty years of history in the "good oak" was one such event in my life. Having read *A Sand County Almanac* several times over the course

of my professional life, most recently in preparation to write this essay, I am struck more deeply at each reading by how much Leopold's view of nature was guided by an interest in and understanding of the broader sweep of time. Aldo Leopold is widely acknowledged as a visionary in the field of conservation. His appreciation for the intimate connections between time and nature is no less prophetic.

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