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Fire and Tree Growth Relationships to Snowshoe Rabbits

WALLACE GRANGE
Pine River, Wisconsin

MANY northern forest trees reproduce best on bare-soil seedbeds, and fire is the major agency that prepares the land for their seeding. Ecologists know that many magnificent primeval stands of timber can be traced back to seeding on land swept by naturally-occuring fire.

It is equally true that periods of abundance for many northern forest animals stand in the relationship *X-years-following-fire*, variable with species, locality and site. Again, fire prepares the necessary seedbed. It is a powerful initiating force. It is not the only such force, and without the reproductive habits of trees, and of animals, its results would be disastrous rather than regenerative. Fire is *one* element in a huge and complex sequence of events which recur from time to time.

Where, how, and when do snowshoe rabbits fit into this fire-related northern forest-community complex?

Most of my observations are from Wisconsin and Minnesota, but in 1963 and 1964 I was able to extend them to parts of Alberta, British Columbia, the Yukon, and Alaska.

The snowshoe rabbit cycle has been known for at least one hundred and fifty years. It is characterized by huge numbers of rabbits for a period of 2-5 years, then their decrease to much lower numbers; or even to local scarcity, or rarity. In general, it averages out, *statistically*, to recurrences about once in ten years. The intervals between peaks have varied from 7 to 17 years. The "regularity" of the snowshoe cycle is a regularity within irregularity. Also, while rabbit abundance is frequently thought of as being universal during highs, this is deceptive—real abundance areas tend to be scattered, or "spotty," with exceptions to be noted later.

My definition and use of the term "cycle" does not depend upon a constant interval between peaks, or between lows, nor upon "regularity." Rather, it refers to a progression and sequence of related events which tend to recur, from time to time, in approximately the same order. This orderly progression of events does not stand or exist by itself. Rather, it springs from the habits and adaptations of animals and of vegetation under the environmental circumstances altered or set in motion by the initiating force (which, generally, is fire).

Snowshoes inhabit all stages of northern forest except those that are primarily hardwoods—maples, oaks, etc. But their chance for great abundance, for "population explosions" (which comprise the classical snowshoe cycle) is limited to *very early succession forest stages* not long after the occurrence of fire. They survive in small numbers even in mature stages: A reservoir of breeding stock carries over in older forests. They leap into spectacular abundance, however, *only* when there are large acreages of new forest reproduction. These commonly follow fire immediately. Nevertheless, anything that can provide a proper seedbed for dense forest reproduction can locally initiate favorable successions, often of small size. Among localized agencies are wind, insect damage, tree diseases, erosion, flooding, solufluxion, frost-heaving, landslides, the retreat of glaciers, and such human activities as cutting, bulldozing and road-building. Such minor agencies of disturbance (if natural) explain the survival of small numbers of snowshoes *even in* advanced forest stages. But fire is the chief initiating force.

Virtually all plant species important to snowshoe rabbits show pronounced adjustment to fire. Jackpine, lodgepole pine, and black spruce all at times cast out seeds from persistent, fire-resistant cones for one, two or more seasons following fire. Quaking aspen regenerates from underground roots, and also from prodigious quantities of seed carried by wind; Alaska birch sends up shoots from burned root collars; balsam poplar develops up to 4-inch fire-resistent bark; willows find new seedbeds on bare soil; dwarf birch shows the same tendency, then colonizes and spreads by "layering," as well as from seed (Viereck, 1959). Blueberry and fireweed both survive aboveground pruning by fire. White pine and white spruce commonly invade stands of earlier succession trees, ultimately replacing them. White cedar, tamarack, hemlock and norway pine all show reproductive relationship to fire. And the list can be expanded. It would be difficult to name a plant species within the northern forest which is no quite extensively adjusted to fire.

On May 22, 1925,* a settler in Lake of the Woods County, Minnesota, set a land clearing fire which then escaped and covered some thousands of acres. The land seeded very densely to jackpine. *Eleven growing seasons later*, in the winter of 1935-36, this pine "thicket" supported what was, and is, the highest snowshoe population I have witnessed, ranging from one to eight rabbits per acre, the maximum numbers representing concentrations.

Throughout that county, throughout northern Minnesota and Wisconsin, at about this same time, there were thousands of other comparable situations, some grown to aspen, rather than jackpine. This period, the 1930's, saw a huge population explosion of snowshoes over perhaps thirty counties of these two states. However, since fire suppression became effective in Wisconsin just a few years later, snowshoe "highs" have dipped lower and lower. Anyone who did not know Wisconsin in the twenties and thirties can scarcely form a proper conception of what the rabbit cycle meant in those days. Nor would he believe the prevalence, extent, the near universality, of fire. To see, today, a snowshoe cycle in this classical sense, on this scale, it is necessary to go to British Columbia, the Yukon, Alaska, or other regions where fire suppression is not a reality.

On this 1925 Minnesota burn, where fire initiated what was essentially a jackpine monotype, not all of the trees grew at the same rate. Some stem counts made in April, 1936, illustrate this.

One area of trees had grown slowly. The average height was 3½ feet. The number of jackpine stems (living and dead) was at the density of 220,000 per acre. Snowshoes apparently made some use of this "short jack" stand in 1934-35. In January, 1936, deep snow engulfed the pines. *The rabbits were forced to move.* The stem count

* In a previous publication, *The Way to Game Abundance*, this date was erroneously given as 1929.

showed that 4383 stems per acre had been killed or injured by rabbits, leaving 215,000 untouched. (In these figures, the nibbling of twigs and use of needles is disregarded).

On this same burn, another site, typical of peak rabbit conditions showed 75,700 stems (living and dead) of which about three-fourths were killed or injured, leaving around 19,000, or about 25%, undamaged per acre. Average height was 7 feet, and I estimated from one to six snowshoes per acre. All trees killed were under 1 inch diameter, 1 foot from the ground.

Again *on this same burn,* an area I classed as "post peak" showed 8700 jackpine stems (living and dead) per acre, of which 6500 were killed or injured, *leaving 2252 trees uninjured.* Almost 90% of these *undamaged* saplings fell in the 1 to 4 inch diameter class—the largest trees on the site. These larger trees were already essentially immune to rabbit damage. With the onset of another growing season, their added girth and thickness of bark would confer further protection. Average tree height was 15 feet. The rabbit population was already down, although still rated at about one per acre at winter's end.

Two nearby sites from a fire about forty years before (1896?) showed jackpine diameters of 4-9 inches (breast high), with 1900 and 1000 trees, respectively, per acre. I estimated the rabbit population at around 1 to 40 to 100 acres.

A mature jackpine site could show as few as a couple hundred large trees. At that stage, there is some resurgence of rabbit habitability due to wind-throw, etc.

These examples illustrate the rise and decline of the rabbit food-shelter resource, and of the rabbits; the period of immunity from winter damage in the very earliest tree growth stages; the systematic thinning and pruning at the point of maximum use; the development of tree immunity to damage, due to growth; the fact that, despite such heavy utilization, a well-stocked jackpine forest survived.

On this one burn, the peak rabbit numbers were spread over five, and probably six, consecutive winters on different but adjacent tracts, and rabbits moved from place to place a great deal.

This type of situation is highlighted best *in extensive monotypes* of jackpine or of lodgepole reproduction.

But a similar situation, different only in degree, applies to other succession types. In pine monotypes, barring further fire, the population explosion is likely to be a one-time-in-a-century affair. In more diverse types, in more open-grown stands, and in slow successions northward, successive peaks may recur on the same tract, at intervals; the duration of abundance is longer. The longest duration I have seen is in the 1924 burn (there may have been several fires) at the eastern edge of McKinley National Park, Alaska and near Deniki Lakes. There, the country is not forest in the usual sense although there *are* stands of good forest interspersed, especially around lakes. Rather, it is a huge opening but there is a scattering of white spruce, with much of the land between trees occupied by dwarf birch. The country is slowly regenerating to white spruce, but it is shrub rather than tree habitat, primarily. Where dwarf birch or willow, or both, can perpetuate themselves for long periods we have fascinating exceptions to the general rule.

On a fourteen square mile tract of land which became Sandhill Game Farm, in central Wisconsin, and which is now the Sandhill Wildlife Demonstration Area of the Wisconsin Conservation Department, a fire which, in all, ran over about 300,000 acres, occurred in September, 1930. Peat and other moist sites regenerated to aspen, both from seed and from runners. Following fire, no showshoes were known to be present. In 1934, they first invaded. By 1938 (eight growing seasons from fire) I saw the first aspen girdling. It required the winter of 1939-40, however, for snowshoes to spread and to occupy all suitable habitat. In that winter, snowshoes were attempting to spread further, into vacant habitat, through 2-inch mesh poultry netting fence. Incidentally, while I had held snowshoes in 2-inch mesh in Door and Rusk Counties, I found, in 1935, in Pine County, Minnesota, that many rabbits escaped from holding pens by squeezing *through* 2-inch wire. My conclusion was that there were many young, late-born rabbits.

The peak snowshoe population at Sandhill occurred in 1939-1940, in which winter I shipped more than 400. From that time on, through the 1950's, snowshoes were dependent primarily upon patches of water-logged, stagnated aspens at or below 1 inch diameters, which still evidenced thicket characteristics; and also upon willow. Willow distribution was affected both by a burning and by a flooding program so there are complications in interpretation. The point is that by 1957 we were cutting some 1931-seeded aspens for pulpwood while at the same time there were still small thickets of tiny aspens of the same age-class, from the same fire. In the late 1950's and early 1960's, snowshoes have nearly vanished from the premises. Again, there are complications in interpretation. I do not know how to assess the effects of snowshoe removal for shipment; nor the flooding program which eliminated the best habitat; nor the extremely heavy red fox population since about 1956, which appears to have severely limited the use of such snowshoe habitat as remains.

At this point, I am reminded of Dr. Adolph Murie's (1944) comment about mountain sheep in McKinley National Park:

> . . . The wolf, rather than the food supply—appears to be the chief factor limiting the size of the sheep population. [And, as he adds, preventing the use of much otherwise good sheep habitat.]

An analogous situation, I believe, for rabbit predators in general, operates *at the snowshoe cycle low.*

I outlined my ideas on the snowshoe cycle in my book, *The Way to Game Abundance*, in 1949. Here, I can touch only a few major points and cover some additional ground.

I called these high-quality, fire-initiated, early tree succession stands "natural propagation areas" within which, for a limited number of years, snowshoes are produced in prodigious numbers, and from which many individual rabbits spread into surrounding country, whether it is good, bad or indifferent with respect to their permanent needs. These rabbits (while they last) add their own production to the total. In the course of a typical "high," snowshoes become spread virtually throughout the length and breadth of every type and condition of habitat, burned or unburned, wherever they can find temporary foothold. Much territory is occupied which cannot support rabbits for long, or in more than small numbers. When the cycle turns, they disappear from these temporary, marginal haunts. *It is an expansion-contraction process.* At the "high," rabbits are in contact with rabbits more or less over enormous, contiguous areas. At the "low", they are apt to be in isolated pockets, in the most favorable remaining habitat, with special emphasis upon shelter quality. Even their habits change. From "tame" and "easy-going" creatures, as they appear to us, they become shy, fearful, secretive ones.

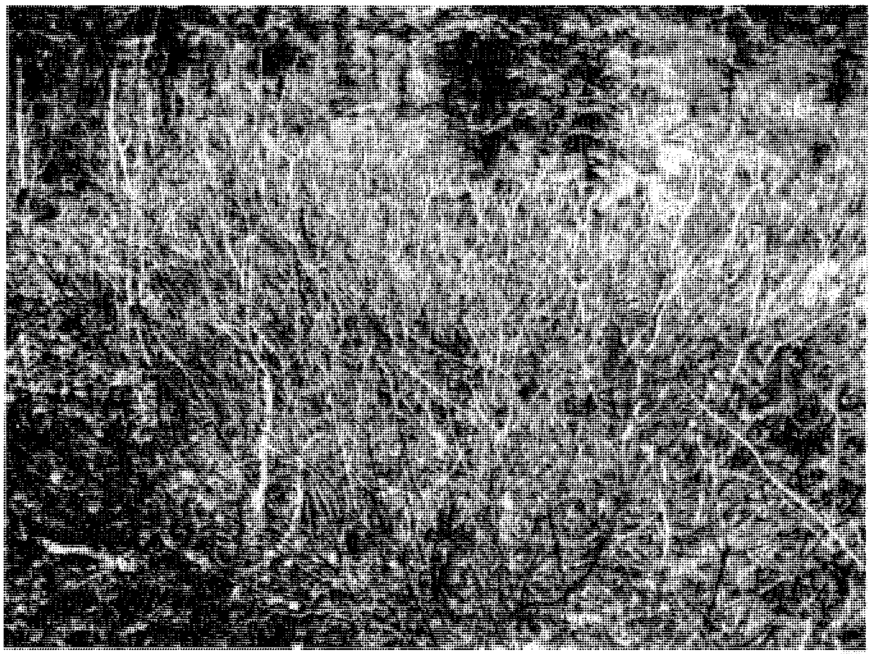

FIG. 3. Maximum utilization of dwarf birch, typical of peak's zenith or just afterward. Above-ground stem survival is variable, many die. *Ring-counts show that ⅛ inch diameters were attained here in + 4–5 years; ½ inch diameters in +11 years.* Several years' growth has thus been consumed. Dwarf birch probably seeded on this burn in the early Twenties and Thirties with or following willows, and is still spreading.

FIG. 4. A willow site near Riley Creek (Probably *Salix pulchra*). Girdling of stems this large, in quantity, usually indicates that food shortage is already acute. Killed willows in open sites often regenerate—slowly—but where the moose population is high (as it is here), the moss cover deepening, and permafrost perhaps rising, willow percentages decrease. Most remaining willow stems are old, up to forty years.

In the phase when "rabbits are everywhere," over-running the country, they can and do *subject enormous blocks of range*, burned or unburned, and embracing almost every cover combination, *to the self-same factor of nipping and pruning away the smallest and most palatable tree and shrub stems*. This was especially observed in British Columbia, the Yukon, and in Alaska, in 1963 and 1964.

But here I must be more precise in describing what happens for there are difficulties of the same sort that two or so decades ago plagued deer researchers. Where northern deer were starving in over-browsed wintering yards (also reflecting a fire-succession cycle, plus an absence of natural predators) many people, including some biologists, had what may be called "*observational difficulties*." They could not seem to see what the researchers saw. As they went into the woods, they found the trees and the brush still there—as well as dying deer. But they could not seem to see, or to believe, that the palatable, nutritious, necessary buds and twigs had been consumed to the point that deer *could* starve. This is still controversial among segments of the public at large. It is not the kind of issue that can be settled by majority vote, or a Gallup Poll, for despite anyone's opinion, natural processes go right on happening in their accustomed manner.

When small stems are consumed by rabbits, there may be very little evidence left of their removal. It quickly disappears. If evidence does persist, it often must be hunted for. The fact of such removal is easily missed under casual observation. I refer particularly to stems ⅛, ¼ and up to ¾ inch in diameter. Even considerably larger girdled saplings do not stand, or last, indefinitely, and are gone without trace in the interval between cyclic "highs." I did find one instance in Alaska where quite large rabbit-killed spruce stems persisted from a previous cycle—they were so rotten they could be pushed over at the touch of a finger. The inconspicuousness of browsing-grazing effects, of course, and the quick disappearance of the evidence of it, is the reason that so many *exclosures* are used in research work to reveal differences of vegetative response.

Outside of pine monotypes, and even in and near them in summer, snowshoes appear *to require* many tiny (and I think, preferably, recently grown) shoots and stems of deciduous plants. In the North, if white spruce, alone, were an adequate snowshoe diet, there could scarcely be food shortage. Snowshoes do eat a certain quantity of white spruce, (on south-facing hillsides and on certain other sites a lot of it) but I do not believe that, by itself, it is adequate. Murie, Peterson, and others, state that moose, a co-inhabitant of the white spruce complex, make virtually no use of white spruce. They, too, must depend on deciduous growth. But, while moose and deer browsing is reasonably conspicuous as is, also, snowshoe rabbit girdling, and the cutting of larger woody stems, the consumption of tiny stems is far less so. It seems to me that Wisconsin snowshoes utilize larger tree stems, and girdle larger trees, than is usual northward; that the importance of tiny deciduous growth increases as one goes north. Utilization is not 100% nor is it, usually, with deer, but it may run to 80%, and down, affecting a vast territory in the same span of four to five years. Where utilization is low, there may be a thousand factors to consider in explanation; especially exposure to winter winds, snow depth, predator abundance, and proximity to concentration areas. Also, why snowshoes particularly relish the bark and foliage from one particular white spruce, or aspen, and neglect others which appear identical, is unknown.

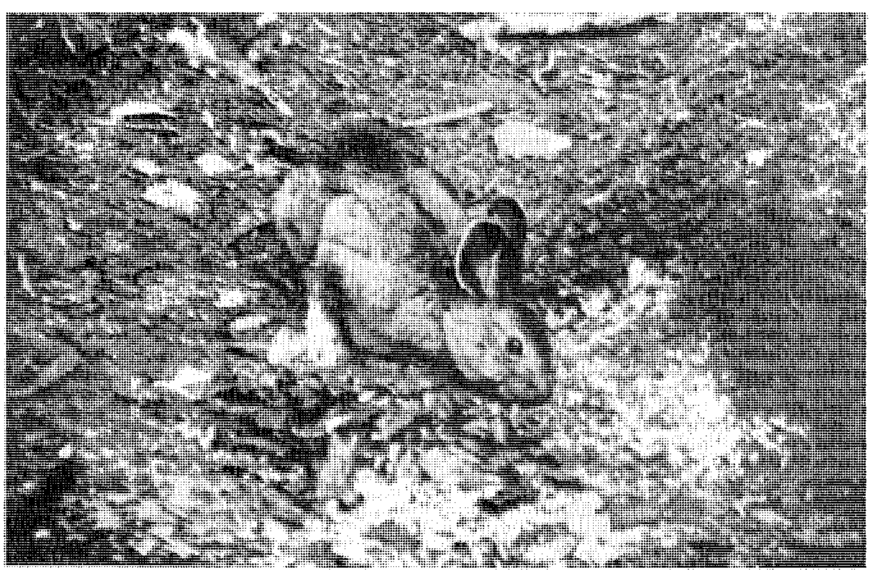

FIG. 5. Snowshoe rabbit, Deniki Lakes, July, 1964. Immediately after some papers were burned, this rabbit came to eat the char.

Last summer, at Ott's cabin at Deniki Lakes, one day I burned a handful of papers, on a bare spot of ground. Minutes later, a snowshoe came from the dwarf birch and ate some quantity of the charred paper (Fig. 5).

When an appropriate point of food and shelter deterioration arrives, the "crash" of rabbits occurs. Crash mechanisms *may* include disease, parasitism, starvation, wandering, climatic factors, reduced litters and numbers of offspring, predation and other agencies. Survival rates are high as the population swings up, and decline drastically when the tide turns. Attention is generally centered on so-called immediate "causes," but the etiology of the crash is to be understood adequately only in terms of expanding-contracting resources. There are those who argue whether deer in deteriorated winter yards succumb to starvation or to pneumonia—for my part I do not care; the underlying, basic cause is malnutrition. And, if rabbit browsing on the scale that occurs at the "highs" were to go on indefinitely, the result to the forest itself would be disastrous. Before this happens, the crash occurs. Seton was close to the heart of the whole matter, long ago, when he said that at their "highs," snowshoes, ". . . threatened their own food supply." I personally have not seen a crash from disease; those I have witnessed have been gradual, a slow but accelerating shrinkage, not sudden "die-offs." But the latter are known to occur.

Keith (1962) states:

> Much of the ecological thinking behind Grange's theory is undoubtedly sound. . . .

And, later says:

> I am—willing to recognize the cogent effect of post-fire successions, but until proof of a ten-year periodicity in the incidence of forest fires is forthcoming, there seems little reason to subscribe to Grange's hypothesis.

However, I have pointed out the differences in timing which occur on the same burns—I see no necessity whatever to claim a ten-year (or any other) cycle in northern forest fires. Nonetheless, there are some interesting coincidences in the dates of "fire years" over continental regions which perhaps those who reject the fire-related explanation of the snowshoe cycle may wish to explain. For example, 1948 was a "fire year" in Wisconsin, Michigan, Minnesota, Maine, California, and portions of Canada and Alaska. I append a list of some of the "fire year" coincidences obtained from incomplete and fragmentary records. More adequate records would probably reveal even better, the fact that there are not infrequently "fire years" in places as far apart as Wisconsin and Alaska, simultaneously.

More important, fire records for Alaska in an eleven year period show 13,000,000 acres burned (about 20,000 square miles), or about 9% of the total forested area of Alaska. Since in slower successions fire effects may persist for decades, the total result may well be more or less cumulative over more than one rabbit high. The list also shows that in the periods prior to real rabbit peaks in Wisconsin, Michigan and Minnesota, fire years occurred which ran up to totals of hundreds of thousands, and of millions of acres. Is this pure coincidence?

I do not know of any figures pertaining to snowshoe rabbit food consumption per day. Dahlke (1942) has produced figures for cottontails, under experimental conditions, of +8 ounces per day. If snowshoes are comparable, each snowshoe may require +100 lbs. of food per winter.

There are references in the literature (Rowan, 1942) to "thirty thousand" snowshoes per square mile.* This would be about 47 rabbits per acre, or one on each plot of 30 × 30 feet. Sometimes they may *appear* to be that numerous, but the most I can claim to have found over extensive areas is around eight (call it ten) per acre, and that was exceptional—a winter concentration. Under certain conditions of snow depth, wind and contour, there can, of course, be temporary areas of rabbit congestion. I should also add that, despite the fact that the snowshoe is a "sedentary" animal, there appear to be large-scale movements in winter, under certain conditions. Cox has reported their crossing Red Lake, Minnesota; other informants have reported their crossing lakes more than 2 miles across; and I myself have seen considerable evidence of shifting about. All in all, the snowshoe at times is a much more mobile animal than is generally supposed, particularly in winter.

* Based on the number shot from less than one acre.

I have not had time, nor much opportunity to study at first hand the abundance-scarcity cycles of lynx, which appear to be closely related to those of snowshoe rabbits (with a time lag on both up-swings and downswings) but will note in passing that they, also, are thus related to the initiating force of fire. Indeed, the ecology of the portions of snowshoe country I have seen is virtually non-understandable unless the role of fire and of vegetative successions which follow it is taken into full account. Fire relationships are also abundantly evident (or were evident formerly) in the case of Wisconsin-Minnesota prairie species such as Prairie Chickens, brushland species, such as Sharptailed Grouse, for other forest species such as the Ruffed Grouse—and for many others—and I have found the three species of grouse mentioned on portions of the same burns which elsewhere provided habitat, simultaneously, for snowshoe rabbits.

I cannot be sure, but I doubt that the spectacular snowshoe rabbit high at McKinley Park, Alaska, in 1964, exceeded the eight rabbits per acre maximum figure mentioned. The impressive thing in Alaska was the enormous expanse of country sustaining high rabbit populations.

There has been at least some tendency on the part of biologists to deal both with the snowshoe rabbit cycle, and with other northern animal cycles, more or less exclusively from a statistical standpoint, with special emphasis upon evidences of regularity in time. Unfortunately, with but rare exceptions, this statistical approach seems to ignore fundamental characteristics—and *changes*—in the habitat situations within which such cycles take place. There is also probably a strong inadvertent bias in recording spectacular, easily-observed "highs" and a lack of adequate equivalent information on *contra-cyclic* local "highs" occurring within the generally "low" periods—of which I have observed several instances. Likewise, the usual tendency is to explain population decreases by the one word "disease" whether or not there is any actual evidence of it. Statistics are extremely useful (and sometimes enlightening) especially in revealing biological events and sequences, geographically distant from one another, which produce approximately like results at about the same time, but with considerable over-lapping and with a not inconsiderable number of exceptions from the general rule (if they are looked for). In this connection, I might mention that bankruptcies occur even at the height of our economic booms, and that some firms and individuals prosper during depressions, irrespective of the statistical picture in total.

From whatever viewpoint or approach northern cycles are seen, particularly that of the snowshoe rabbit, it is of primary importance that they be seen in the context of habitat—especially of *changing* habitat conditions—and that due regard be given to the forces which initiate and alter vegetative successions. Not least of these forces, in the snowshoe cycle, is the rabbit itself! Rabbit browsing, which is selective in nature, of itself accomplishes profound changes, inconspicuous as they may sometimes be, over truly enormous blocks of land. Somehow it seems to be provided for, in the orderly processes of Nature, that, like the accumulations of puddles following heavy rain, there shall be a deluge of rabbits for a time, and then, in course, the drying up and virtual disappearance of the onetime hordes, also for a time. I might liken the process to an activity cycle, with periods of high population and great activity, followed by periods of rest—for land and vegetation—reflecting the fundamental pulsations of energy everywhere. Involved in this is energy from the sun, alternating periods of rain and drought, the occurrence of fire, and vegetative and animal response, all interlocked.

In any event, reverting to the matter of high snowshoe rabbit populations, there are a number of questions which require answer before the fire-related habitat succession explanation of the cycle is dismissed out of hand.

1. Upon what did (or could) those thirty thousand snowshoe rabbits per square mile reported in the literature, subsist over a winter of five to seven months? And, over 3-5 consecutive winters?
2. Where did they find the necessarily prodigious quantities of food?
3. Does such food production occur year in and year out?
4. What was the condition of the site when the crash came?
5. And was this site—by some random happenstance—*on a burn* where, ten or twelve or so years preceding the snowshoe "high," fire had exposed bare soil and provided the seedbed for a new forest, and for whole legions and new generations of snowshoe rabbits?

Partial List Suggesting the Extent of Major Forest Fire Acreage, Wisconsin, Minnesota, Michigan and Alaska, and Some Coincidental Dates of "Fire Years."

(Acres reported burned, or name of historic fire)

Year	*Wisconsin*	*Minnesota*	*Michigan*	*Alaska*
1864	+ 1,000,000			
1868	+ 1,000,000			
1871	1,280,000	....	2,000,000	
1881	....	....	1,000,000	Kenai Fire
1894	Phillips Fire; Barron, Rusk, Chippewa Counties	Hinckley Fire	....	Schwatzka Fire
1896	....	....	228,000	Canyon Creek Fire
1908	1,200,000	Chisholm Fire	2,369,000	....
1910	892,000	Beaudette Fire 300,000	....	....
1914	....	....	408,000	....
1915	46,000	....	157,000	Copper River Fire, etc.
1917	16,000	1,245,000	193,000	....
1918	....	Cloquet Fire 770,000	238,000	....
1919	....	....	418,000	....
1920	424,000	96,000	76,000	115,000
1922	33,000	511,000	38,000	921,000
1923	528,000	502,000	460,000	....
1924	77,000	168,000	242,000	350,000
1930	527,000	....	290,000	134,000
1936	Douglas Co. Fire	Markham Fire	....	Black River Fire
1948	Fires of substantial scale reported in Wisconsin, Minnesota, Michigan, Maine, California, portions of Canada, and Alaska. Acreages covered in Wisconsin and probably elsewhere held down by fire suppression work.			

Alaska Fire Data Only, indicating extent

1940	 4,500,000	acres
1941	 3,600,000	"
1946	 1,438,000	"
1947	 1,431,000	"
1950	 2,063,000	"
	+ 13,032,000	" (11 years)

(Information in list available for years as follows: Wisconsin, 1910 through 1950, plus scattered records; Minnesota, 1916-1926; Michigan, 1911-1930; Alaska, 1940-1950. A complete, collated list should be prepared).

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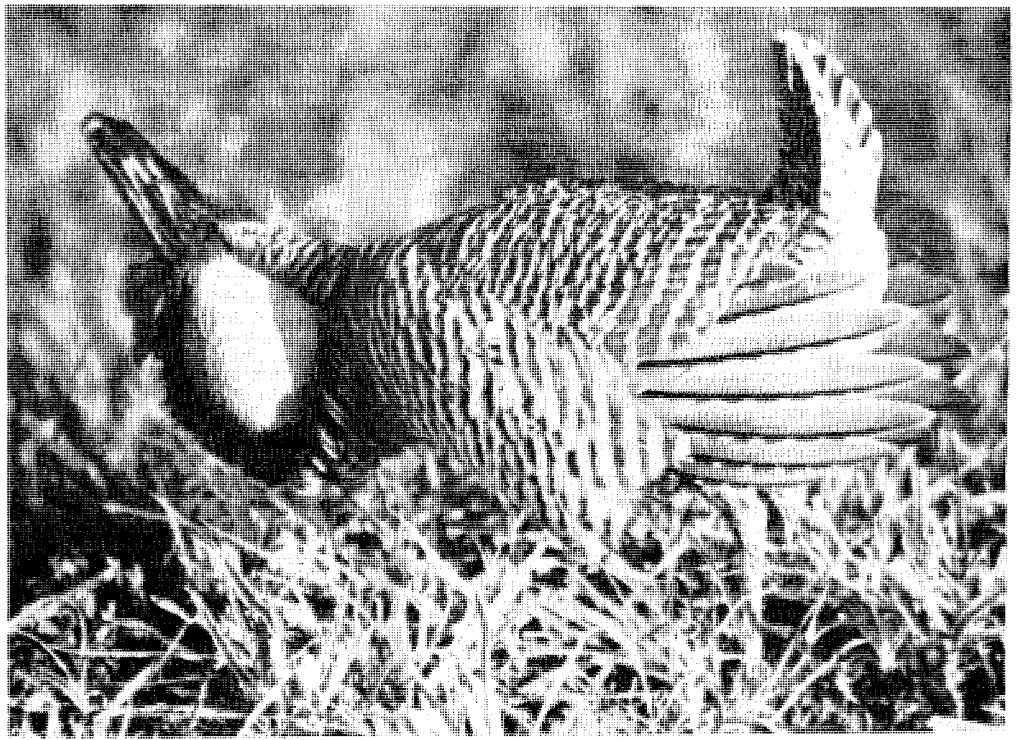

FIG. 1. Strutting male Attwater's Prairie Chicken. Photo by Roger Fleming.

FIG. 2. Ranch in Jackson County Texas east of Edna. Area deferred from grazing May–October. Tall grasses include big bluestem, switchgrass, Indiangrass and little bluestem. All plants had vigorous growth and produced maximum forage. Photo courtesy Texas A. & M. University, Dept. Range and Forestry.