CHANCE *and* CHANGE

ECOLOGY FOR CONSERVATIONISTS

WILLIAM HOLLAND DRURY JR.

EDITED BY JOHN G. T. ANDERSON
WITH A FOREWORD BY ERNST MAYR

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7 Secondary Succession

In 1942 I took a course in ecology that used the standard text by Weaver and Clements on plant ecology (1938), which described the theory of succession as consisting of two important components: primary and secondary succession. I have alluded to portions of both of these components in previous chapters, but I feel it is important to address the theory as a whole and point out where it conflicts with Darwinian natural selection.

The scientific concept of succession is an abstraction of a higher order than simple recognition of the facts that: patches of vegetation vary from place to place; time sequences among patches can be found on river floodplains, sand dunes, or old fields; and the occupants of the patches can be arranged by categories of height, number of species present, and the rate at which plant material is produced.

Almost everybody has his or her own special meaning for "succession," akin to what Humpty Dumpty recognized in his discussion of definitions in Lewis Carroll's *Through the Looking-Glass:*

> "There's glory for you!"
>
> "I don't know what you mean by 'glory,'" Alice said.
>
> Humpty Dumpty smiled contemptuously. "Of course you don't—till I tell you. I meant 'there's a nice knock-down argument for you!'"
>
> "But 'glory' doesn't mean 'a nice knock-down argument,'" Alice objected.
>
> "When I use a word," Humpty Dumpty said in rather a scornful tone, "it means just what I choose it to mean—neither more nor less."
>
> "The question is," said Alice, "whether you *can* make words mean so many different things."
>
> "The question is," said Humpty Dumpty, "which is to be master—that's all."
>
> Alice was too much puzzled to say anything.

The very ill-defined nature of succession allows it to enrich nearly everyone's perception of nature. To many, it is simply change in vegetation and is used only to describe: the sequence of flowers from spring through summer into fall, the zones of vegetation evident on mountainsides, or the zones of vegetation from the tropics to the Arctic. Foresters and wildlife biologists in their practical applications, use "successional habitats" or "second growth" for almost any vegetation on the spectrum, from grassy fields, brambles, and brush to thickets and stands of saplings that "invade" cutover or burned-over land, blowdowns, old fields, river valley thickets, and sand dunes.

But succession has additional implications: the succession of fossil forms in geological ages, the "stages of evolutionary progress," the succession at the end of a dynasty inevitably involving a struggle for power. Succession comes to imply replacement and successful competition. For example, it has been applied to the zones of aquatics through emergent sedges to bushes and forest on the margin of a pond; the zones of plants on sand dunes, from the outer beach to the back dunes; the zones of plants from grasses and sedges, through willows and alders to trees on a river floodplain; the sequence of plants following a fire; the sequence of plants on abandoned farmland.

The Linnaean concept of morphologically defined species has had an important impact on how botanists think about vegetation. Plant ecologists accepted plant communities to be vegetation's equivalent of species —entities whose morphological features clearly distinguish them from neighboring forms. In this context Cowles emerges as the giant who founded the American school of ecology. He introduced the idea that vegetation is dynamic, in contrast to the idea then current in Europe that vegetation is static. Cowles studied and described the vegetation of the sand dunes on the south shore of Lake Michigan (1899, 1901). He identified the plant community as the unit of study and determined what he considered to be a sequence of vegetation, from the sparse grasses along the lakeshore, through brushy hollows, to forests of pine and oak or beech and maple on the dunes farthest inland.

Clements identified the long-term development of vegetation that occurs under natural conditions on geologically young surfaces such as mountains, river floodplains, and sand dunes as "primary succession" (1916). Clements hypothesized that during primary succession pioneer species colonize bare ground and, as they die, add organic material to the soil. As the soils deepen and increase in organic content, additional species colonize until the vegetation reaches its maximum development, the climax, which remains at equilibrium on the reduced relief of the oldest topography.

An important component of this theory is that species at each stage of the succession *prepare the way* for the species that will replace them. Early successional species alter their environment to make it better for subsequent species and worse for themselves. While individuals and species are replaced, the community as a whole moves toward some stable equilibrium ultimately determined by climate.

Clements applied the term "secondary succession" to changes resulting from windstorms, fire, and human effects because he considered them to be temporary deviations from the original climax. Since much of the initial "preparatory" work had already been done during the original or "primary" succession, secondary succession would take less time to achieve climax conditions. The actual amount of time required would of course depend upon how many "seral stages" were needed to restore conditions to equilibrium. It is important to note that inherent in this worldview is the notion that balance is the fundamental nature of things, and anything that disturbs this balance is considered "unusual" or an aberration that will be eliminated by the self-correcting mechanisms of the community.

The degree to which this view came to dominate much of ecology is evident in a paper by MacArthur and Connell published fifty years after Clements's formulation (MacArthur and Connell 1966): ". . . a clue to all of the true replacements of succession: *each species alters the environment in such a way that it can no longer grow so successfully as others.*" Twenty years later the notion of a climax equilibrium was alive and well in a widely used textbook in general ecology: "The climax is recognized as a steady-state community with its constituent populations in dynamic balance with environmental gradients" (Krebs 1985). Today, many environmentalists still hold onto its tenets, although many scientists have abandoned the essential elements of the theories.

[Editor's note: The notion of climax equilibrium is still going strong, as is evidenced in a recent ecology text by Rickleffs (1993): "Once forest vegetation establishes itself, patterns of light intensity and soil moisture do not change, except in the smallest details, with the introduction of new species of trees. . . . At this point, succession reaches a climax; the community has come into equilibrium with its physical environment."]

THE ORDERLINESS OF SECONDARY SUCCESSION

Secondary succession in abandoned fields has been widely used to illustrate succession in high school and college textbooks. Changes in vegetation in old fields have been observed on an almost infinite number of abandoned farms nearly everywhere in the eastern United States during the last 150 years.

Once a farm or garden is abandoned, the first plants that appear on the site are small, herbaceous, and fast-growing annual or biennial garden weeds. Perennial weeds follow the annuals, then woody brush overtops the wildflowers. Soon, trees appear—usually eastern red cedar and gray birch on sandy soils in southern New England, white pines in central New England and paper birch or white spruce in northeastern New England. Variations on the theme are common. Eventually, obvious change slows and "succession stops."

These changes have generally been explained by plant ecologists in the way that Whittaker did in describing succession on an old landslide: "One dominant species modified the soil and the microclimate in ways that made possible the entry of a second species, which became dominant and modified [its] environment in ways that suppressed the first and made possible the entry of a third dominant, which in turn altered its environment" (1975). But do the early species facilitate the establishment of the later arrivals, or, once established, do they just live out their lives until displaced by plants that overtop them? Where do the species come from that appear in succession? Is a particular stage in succession the adaptive habitat of particular species or do these species occupy other, geologically defined habitats, from which they expand their ranges opportunely and temporarily?

DIRECT EVIDENCE FROM ABANDONED FIELDS

McCormick examined the effects of early pioneers on succession in an old field, and his observations indicate that the early arrivals inhibited the establishment of later arrivals:

> Annual plants were removed as seedlings from some sections of a recently plowed field, but were allowed to grow elsewhere. According to reaction theory, an annual vegetation is necessary to "prepare the way" for perennial plants on such a site. By the end of each summer, however, perennial plants were several times as abundant on areas kept free of annuals. The biomass (dry weights) of individual perennial plants on the annual-free areas were many (15 to 82) times as great as those on areas with annuals. Many goldenrods, asters, black-eyed Susans, and other perennial plants flowered on annual-free sections, but were sterile on plots covered with annuals. . . . This experiment does not refute the general theory of the reaction mechanism. However, it does seriously question the reality of the theory and indicates that the theory was not valid for the early old field situation in which it was tested. (1968)

Note that McCormick, like most botanists at the time, was willing to consider his observations to be anomalies in a general law, rather than falsification of a preestablished hypothesis.

A long-term experiment in New Jersey by Pickett both explained how traditional old field succession may appear to occur and examined the detail of plant composition that refuted the theory. Pickett stated,

> Changes in species composition and cover were followed in an oldfield abandoned after plowing in the spring of 1960. Twenty years of data collected since then show the succession to be individualistic, that is, composed of broadly overlapping population curves through time. In general, the population curves exhibit long, persistent tails, indicating that, through this time span, succession is a process in which species that are present for much of the time become dominant at different times. Invasion and extinction are not the major mechanisms of community change. Bi- or multi-modal peaks were discovered in some species, . . . Many species which are important later in the sequence invade early. . . .
>
> . . . The community pattern is clearly a temporal continuum as has been long expected. . . . Examining only the *peaks* of the 10 or 12 leading species, i.e. ignoring the lower portions and tails of the species distributions, would allow the description of groups that correspond to the aspect dominant stages of succession often referred to. Clearly, however, examining the whole suite of species and their complete responses shows that the mechanism of community change is not one of sudden shifts between discrete compositional communities. (1982)

A major argument has been that some species, like alders and willows, prepare the way for "later successional" species, and hence that the delay in development of boreal forests could be attributed to the relatively recent retreat of the glacial ice. This seemed to have been confirmed by Cooper's studies of the colonization of raw soils in Glacier Bay, Alaska, where glaciers have been rapidly retreating during the last one hundred years (1923). Many textbooks have used this sort of observation to illustrate the "principle" that pioneer mat plants, shrubs, willows, and alders prepare raw soils for colonization by trees of the mature forest. But, recall from chapter 5, Sigafoos and Hendricks found that the time between the point when the ice left glacial moraines at Mount Rainier, Washington, and when tree seedlings became established was indeed short (1969). All of these examples show that different species respond in different ways, and that the reasons for events differ from place to place.

VEGETATION CHANGE AS OBSERVED IN THE FIELD

I spent the first summer of graduate work taking courses at the Harvard Forest on the Massachusetts uplands in Petersham, about seventy-five miles west of Boston. When Harvard acquired the forest at the end of the nineteenth century the university planned for the forest to support itself through continuous cutting of its maturing stands of white pines according to principles of sustained yield.

It emerged from the detailed and long-term studies carried on at the Harvard Forest that the rolling hills and upland soils around Petersham had been cleared first by veterans of the American Revolution. By the 1840s, 85 percent of the land was cleared and in farms. Then in midcentury the economy of hill farms on the sterile upland soils of New England collapsed, and they were rapidly abandoned (Raup 1966). White pine seedlings, whose seed source was the trees that stood along fence lines and in woodlots, took over the abandoned farmland. These trees reached harvestable age at the end of the nineteenth century.

Sustained yield cutting of white pines preoccupied the early research at the Harvard Forest. This research became politically relevant when the Yale foresters were able to regenerate white pines at their experimental forest on the extensive sand plains of southern New Hampshire, while the Harvard foresters were unable to do so on the heavier soils of the uplands of western Massachusetts. The first director and the staff at the Harvard Forest expended a plethora of experimental efforts in order to maintain a sustained yield of white pine lumber, only to meet with perennial frustration. It became increasingly clear that seedling hardwoods had established root systems and grown up under the pines during the years of the original white pine stands. These seedlings were cut back, but after the mature white pines were cut the hardwoods sprouted from stumps. Because the hardwoods already had an extensive root system, they rapidly overtopped volunteer or planted white pine seedlings. The labor costs necessary to suppress the hardwood sprouts could not be justified economically.

The failure and frustration culminated in 1938, when a major hurricane crossed Long Island and passed up the Connecticut River valley, virtually eliminating the remaining mature growth of white pine. At that point, Hugh Raup was appointed director of the Harvard Forest. The 1938 hurricane not only ended attempts to reestablish white pine, it also gave Raup the opportunity to establish his own program of research. His central philosophy was to ask "naive questions." In this case he asked what the forest had been before it had been cleared by the settlers.

The summer that I was at the forest, Raup was planning a new program of research with the help of Steve Spurr, a professional forester. Spurr identified the oak-hickory stands on dry, coarse soils on south-facing slopes as successional, and he reserved the category *mature* for beech, yellow birch, paper birch, and sugar maple stands, all of which require moist, fine-grained soils (1950, 1956). These trees are indeed the most shade tolerant species. Over most of the slopes, Spurr pointed out, "two species are practically omnipresent. Red oak and red maple are equally prominent on all successional stages and one or the other is prominent on all sites. . . . Both exhibit a marked relationship to soil moisture, red oak being most frequent on the drier, and red maple on the wetter, sites" (1956).

Actually, most of the second growth covering the uplands consisted of patterns and mixtures of sugar and red maples, red oaks, white ash, paper birches, white pines, hemlocks, black birch, and some hickories. The patches seemed to vary strikingly from place to place, here approaching the transition hardwoods, there the northern hardwoods.

Spurr was already thinking in terms of delineating species distributions by site preference, using five categories of soil moisture. This eliminated the need to use the categories of successional stands that most foresters use: pioneer, transitional, and late successional. For example:

> Of the other species, the various birches are the most important. Paper birch is best adapted to the drier sites, black birch to the average well drained sites, and yellow birch to the wetter sites. White ash is locally important on the imperfectly drained soils, but shows little persistence into late successional stages. White oak is important in all successional stages

Paper birch, pen-and-ink botanical drawing, 1941.

> on the drier soils, while hickories are somewhat less xerophytic, being found on the well drained as well as on the very well drained sites. Beech and sugar maple are occasionally found on the intermediate sites; while red and black spruce, tamarack, elm, and black gum are found on the wettest sites. (1956)

Note that this sort of description emphasizes the relationship of individual species to their environment, rather than stressing interrelationships between species.

Egler offered two testable alternative hypotheses focusing on "process" in successional theory (1954): relay floristics (each community alters the site in ways that allow others to colonize and displace it); and initial floristic composition (species colonize the area in a scramble, and some appear earlier because they disperse and grow more quickly). It is important to note the differences in process involved in these two hypotheses. In relay floristics early species "foul their own nest," creating an environment where they can no longer persist. Under initial floristic composition, seed dispersal and seed sources become the critical factors. In the 1950s, Egler offered a $10,000 prize (republished in 1975) to anyone who presents confirmable evidence that relay floristics occurred. Over the last forty years, no one has submitted a claim for the prize.

Under Darwin's theory of natural selection, individuals possessing heritable traits that enhance their survival and reproduction are likely to persist and spread. Individuals lacking these traits will die out. It would seem that the theory of relay floristics violates this process or at least consists of an easily circumscribed sequence. There would be strong selection pressures favoring members of "early successional" species to suppress their successors, and strong selection pressures opposing those individuals that enhanced the growth of competitors.

THE SECOND GROWTH: WEED SPECIES OR OLD GROWTH?

The vegetation that grows in a disturbed area is often patronizingly referred to as "second growth." Raup pursued the identity of such plants, and studies by his student Carlson showed that the species that follow the old-field "pioneers" deserve more respect. Raup and Carlson compared the distribution and abundance of the trees found during their study in the Harvard Forest with information recorded in one of those historical gems that occasionally come to the aid of a biologist interested in history (1941): Whitney's *History of the County of Worcester* written in 1793. Whitney had listed the trees found in remaining stands of upland forests and the tall trees that grew along the fence lines that had been left when the farmer cleared. Through this comparison Raup and Carlson found that the species composition of the second growth closely resembled that of the forests that covered Petersham when the first white settlers arrived.

Raup and Carlson compared the distribution and relative frequency of tree species in contemporary stands with that in the precolonial stands.

$10,000 Challenge

Challenge, to any believer in "plant succession to climax."

I, *Frank E. Egler,* hereby and herewith agree to wager any sum up to

TEN THOUSAND DOLLARS ($10,000)

against an equal amount, the money to be donated to a nonprofit organization scientifically investigating the subject of Vegetation Change under natural or seminatural conditions, thru a period of more than 25 years, if any such believer will produce the evidence, either from the published scientific literature, or from unpublished research.

I stipulate that such research must support the Belief that natural and seminatural Vegetation change is a cause-and-effect phenomenon of ingoing and outgoing populations of plants, involving at least five stages, as indicated in diagrams published by me, in the sequence referred to as classical "Relay Floristics." Any contender will give advance notice in writing. He will prepare to submit all evidence in writing within six months of that time to a Commitee of Six Judges composed of ecologists Roland C. Clement, William H. Drury, William A. Niering, Ian C. T. Nisbet, and any two others they may appoint. The decision by the Judges will be reached within six months of the date of submission of the evidence.

Figure 2. In the more than forty years between the first publication of this challenge and his death in 1997, Dr. Egler's challenge was not met. (Quoted from Appendix VII in Egler 1975.)

When they compared the patterns of trees that had volunteered as second growth with the patterns of trees on land occupied by the linear descendants of trees that stood before European settlement, they found the patterns to be the same. The "old growth" matched the "second growth," even in the case of trees that followed old-field pines on plots that had been cleared, stumped out, planted to gardens, turned over to pasture, and finally abandoned.

This study indicates that once the white pines, which were in fact opportunistic old-field weeds, had lived out their lives, the tree species best adapted to the site grew back on their native habitat. The "best adapted species" are those of the wilderness forests, the same ones found by the first European settlers coming into the country. Obviously, this understanding markedly reduces the "turnaround time" involved in the story that regional forest development takes many thousands of years to reach climax.

RARE EVENTS OF EXCEPTIONAL INTENSITY

Over the years, Raup became more and more convinced that natural disturbances are so frequent that there is not sufficient time available for the sequence of generations implied in the theory of succession. He wrote:

> Wherever old American forests dating back to pre-settlement time have been studied historically they have failed to satisfy the requirements of the self-perpetuating "climax." One of the most important of these requirements is that the trees shall be all-aged. However, a universal feature of our old forests is that they are even-aged or have one or more well-defined age-classes in them. This phenomenon is known in so many parts of the continent, and in so many types of forest, that we cannot ignore it. We know of no way to account for it other than by the occurrence in pre-settlement time of disturbances that destroyed or decimated whole forest stands. (1964)

Henry and Swan found supporting evidence for Raup's view in the old growth forest of the Pisgah Tract in Southern New Hampshire (1974). They determined the age of stumps, sections of fallen logs, and even buried wood. They showed that the major species in this patch of old growth seeded during two exceptionally intense disturbances, a disastrous fire in 1665 and a major windstorm in 1938. As they put it: "We can say that tranquillity does not appear to be an important mediator of change, but that external events (fire and wind storms) are extremely important. The vegetational composition on one site may change considerably over time, and studies that examine compositional change associated with disturbance may provide a key to predicting its progress."

Periodic windthrow may serve a role similar to that performed by fires and agricultural clearing. Windthrow increases sunlight in small glades where several trees have fallen. Herbaceous plants may seed into these patches, as may tree seedlings.

Stephens's 1956 study in the Harvard Forest showed how the effects of windthrow have permeated the history of the forest. Stephens estimated the ages of trees in a patch. His counts showed first that the diameter of stem was not simply related to age. Second, and equally important, he showed that tree ages came in clusters, and each cluster was associated with some identifiable "disturbance," such as fire or a windstorm. He found evidence of powerful disturbance sometime between 1400 and 1500 and in 1635, 1730, 1750, 1815, 1851, and 1938. Note the long period without serious storms during which many inland New Englanders came to think that big storms were abnormal.

The mounds from trees felled by the oldest hurricanes were barely detectable on the surface, but Stephens found eighteen of them. He made a map of the locations and age classes of the fallen trees of the past, using it to draw in the area subjected to windthrow. The average areas and age classes turned out to be very nearly the same for each mound, however long ago the storm had come. The trees uprooted in the earliest recorded storm weren't much bigger than those later victims. The disturbances occurred well within the life expectancy of the major constituents of the "old growth stands." It seems likely, then, that few forest trees in the northeast live out their life expectancy, let alone provide for truly successional replacements.

Later, Oliver reworked Stephens's data and showed that the size of the area disturbed (the number of mounds created by each event) affected the species that became established in the patch (Oliver and Stephens 1977).

This suggests that the chance to win a place in the canopy may be a lottery in which failure may be the fate of most of the progeny of existing species. Species are sorted out in response to local differences in soil, microtopography, subsoil structure, and exposure. The change is highly probabilistic and indeterminate.

PATCH DYNAMICS

The ideas inherent in Oliver and Stephens's work on small patches of forest that are disturbed have been developed primarily by Pickett and White into a more widely recognized phenomenon: patch dynamics (1985). Following the theory of patch dynamics, death strikes individual trees in the canopy capriciously, and when the individual dies, it falls and opens up a glade. Then a scramble ensues until another individual that has the "right stuff" and the luck to be at the right place at the right time establishes itself.

Pickett and White's ideas represent a concept that has come to be identified as the fine-grained study of "disturbance" in "natural systems." I have come to think of this as being a sort of calculus, in which change is reduced to minimum space and time for analytical purposes, with the idea that once the major themes have been identified, they can be applied to vegetation in general.

When ecologists turned aggregations of plant species into "communities," they created the need for a theory to explain why so much of the vegetation is intermediate between the "pure types" that they conceived as pigeonholes. This need is filled by the theory of succession. In a similar fashion Pickett and White need a theory of succession on a micro scale.

As long as people regard death as disturbance and accept the idea that a tendency in the direction of equilibrium is universal, we will need a theory of disturbance and succession. But I don't think that either is valid as an abstraction. For those who believe that natural communities are orderly, succession has been needed to explain why disorder is so pervasive.

When "disturbance" has been reduced to the area under an individual, it becomes synonymous with death. Death has long been recognized as necessary for life, but its pervasiveness can seem remote when the generation time of the individuals is several times our own. Few zoologists would take seriously assertions made about population phenomena in chickadees unless they were based on observations over several chickadee generations. Unfortunately, in much of ecology, the absence of evidence does not lead to skepticism regarding the underlying assumptions of theory. The degree of belief is shown clearly in Watt's comment: "On account of the lag in response or repeated and fortuitous checks to normal orderliness, or the long delay between the incidence of the disturbing factor and return to a possible normal, anything like phasic equilibrium may rarely be achieved even although the tendency is always in that direction" (1947).

The colonization of an old field demonstrates the tremendous potential for seed production and dispersal in the species involved. When an opportunity is offered, many become established; otherwise they die. The ordinary trees that push into gaps in the bushes or among the pine stumps are the species of the old-growth, wilderness forests. It is important to realize that romanticizing wilderness distracts attention from the impressive performance of ordinary species.

Henry and Swan found no suggestion of a trend toward an equilibrium hardwood stand–type in Harvard Forest, even over a century free of disturbance (1974). They found that the tree species that seeded into the large blowdowns held on until the next disaster. Hack's work that we saw in chapter 6 indicated that local details of the shapes and direction of slopes, relative soil moisture, and nature of the mineral soil, together with a generous dose of chance and historical accidents, helped to define species composition.

Egler's challenge to show that later successional types appear after the early ones have lived out their lives has not been met. It seems worthwhile to search for yourself in a New England field abandoned within a dozen years or so to see whether seedling birches, aspens, and pines (even red maples and oaks) are already showing up among the meadowsweet and sumac bushes.

The most important idea to carry away from this chapter is Egler's: all plant species that will be seen in an old field appear soon after the site has been abandoned. Egler's idea is a challenge to the fundamental assumption that certain species prepare the site so that others can more readily colonize. He says that succession is a series (to us) of individuals that live out their troubled lives, then die. The classical theory of succession sorely needs evidence of relay floristics—that certain sets of species actually replace each other. There is no evidence from the field to support Watt's idea that in the absence of disturbance, change occurs steadily, moving the vegetation towards an equilibrium. This remains an unfounded article of faith.

The classical concept of succession has become one of the most frequently cited examples of an ecological explanation for "the way the world works" and is featured in virtually every introductory biology textbook from grade school to college. Discussion of possible alternatives are not mentioned or are relegated to brief footnotes.

Successional theory has become a key component of much of the conservation movement. If natural areas—that is, those "uncontaminated by humans"—tend toward some sort of stable climax community through a predictable sequence, the best strategy that a conservationist can adopt is to remove human influences from a region, and wait for the inevitable reestablishment of the climax.

A first sign that an ecologist accepts the developmental model is a reference to "a relatively uniform habitat of regional extent." This suggests lack of interchange with neighboring, incrementally different species associations, hence the community is a closed system. Without exchange with neighboring populations, the local population must regulate its own numbers. Hence, stable animal populations must have inherent mechanisms that regulate their own populations. Again, because the habitat is assumed to be uniform and of considerable extent, subdominant individuals do not have places in which to escape or to hide in less preferred sites. Lacking heterogeneity of habitat for refuges, subdominant species develop mechanisms to avoid competition with their species neighbors.

Thus the acceptance of closed systems and developmental models in animal ecology is manifest in emphasis on density-dependent mechanisms of population regulation and on primacy of competition in limiting or determining the species composition of the community. We shall examine the consequences of these manifestations in subsequent chapters.

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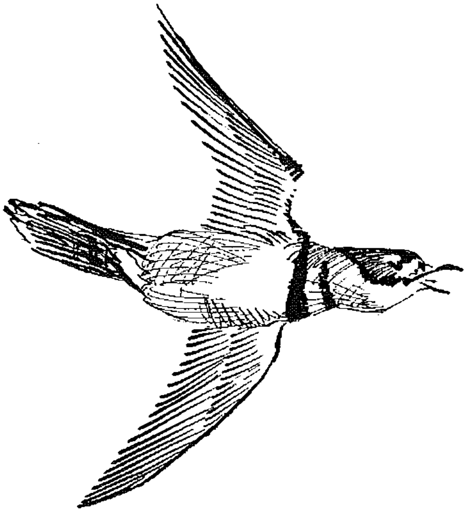
When your views on the world and your intellect are being challenged and you begin to feel uncomfortable because of a contradiction you've detected that is threatening your current model of the world or some aspect of it, pay attention. You are about to learn something.

WILLIAM H. DRURY JR.

About the Author

WILLIAM HOLLAND DRURY JR.

MARCH 18, 1921–MARCH 26, 1992



William H. Drury Jr. was the fifth child, first son, of the artists William H. and Hope C. D. Drury. As the only boy in the family, he learned to entertain himself by roaming the fields, marshes, and beaches of rural Middletown, Rhode Island, and sketching the animals and landscapes he found there. He was educated at home and at a neighbor's until he entered the Saint George's School, and he later spent a critical postgraduate year at Haileybury College in England, where watching birds was a recognized and respected vocation enjoyed even by the school's headmaster.

He graduated magna cum laude in biology from Harvard College in 1942 and was elected to Phi Beta Kappa. During World War II, he served as a chief quartermaster in the U.S. Naval Reserve in the European, Atlantic, Pacific, and Asiatic theaters. After the war, he returned to Harvard University and was elected a Junior Fellow in 1949. For his Ph.D. in biology and geology, Drury explored the relationship between geology and vegetation patterns in Alaska and northwestern Canada. He taught at Harvard University as an assistant professor and lecturer in biology.

The chance to create an ornithological field research station for the Massachusetts Audubon Society lured Drury away from academia for twenty years, during which he served as Audubon's director of education, director of research, and director of scientific staff. Herring gulls, friends since his early years, were his favorite research subjects, but he also spent much energy supporting Rachel Carson's views on DDT and other pesticides. He served on the Science Advisory Committees for Presidents Kennedy and Nixon, as well as on several state boards.

Drury returned to the north in the 1970s to study seabirds in Alaska's Seward Peninsula for the National Oceanic and Atmospheric Administration's Outer Continental Shelf Environmental Assessment Program. The opportunity to work at a new, ecologically focused college on the coast of Maine returned him to teaching in 1976. With his varied interests and background, he brought a unique perspective to students of "human ecology" at the College of the Atlantic. His course offerings included landforms and vegetation, populations and species, ornithology in the field, natural history drawing, and animal behavior. His research efforts were spent on pragmatic projects such as the return of terns and other seabirds to traditional nesting islands in the Gulf of Maine, restoration of peregrine falcon populations in the east, and the gathering of baseline vegetation data on Gulf of Maine islands for long-term studies. He was working on the final drafts of this manuscript at the time of his death.

Illustration, previous page: Killdeer, pen and ink.