WILDLIFE-FOREST RELATIONSHIPS: IS A REEVALUATION OF OLD GROWTH NECESSARY?

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ABSTRACT

The lack of a uniform and ecologically meaningful definition of old-growth forest has caused confusion and led to a misunderstanding of certain wildlife-forest relationships. Many of the currently accepted theories regarding these relationships were originally postulated during the period 1930 to 1960, after old growth had largely been eliminated from much of North America. Some of these theories, which have come to be accepted as facts, were either based on work conducted in mature, second-growth forests (often mistakenly called old growth), or were simply the product of speculation. For this reason it is imperative that resource managers take a fresh look at old growth and reevaluate its importance to associated wildlife species.

Old growth, as we define it, consists of uneven-aged, silviculturally overmature stands which have reached a dynamic steady state condition. Such stands have been variously labelled pristine, virgin, or climax, and typically exhibit high habitat complexity and diversity. Under present forest management practices of clearcut logging over relatively short rotations, old growth is a nonrenewable resource.

Industrial-scale logging, which was responsible for removal of much of the old-growth forest, spread generally east to west across the continent from the early 1800's through the mid 1900's. Today, old growth in significant acreage exists only in a handful of Western states and much of what remains occurs in remote areas and at higher elevations. Vast tracts of unbroken old growth occur today only in Alaska. Evidence that old growth has high wildlife values is drawn, in part, from the historical record using deer (Odocoileus spp.) as an example. Prior to and concurrent with the expansion of lumbering in the virgin forests, this record showed deer to be in high numbers, and lucrative, market hunting existed? on a large scale. In many areas, deer populations declined following removal of old-growth forests. Though it is difficult to separate the relative effects of habitat loss and increased hunting pressure on this decline, deer appeared to have thrived in many old-growth forests.

More direct evidence showing old growth to be important wildlife habitat comes from recent and ongoing research in old-growth forests in Alaska, British Columbia and the Pacific Northwest. Old growth is considered to provide optimal or essential habitat for black-tailed deer (Odocoileus hemionus), numerous bird species, and some small mammals and furbearers; and the list is growing as more attention and more research is directed toward old-growth forests.

Old growth today is a limited and nonrenewable resource of great importance to some wildlife species and of unknown importance to many others. The opportunities to study wildlife/old-growth relationships will, for some species, be very difficult since old growth habitat, in many areas, is disappearing faster than we can develop an adequate understanding of it. There is a pressing need to understand more completely the ecology of old growth in order to provide responsible wildlife-forest management.

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INTRODUCTION

Early in the establishment of wildlife management as a profession, theories were commonly presented as facts. It is not surprising then, that subsequently we have often been confused with contradictory evidence. One example is the aphorism that good timber management is good wildlife management. Bunnell (1976:147) protested that advocates of this doctrine espoused it "on the basis of ingenuous faith in the term 'good' with little supportive data."

This principle apparently was not based on experience with timber management practices that resulted in "good" things for wildlife, but, instead, on the undocumented belief that higher populations of some game species in certain areas occurred after industrial-scale logging and/or widespread wildfire had removed much of the virgin forest. A corollary, therefore, was that "old-growth" forest was relatively unproductive of wildlife (as stated by many authors including, for example, Leopold 1949, 1950, Cowan 1956, Severinghaus and Cheatum 1956, Robinson 1958, and Jenkins and Bartlett 1959). Therefrom, it seems to have been concluded that any means used to eradicate "old growth" would yield the nebulous "good for wildlife."

Recently, Thomas (1979:11) citing Bunnell (1976) warned "it has become increasingly obvious that such cliches . . . will no longer suffice." We agree, but should concede our doubts were not quickened until we were assigned to study the influences of timber harvesting and management on wildlife habitat in southeast Alaska where there is a unique opportunity to contrast truly pristine forest with logged areas in various stages of succession. Early in the program we acquired data (discussed later) that did not fit the theory. One possibility, of course, was that the Alaskan forests were somehow different from other North American forests. Consequently, we searched the literature for information on those earlier forests and the data that lay behind the doctrine.

THE HISTORICAL RECORD

Harvesting the "Old-growth" Forests

The extent of "old-growth" forest today is much different than when European settlers first colonized this continent over 300 years ago. According to rough estimates the original forests of commercial quality equalled about 850 million acres (344 million ha) with about 75 percent of this area occurring east of the Great Plains (Clawson 1979, Kellogg 1907). Much of today's commercial forest land, about 500 million acres (202 million ha) (Clawson 1979), is in second or third generation timber stands. Although it is difficult to accurately trace the demise of "old growth" because of limited, inaccurate, and noncomparable data, several sources allow us to describe this history generally.

Following early colonization on the Eastern Seaboard, trees were harvested for firewood, lumber, and to clear the land for agriculture (Brown 1948). In the early 1800's, wood was in demand in the Northeast for fuel, charcoal, and shipbuilding. By the mid 1800's, lumbering was developing rapidly and expanding to the west and south from New England (Reynolds and Pierson 19 3, Brown 1948), reaching its peak about 1900 (Clawson 1979). The progression of the timbering industry in the United States through the nineteenth century was described by Reynolds and Pierson (1923:11) as follows:

> For 100 years the lumber industry has been in the process of migration from one forested region to another. . . . As the first cut of pine in the more thickly settled coast regions drew near its end, the exploitation of the white pine forests

> of the Lake States began and the hardwood regions of the central Appalachians were opened to the market. As the cut of the Lake States drew to its close many lumber manufacturers of that region removed their operations to the South and began the attack upon the great belt of long-leaf pine stretching from Virginia to Texas. . . . Now [1920] four-fifths of the original southern pine is gone, and there is in progress a marked drift of lumbermen from the Southern States to the Pacific Coast, and to the northern part of the Rocky Mountains, known as the Inland Empire.

Reynolds and Pierson (1923) reported that by 1920, 96 percent of the virgin timber had been cut from the Northeast and Central States, 90 percent from the Lake States, and the South was not far behind. They reported that 61 percent of the total remaining sawtimber was west of the Great Plains. In the West, as of 1920, 17 percent of the timber had been cut and this was from the best and most accessible stands (Reynolds and Pierson 1923). These authors further stated that even Colorado, Utah, and Wyoming were well past the peak of their production. By 1920, Reynolds and Pierson (1923:21) stated, "we are beginning in earnest to cut our last reserve of virgin timber . . . ."

As of 1938, the Society of American Foresters (1947) classified 22 percent of the total forest area (about 460 million acres [186 million ha]) of the United States as "old growth." "Old growth" was defined here as "original forest"; however, portions of the so called "old growth" were described as having been culled. East of the Great Plains, the forest was largely cut over with remnants of "old growth" representing about 11 percent of the commercial forest land (Society of American Foresters 1947).

In 1953, "old growth" (which in this report was not defined) represented only 10 percent of the commercial forest land, (USDA Forest Service 1958). Thirty-three percent and 10 percent of this limited "old growth" was in the Pacific Northwest and Alaska, respectively, and no significant old-growth acreage remained in the Eastern forest area.

In 1963, "old growth" was defined as being trees past rotation age (USDA Forest Service 1965:225). To our knowledge, "old growth" has subsequently been poorly defined or its occurrence has been unreported in nation-wide inventories. We know that some "old-growth" stands exist in the Eastern deciduous forests but these are scattered, of small size, and rare (Bormann and Likens 1979, Lorimer 1980). The major states where significant "old growth" still exists today are Washington, Oregon, Idaho, Montana, California, and Alaska. According to Juday (1978:498) in the Pacific Northwest, "The elimination of old growth on forest industry lands is now virtually complete." There, most of the remaining "old growth" occurs primarily on public lands in remote areas and higher elevations. Vast tracts of unbroken "old growth" occur today only in Alaska. All of the timber harvest in Alaska today is in "old growth," and, following the historical pattern of logging in other regions of the country, the present harvest is concentrated in lower elevation stands of highest quality and volume.

Deer Populations in North America

Within the limitations of these proceedings, we can only present a cursory review of some of the historical accounts that are relevant to the topic. We have selected deer (Odocoileus spp.), because their history in North America is well documented, probably due to their high market and sporting value.

The numerous anecdotal records reviewed by Young (1956) in The Deer of North America suggest that before the virgin forests of this continent were significantly altered by man, deer apparently were very abundant: Ernest Thompson Seton "estimated" the original North American deer population at more than 50 million animals; between 1755 and 1773, over two and one-half million pounds (1.13 million Kg) of deerskins from about six hundred thousand deer were shipped to England from Savannah, Georgia; in 1753, 30 thousand deerskins were shipped from North Carolina; in 1786, Quebec exported 132,271 deerskins.

Presettlement deer Abundant

Schemnitz (1973:12) said, "Historical accounts in the Northeast reveal an abundance of wildlife in the period 1605-1820 (Banasiak 1961). . . . In the period between 1820-1880, logging, agriculture and livestock grazing increased. Commercial hunting was prevalent. Deer populations declined greatly (Silver 1957)."

In the Lake States, heavy market hunting of deer began about 1860, and enormous quantities of venison were shipped by rail to the Milwaukee and Chicago markets (Bersing 1956:10). In Michigan (Jenkins and Bartlett 1959:11), "an average hunter could take 10 or 15 animals a day . . . and in 1878 . . . 70,000 carcasses [were] shipped out of the Lower Peninsula. In 1880, rail stations handled 100,000 deer." By the end of the century, both timber and deer were nearly gone from the Lake States. (Bersing 1956, Jenkins and Barlett 1959).

In the Gulf South, according to Davis (1945:92-94), "The sale of deer hides was an important item of trade before 1900. . . ." Impressed with this volume of trade, Strecker (1927:108) said, "This animal [white-tailed deer] must have been excessively abundant before the country was settled by whites." Logging activity peaked in this region around 1910 (Maxwell 1973). Subsequently, the deer population declined radically as wanton hunting -- and logging -- continued, and reached a low point in eastern Texas (the timber country) about 1930 (Davis 1945).

In the Northeast and the Lake States, as in Texas, the fantastic market harvests of deer occurred during the logging era. Concern over declining deer populations led to strict hunting regulations. In Michigan (Jenkins and Bartlett 1959:13), "we were scraping the bottom of the deer barrel between 1900 and 1910"; in Wisconsin (Bersing 1956:15), "probably the population reached the lowest point before World War I."

If we are to believe more recent studies on post-logging habitat conditions (Leopold 1949, Verme 1965, Wallmo et al. 1976, Blymeyer and Mosby 1977, Wallmo and Schoen 1981), deer populations declined radically exactly when they should have increased, if removal of the "old-growth" forest had resulted in its supposed influence. DeGarmo and Gill (1958:2) were similarly confounded: "Two paradoxes are evident from the early history of deer in West Virginia; one that they were reported to be abundant in virgin forests; the other that they nearly disappeared when heavy timber harvests began to stimulate an abundance of food and escape cover. . . . Virtual disappearance of the deer from most of the State coincided with the big timber-cutting years between 1880 and 1910." We should acknowledge, however, that because excessive market hunting took place concurrent with or just preceding removal of "old growth," it is difficult to separate the relative contribution of each to the deer decline.

In the West, Murphy (1879; as cited in Young 1956) gave similar pre-logging accounts of deer in great abundance and market hunting on a massive scale from the northern Rockies to the Pacific Coast. Gill (1976) and Wallmo et al. (1976) pointed out that there were no reliable estimates of deer populations in the Rocky Mountain region before or after the advent of extensive logging.

In the Pacific Northwest, Einarsen (1946), Cowan (1945, 1956), and Brown (1961) were perhaps most influential in legitimatizing the concept that "old-growth" forests supported few deer -- despite Young's (1956:3) accounts of phenomenal market hunting along the Pacific Coast and in interior Oregon and Washington. Cowan (1945) arrived at deer density estimates of one deer per square mile (2.59 km^2) on the southwest coast of Vancouver Island. He did not present any data or describe how these estimates were derived, however. Later Cowan (1956:606) offered only one source of documentation -- Einarsen's (1946) report of the response of deer to the Tillamook Burn in western Oregon. Later, Hine (1973), in summarizing a long-term study of deer in the Tillamook Burn, also offered only Einarsen's record of the early event.

Einarsen (1946:56-57) said, "This was originally a rugged area covered by a heavy stand of giant spruce, hemlock, Douglas fir, and cedar. . . . As a result of two severe fires, in 1933 and 1939, . . . the deer population was reduced [our italics] to less than one animal per section [square mile; 2.59 km^2] of land. . . .

The area was closed to hunting until September 26, 1942. . . . During the protection period, deer increased from one to over 15 per section." There was no comment on the population density before the fire, or how any of the later estimates were obtained, or on the role that protection from hunting may have played in the increase.

Brown's (1961) verification of the reaction of deer populations to logging is limited to the results of pellet-group surveys conducted in southwestern Washington and the Olympic Peninsula in 1951. He measured four successional stages. His final successional stage consisted of "dense second-growth or mature old-growth timber areas that were considered to have a low productivity of deer forage." (Brown 1961:56). Because "old growth" and second growth were considered a single successional stage, it is difficult to evaluate the relative importance of "old growth" as deer habitat especially since, on his intensive study area, true "old growth" was virtually absent (Brown, personal communication, 7 January 1981).

In our literature search we found few records of measured deer densities in "virgin" forest, but these were of interest because of their high levels. Hebert (1979:139) reported densities of Columbian black-tailed deer in previously unlogged forest on Vancouver Island: "25-60 per square mile on a watershed basis" and "75-150 per square mile [on] specific winter ranges" (10-23 and 29-58/km^2). Barrett (1979) estimated winter densities of 53 to 75 deer per square mile (20-29 Km^2) on Admiralty Island in southeast Alaska. These estimates were based on pellet-group counts. Such estimates do not support the thesis that "old-growth" forest is poor deer habitat, but neither does the rest of the historical record. Furthermore that record does not provide reliable documentation of remarkable increases in deer populations attributable solely to the removal of "old-growth" forest.

There are only limited records and some photographs of the structure and composition of remnant stands of Eastern "old-growth" or virgin forests. To our knowledge, there were few, if any, deer studies in such forests. Moreover, many of the "old growth" forest ecosystems of North America had been greatly reduced before there was an intellectual discipline capable of interpreting them. The term ecology was not even coined until 1869, and the science was not formalized until around the turn of the century. The concepts of wildlife management, biotic communities, and succession developed thereafter (Leopold 1933, Allee et al. 1950). The simplistic notion that logging and timber management are "good" for deer, at least, seems to have come about more through a speculative process than through objective evaluation of data.

FOREST ECOLOGY

On the preceding pages, we have made a point of setting the term old growth in quotation marks, because it is used so indiscriminately. In the field of silviculture, old growth refers to forests that have reached the plateau of volume increment or, even, to an earlier age beyond which maximum economic return per rotation interval declines. But, those distinctions apply to managed forests, and much of the timber harvesting on this continent, to date, has consisted largely of first entries into unmanaged forests. So, for convenience in classifying that resource, the U.S. Forest Service applies the term old growth to stands older than some arbitrary age; in the Northwest it is 150 years. For the purposes of interpreting wildlife ecology, this definition is not adequate.

Silvicultural systems fall basically into two classes, even-age and uneven-age. The former takes advantage of the most common pattern of secondary succession. When old growth is completely removed by clearcutting, wildfire, or other agents, the trees that regenerate are all of about the same age. They tend, then, to grow apace toward the "green-up" stage, when their developing crowns have formed a more or less uniform canopy. As the trees continue to grow, each needs more space, and competition overcomes the weaker trees, but the stand retains its even-aged character (Figure 1). This is the aggradation phase, described by Bormann

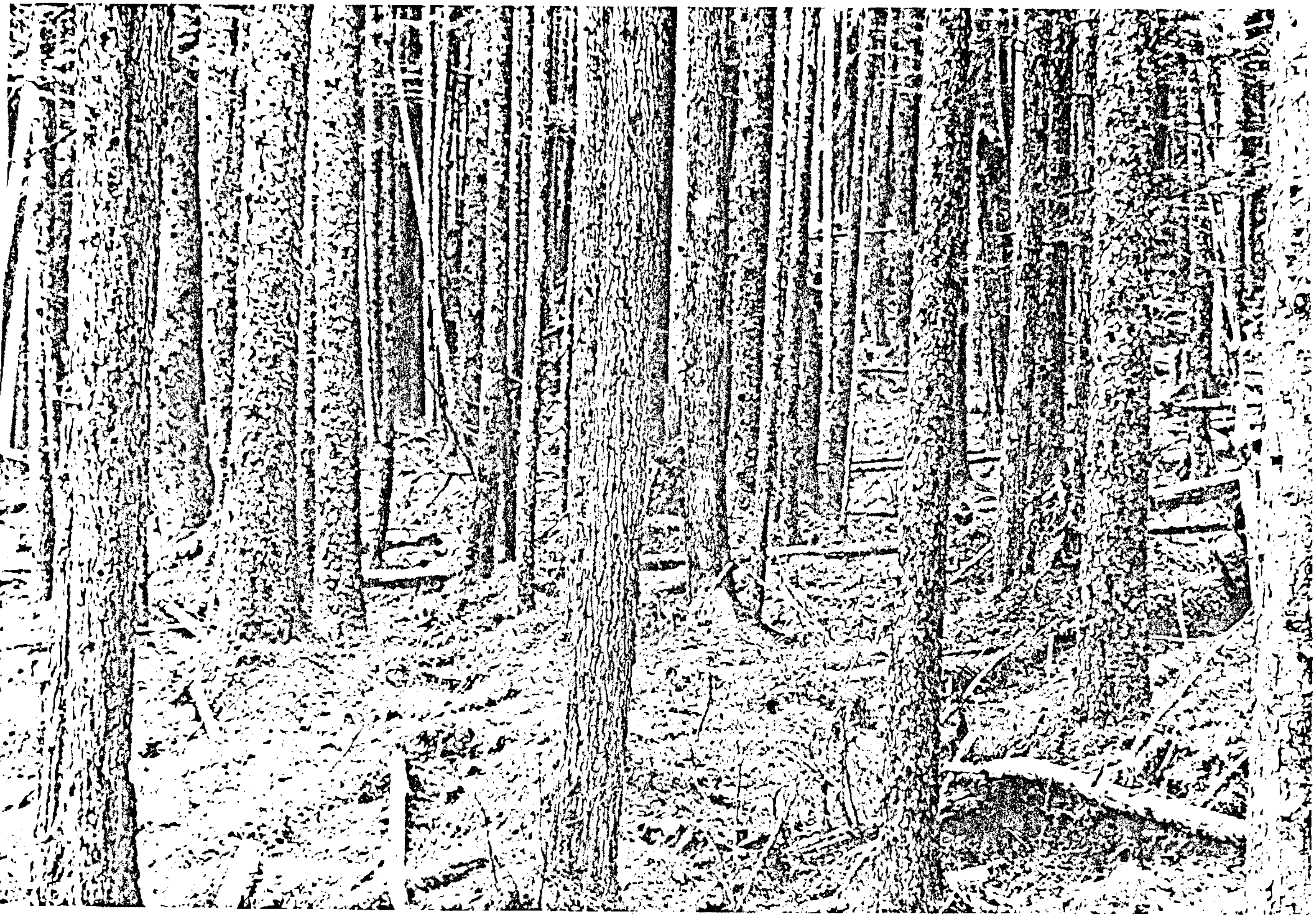

Figure 1. This second-growth forest in southeast Alaska is about 150 years old. It is even-aged, silvicultrually mature, and has low habitat diversity compared to old-growth forest.

and Likens (1979), during which biomass increases more or less steadily to a maximum.

From the standpoint of timber production, it is most efficient to harvest at or below maximum biomass for it is followed by a transition phase of declining volume as growth of individual trees slows down and some succumb to disease, insects, or windthrow. Over a long period of time, perhaps centuries in spruce-hemlock forests of Alaska (Harris and Farr 1974), the forest reaches a point at which the standing crops of living, and total biomass begin to oscillate about a mean. According to Bormann and Likens (1979:174,175) an ecosystem in this dynamic but relatively unchanging condition can be labeled a "Shifting-Mosiac Steady State," which structurally, "would range from openings to all degrees of stratification....The forest stand would be considered all-aged and would contain a representation of most species, including some early successional species, on a continuing basis."

Although there may be no immediate reason for the timber manager to preserve the Shifting-Mosaic Steady State, it has some important characteristics for wildlife. In southeast Alaska, for example, most of the forest exists in this uneven-age stage (Figure 2), and as such, exhibits high structural complexity and variability in both a vertical and horizontal plane as compared to second-growth stands. In areas of recent disturbance, or where older trees have fallen, herb and shrub communities occupy the

Figure 2. This old-growth forest in southeastern Alaska is uneven-aged, silviculturally overmature, and has high habitat diversity compared to second-growth forest.

openings, or thickets of saplings may develop. Wet or rocky sites, or areas subject to soil sliding may remain permanently brushy. With trees of a wide age span, the forest has a multi-layered canopy. Thus, in the vertical plane, the structure of the community includes an herb layer, shrubs varying from a few inches (cm) to over 6 feet (2 m) in height, sapling-size and pole-size trees, and subdominant and dominant trees many centuries old with crowns ranging from, perhaps, 100 to 200 feet (30-61 m) in height. Fallen trees in various stages of decay, standing dead trees ("snags"), and a variety of epiphytes, including mistletoe, fungi, mosses and lichens, add to this vertical complexity.

Even-age silviculture stops development at or below the end of the aggradation phase when forest structure is comparatively simple. At that stage, in most coniferous forest types, vertical structure consists of the forest floor stratum, mostly devoid of vascular plants, an intermediate stratum of even-aged, even-sized, more or less evenly distributed tree trunks, and a dense, one-layered canopy. Obviously, there is much less structural complexity and variability (i.e. diversity) in such a stand compared to old growth. In Alaska, this condition persists for close to two centuries following clearcutting (Alaback unpublished report, Harris and Farr 1974, Wallmo and Schoen 1980). It is the kind of "mature forest" illustrated by Cowan (1956:566) as an example of poor deer habitat in the Pacific Northwest. Bormann and Likens (1979:170), in reference to the northern hardwoods state, "Interestingly, it seems in the minds of many novelists, conservationists, foresters, and ecologists this type of massive, more or less even-aged successional forest is equated with 'virgin,' 'climax,' 'pristine,' or steady-state forest."

In the remainder of this paper, the term old growth will be used to refer to forests that have reached the "Shifting-Mosaic Steady State." This concept says more about the potential biotic community than the term climax.

WILDLIFE ECOLOGY

The importance of old growth to many species of wildlife remains largely unstudied and poorly understood. We intend to direct our primary focus here to one subspecies, Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), which we have had recent opportunity to study in a true, steady-state, old-growth forest in southeast Alaska. Our investigations revealed that these deer used old-growth forest considerably more in both summer and winter than any seral stages from 1 to 150 years of age (Schoen and Wallmo 1979, Wallmo and Schoen 1980, Schoen et al. 1981a). Other researchers in southeast Alaska revealed that relatively shallow snow and an abundance of available forage are among the reasons for this preference in winter (Bloom 1978, Barrett 1979). In comparison to old-growth forest in Alaska, even-aged, second-growth stands (30-150 years old) produce minimal understory forage. Recent clearcuts (3-20 years old) produce abundant forage but snow accumulation during winter periods often makes this forage unavailable to deer.

Encouragement that our observations of the importance of old growth were not anomalous comes from studies of Columbian black-tailed deer (Odocoileus hemionus columbianus) which have exhibited similar responses. In British Columbia, it has been suggested that clearcutting in the hemlock-spruce climax would not improve game production (Robinson 1958) or benefit deer populations (Gates 1968) due to reduced range quality associated with rapid succession. On Vancouver Island, Jones (1974, 1975), Weger (1977), and Harestad (1979) obtained data supporting the importance of old-growth forests as winter deer habitat. The results of these British Columbia studies were reiterated and emphasized further by Bunnell and Eastman (1976), Cowan (personal communication, 2-13-78), Bunnell (1979), and Hebert (1979). Hebert (1979), in addition, presented evidence of deer declines, following logging of old growth on Vancouver Island, of as high as 75 percent. He indicated that declines as great as 80 to 90 percent may be expected.

In eastern North America, the effect of snow in reducing white-tailed deer (Odocoileus virginianus borealis) use of clearcuts has been described by Krull (1964) in New York and by Drolet (1978) in New Brunswick and Nova Scotia. Mundinger (1980) reported the same for northwest white-tailed deer (Odocoileus virginianus ochrourus) in western Montana, and he recommended a 250-year timber harvest rotation to retain suitable forest for winter habitat.

Numerous graphic models have been presented to illustrate the value of sequential stages of forest succession as deer habitat (e.g., Leopold 1949, Brown 1961, Mohney 1976, Lowe et al. 1978, Wallmo and Schoen 1980). They are based on many reports of increases in potential forage supplies and deer use levels in young clearcuts or burned areas relative to adjacent forest. None of these models, except that developed by Wallmo and Schoen (1980), carry the theoretical results to the ultimate stage of uninterrupted succession. When considering deer response to forest succession, it is important to adequately evaluate the entire chronological sequence of succession. In Alaska, the effect of cutting an old-growth stand is to increase for a short (15-20 year) period understory productivity, recognizing however, that understory availability may actually decline due to excessive snow accumulation in these openings. This is followed by 80 to 85 years (on a 100-year rotation) of relatively nonproductive second growth. The net result for deer is a decline in carrying capacity over the entire rotation.

In southeast Alaska, we have only begun to study how deer respond to certain characteristics of their old-growth environment (Schoen et al. 1981a). Many other wildlife-habitat relationships, with respect to old growth, will require review and further study. Lacking these data, one might safely assume that a goal of maintaining the greatest wildlife diversity (i.e., variety) is more a matter of maintaining the greatest habitat diversity. This relationship has been discussed generally by Odum (1971) and Ricklefs (1973), and is perhaps best demonstrated by the numerous studies correlating bird species diversity with habitat diversity (MacArthur and MacArthur 1961, MacArthur 1965, Balda 1975, Shugart et al. 1975, Meslow 1978, Anderson et al. 1979, Mannan 1980, and others).

Ecologists generally believe, with some exceptions (Whittaker 1970, Ricklefs 1973), the diversity and complexity of community organization increases with succession (Whittaker 1970, Odum 1971, Ricklefs 1973). In southeast Alaska, it is readily apparent that habitat diversity in the old-growth, or climax stage of succession (e.g. Figure 2) exceeds that found within early or intermediate successional stages (e.g. Figure 1). A conceptual model of a few seral relationships within the forest ecosystem of southeast Alaska is presented (Figure 3).

In the Pacific Northwest, old growth is considered an optimal or essential habitat for some bird species (Meslow and Wight 1975, Meslow 1978, Forsman et al. 1977, Bull 1978).

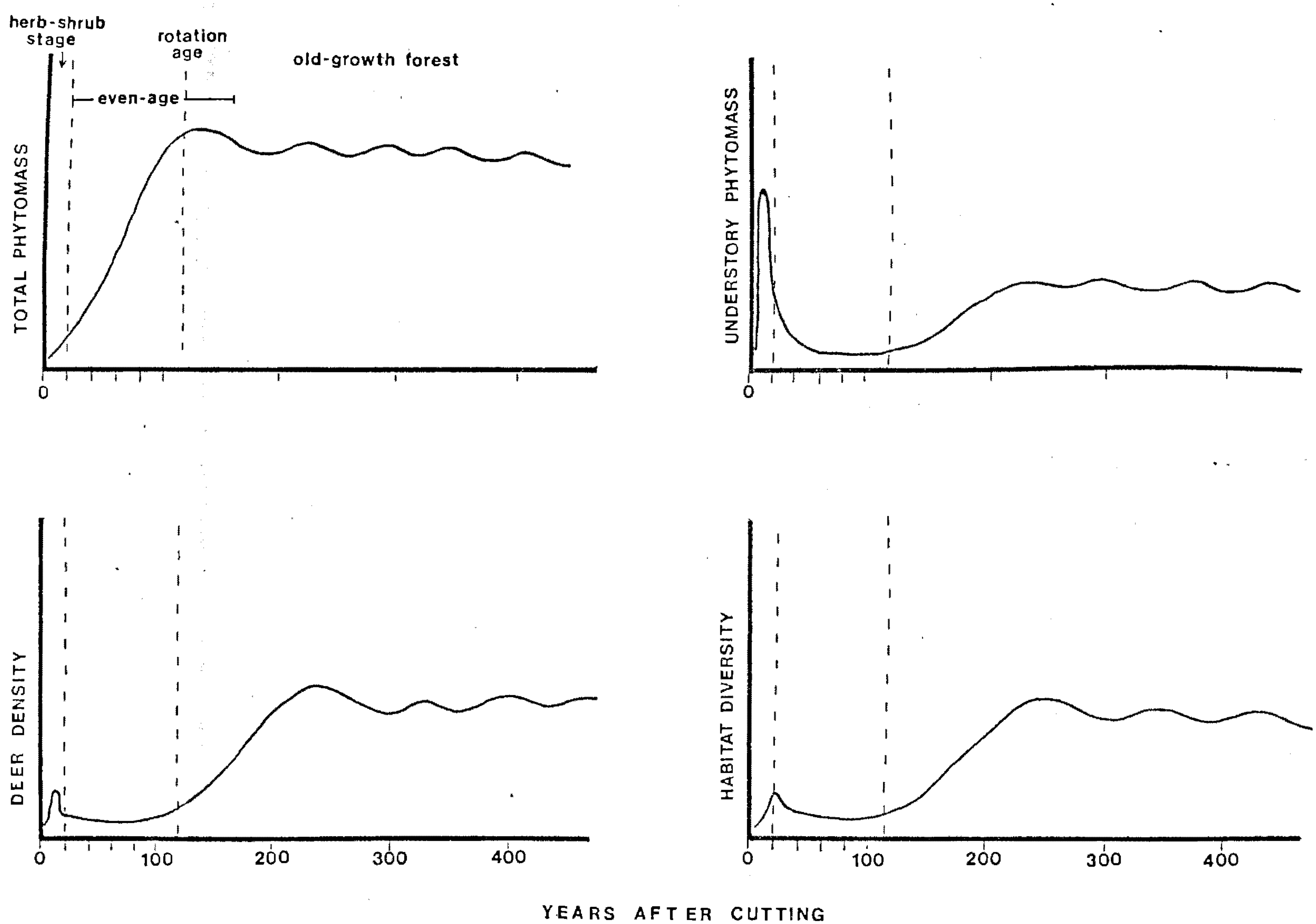

Figure 3. Conceptual models of several seral relationships within the forest ecosystem of southeastern Alaska.

In discussing breeding bird diversity and vegetative structure, Balda (1975) stated, "Until we have the necessary information on specific habitat types on a regional basis a goal of land managers should be to maintain as many naturally occurring habitats (especially climax communities) as possible. . . ."

Luman and Nietro (1980) listed several wildlife species in the Pacific Northwest whose complete or partial dependence upon old growth is such that preservation of their present populations may require the retention of large areas of old-growth timber. They included the northern spotted owl (Strix occidentalis caurina), goshawk (Accipiter gentilis), pileated woodpecker (Dryocopus pileatus), Vaux's swift (Chaetura vauxi), marten (Martes caurina), fisher (Martes pennanti), northern flying squirrel (Glaucomys sabrinus) and red-backed vole (Clethrionymys c lifornicus).

Some species that may not have primary dependence on old-growth forest throughout their geographic range have been observed to utilize it seasonally, and may be dependent upon it in some areas at some times. Examples are moose, Alces alces (Doer et al. unpublished manuscript), mountain goats, Oreamnos americanus (Schoen et al. 1981b), black bears, Ursus americanus (Kelleyhouse 1980), grizzly bears, Ursus arctos (R. D. Mace, personal communication and in press), white-tailed deer, Odocoileus *virginianus* (Mundinger 1980), and Vancouver Canada geese, *Branta canadensis fulva* (Lebeda 1980).

The Vancouver Canada goose is interesting because of its remarkable departure from typical habitat use by the species. On Admiralty Island in southeast Alaska, their preferred habitat for nesting and early brood rearing was found to be old-growth forest (Lebeda 1980). Also in southeast Alaska, which has the largest population of bald eagles (*Haliaeetus leucocephalus*) in the United States, nesting habitat of bald eagles consists almost exclusively of old-growth forest usually within close proximity to the marine shoreline (Robards and Hodges 1976).

It is significant that many of the examples of old-growth use by wildlife are taken from the Pacific Northwest or southeast Alaska because this area is the last stronghold of extensive, though rapidly diminishing, old growth left in the United States. Here, opportunities are still available to observe natural phenomena that have long disappeared over much of the continent. In North America, generally our understanding of early seral ecology is much more complete than that of old-growth forest ecology for the reason that relatively few ecologists have studied or have had the opportunity to study the biotic communities of true old-growth forests. We have been able to cite only a few examples of the value of old growth to some wildlife species. It is regrettable that the interest developed so late, because such habitat may be disappearing faster than we can develop an adequate understanding of it.

CONCLUSION

The diverse goals to which wildlife managers are responding today require a better process than is currently used for integrating wildlife and forest management. Thomas (1979) has offered the first realistic attempt to face up to the enormity of that charge, and his planning system has been widely acclaimed as a means for providing responsible multiple use management of forest lands. However, as we develop new approaches for integrating wildlife goals and objectives into forest management, we must ensure that such guidelines are based on current quantitative data and are applicable to the area in question. We must also be cautious in our application of generalities and keep in mind that "Progress in any field may be measured by the rate at which generalizations are broken down and reformulated." (Leopold 1930:332).

Our purpose here has been to point out the scarcity of old growth in North America today, and to draw attention to the need for a greater understanding of the role old growth plays in wildlife-forest relationships. Old-growth forests are today very limited and, under standard rotations, nonrenewable. Thus our approach to forest management of old growth will have substantial and long-term consequences. The magnitude of our responsibility is well stated by Juday (1976:158) who cautioned that "despite the enormous temptation of great economic gain from the sale of old-growth timber, resource managers must always remember that old-growth is a phenomenon that pre-dates them and the human species...It functions according to rules that the human species must understand if we are truly serious about managing forest ecosystems on a long term basis." More research and less speculation will be required if we are to meet our responsibilities in providing enlightened and knowledgeable wildlife-forest management.

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