The Ruffed Grouse

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ITS LIFE STORY, ECOLOGY AND MANAGEMENT

By FRANK C. EDMINSTER

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To my sons

DAVE and STEVE

to whom I
consider my greatest
duty is to help them
become good sportsmen

Acknowledgments

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Introduction

Three times since the turn of the century the ruffed grouse has suffered severe and quite sudden reduction in numbers in the northeastern states. Similar declines occurred in the lake states and Canada. Each time it has appeared to be threatened with extinction. Each time the sporting and nature-loving public has become aroused. And following each of these occasions, there have been investigations of the causes of the catastrophe. Woodruff in 1908 reported promptly on the severe but rather short-lived decline of 1907 in New York. Stoddart likewise pursued his questionnaire study of the 1917 scarcity promptly and published the results the next year. When the great decline of 1927 occurred (possibly the most severe of all), studies were already under way by Allen and Gross in New York and New England respectively. By the autumn of 1929, with two more hunting seasons passed and no apparent improvement in the numbers of grouse in New York, sportsmen urged that the state again undertake to determine the cause of, and cure for, the periodic decimation of the ruffed grouse. As a result the Conservation Department undertook a complete, scientifically conducted study of this species. I worked on this study for over seven years, mostly at the Connecticut Hill Game Refuge, near Ithaca, N. Y. These studies are the nucleus of experience about which this book is written, but insofar as possible its application has been broadened to cover the whole northeastern region. Eight years' additional work on wild life throughout the northeastern states with the Soil Conservation Service, U. S. Department of Agriculture, has aided in providing the breadth of field observation that makes this possible.

Many other studies of the ruffed grouse have been carried on in recent years. I have cited freely from the reports of these in order to provide a comprehensive picture of this most fascinating bird. State game agencies and colleges in Maine, New Hampshire, Massachusetts, Connecticut, Pennsylvania, Virginia, Ohio, Michigan, Wis-

consin and Minnesota are among those reporting on various aspects of the subject.

It is not intended that this book be an exhaustive treatise on all phases of study of this species. Rather it is hoped to cover the high spots of the life story, the ecology, and management of the ruffed grouse in a manner interesting to the sportsman, the nature lover and the lay reader, and at the same time be accurate and adequately documented for the technical man in the field of wild life management.

I want to emphasize that the responsibility for this writing is entirely mine and it is not sponsored by any public agency. In particular, it should be understood that this is not a report of the New York State ruffed grouse investigation. Throughout, where the editorial we is used, it refers only to the author.

Preface

The ruffed grouse is a creature that has evolved over millions of years along with thousands of contemporaries in the animal and plant world of today. The fact that the species exists at all is evidence of its ability to compete successfully in a world of constant strife. Like all other creatures it developed certain innate reproductive abilities, together with skills of escape and concealment that enabled it to increase and maintain its numbers. Also, other conditions developed to offset these increases. These opposing forces that play on each species tend to preserve the status of each. In discussing this mechanics of ecology for game species these forces have come to be called the factors of abundance.

These elements, or factors, that control the numbers of a species are essentially the same for all. But the different factors assume vastly different degrees of importance with different species and under varying circumstances with each species. Under any set of conditions, some one of the factors will keep grouse from increasing beyond the level it actually does; or, stated another way, will reduce grouse to the minimum numbers they decline to prior to the breeding season. This limiting factor does not cause all the mortality; merely the ultimate part. But if the limiting factor is reduced or eliminated, some other will take its place at a somewhat improved level of population. There will always be some factor to set the actual limit of survival for each species. And other factors, no matter what their importance or how man may affect them, cannot change the survival level of our game species. The limiting factor determines the greatest number that will survive on a particular area.

The eight major factors that control grouse populations may be divided into two types, as shown graphically in Fig. 1, page 3. The ones that compose the environment are in one group, while those that are inherently a part of the species are in the other. These we will describe briefly.

SHELTER

Fundamental to the environment that supports grouse is the vegetation that provides its home. Shelter includes the trees, shrubs, and herbs that compose the crown cover, undergrowth, and ground cover as well as the surface litter on the ground, and occasionally boulders, ground holes, and other protective materials. For the grouse, the evergreen conifers and broad-leaved trees and shrubs are important shelter, especially in the winter. Brush piles, fallen tree tops, and deep snow also furnish important winter protection. In the summer the leaf litter and vine and brier tangles are important shelter. Shelter must furnish not only protection from the elements and from mortal enemies, but the medium for all of life's functions including nesting, courting, sunning and dusting.

FOOD

Probably the most obvious factor affecting abundance is the food supply—an ample supply for good health at all seasons of the year. Water and grit requirements are a part of this factor. With the grouse, food as an independent factor is not often as limiting in effect as it is with many animals. Cover which furnishes adequate shelter usually possesses considerable numbers of grouse food plants. But the distribution and quality of grouse foods has a vital bearing on the distribution of the birds, even though grouse rarely succumb directly from diet deficiencies.

The cover which furnishes both shelter and food for grouse is termed the habitat, and is the foundation of the environment.

PREDATORS AND OTHER ANIMALS

Those creatures other than man that utilize the grouse for food are its predators. Primarily mammals and birds, they are the most common immediate cause of death for adult grouse. However, in considering the importance of the predators and other animals in determining grouse abundance, the correlation with other factors must also be considered. Most of the other factors of abundance are closely associated with predation. The snow that makes the roosting grouse vulnerable for attack, the parasite that weakens its flight,

the innate urge that forces a grouse to expose itself in order to perform for the benefit of other grouse—these and many other conditions predispose the predation which actually disposes of the grouse. The lack of adequate shelter in the cover, an inconvenient distribution of staple food supplies, man's sudden changes in the habitat, are examples of environmental deficiencies that may induce grouse mortality from predator attack. The density of the grouse population itself affects the degree of predation.

Even under the best of physical circumstances, predators will affect grouse population to some degree, and over most of the northeastern range they constitute one of the major factors. Many other mammals and birds that are associated with grouse habitat tend to serve as buffers for grouse by furnishing the predators with the bulk of their food.

DISEASES AND PARASITES

Organisms that derive both food and shelter from the grouse are parasitic upon it. Those that live upon its skin are ectoparasites and belong to the insects and other arthropoda. Endoparasites, those that live inside the body, are generally roundworms, flatworms, or free-floating protozoa or bacteria. Some of the disease-causing organisms are classed as viruses, while one is a fungus. Many are capable of causing death, either alone or in combinations.

Most animals have a rather large population of parasitic organisms, even when in excellent health. This is true of grouse. Most specimens of grouse when thoroughly examined will be found to have parasites of various types. Ordinarily they do the bird no harm. When certain destructive kinds gain access, the bird may be seriously affected. Other kinds of parasites, when present in large numbers, may have serious effects.

Generally a grouse, so ill from the effects of parasitic organisms that its functions are impaired, is picked off by some enemy before it can die from its affliction. Some do actually die without violence, at times in such numbers that the presence of an epidemic is indicated.

When disease is rampant it is a grave matter. Fortunately this is not commonly the case, and the direct losses from this source are generally occasional and scattered.

WEATHER CONDITIONS

Violent changes in the physical conditions surrounding grouse are exceedingly important in affecting abundance. Weather conditions and some of man's activities come in this category.

As with ourselves, weather conditions affect the grouse's activities. The wind, rain, snow, sleet, heat, cold, and sunshine all play a part in determining where a grouse will be and what it will be doing. For the young ones, the exposure to the elements may cause death, quickly and surely. To the grownups it often makes them more vulnerable to their enemies than they might be under more favorable weather. For the grouse, as for most living things, the weather is of the utmost importance in their lives.

MAN'S ACTIVITIES

Man may be either beneficial or destructive to grouse. As a hunter he is a killing agent, yet the removal of the surplus population may actually be beneficial to the species he kills. In other ways he affects the physical conditions of the environment. As a farmer he both improves and destroys habitats, through plowing, cutting, and fencing; he constantly arrests and alters the natural plant succession. His use of fire is often detrimental to wild life, yet sometimes helpful. His livestock and pets affect both plants and animals of the wild.

Man as a lumberman creates desirable openings and bushy growth by breaking up the forest cover. But by making forests into open land, he has often completely destroyed the range for grouse. As a conservationist he recreates habitat, offers protection in refuges, and makes laws to improve wild-life conditions. With some definite limitations, it may be said that the future of the ruffed grouse, as with all wild life, rests with him.

HABITS OF THE SPECIES

Even as with you and me, the grouse has habits imbued in him that he could do better without, at least in some respects. Many inherent urges affect survival. With us it may be to drive automobiles at breakneck speed, to jaywalk in traffic, or to eat or drink excessively. With the grouse it is to drum on an exposed log, to strut

around in the open to please a lady, or to fly at breakneck speed where obstacles are everywhere. But even though it is courting death to indulge in these whims, the grouse will continue to do it.

REPRODUCTIVE CAPACITY

The second of the major survival and increase factors that is inherently a part of each species is its innate ability to reproduce. It is elemental that, other things being equal, a bird that habitually lays eleven eggs (like the grouse) has a higher reproductive capacity than one that lays, let us say, four eggs (like the woodcock). Likewise, a species that is polygamous is better fitted to assure complete fertility than is one that is monogamous; a creature that matures to breed in a single year has a higher reproductive capacity in that respect than one that cannot breed until it is two or three years old. So in these and in other reproductive constituents, the survival and population of the grouse is vitally affected.

When we combine all the forces involved in these eight major factors of abundance, we have the whole ecology of the grouse and its associates with all the tragedy, pathos, drama, and comedy of their dynamic existences.

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The Bird Itself

CLASSIFICATION, NOMENCLATURE

Bonasa umbellus (Linnaeus),[1] the ruffed grouse, belongs to the great, almost cosmopolitan order *Galliformes*. Four families of this order are found in North America, the Cracidae, Tetraonidae, Phasianidae, and Meleagrididae—respectively the curassows, guans, and chachalacas; the grouse and ptarmigan; the pheasants and New World quail; and the turkeys. The family to which the ruffed grouse belongs, the Tetraonidae, is represented by seven genera and eleven species on the North American continent.

The generic name *Bonasa*, derived from the *Greek* Βόναγμς and Latin *Bonasus* (classical nouns meaning "a bison") embodies the idea of a bison's bellowing, hence that of a ruffed grouse's drumming. The zoologist Stevens, who named the genus in Shaw's *General Zoology* in 1810, may never have seen a living ruffed grouse, but he obviously had heard of its courtship performance. The specific name, *umbellus*, is a Latin word meaning an umbel or umbrella. It is descriptive of the bird's striking ruffs. The genus *Bonasa* is found only in North America (in the United States and Canada) and has but one species.

The accepted common name is ruffed grouse. However, the bird is known colloquially by many other names, some of which occasion considerable confusion with other species. The various Indian tribes called it by many names, including: Wen′-gi-da-bi-ne′ or Pinai (Chippewa); paupock (Narragansett); papahcogh (Mohican); cutquass (Pequot); ohquase (Oneida); pabhackoo or mimituiis (Delaware); Mūtch-i-es′—"Bad Bird" because in old times he was medeoulin, had magic power, and plotted against Gluskap, according to old stories—(Malecite, in New Brunswick); Pul-o-wetch (Micmac); Ajack, Puskee, or Pupuskee (Algonquian around Hudson Bay); Kh-

[1] *A.O.U. Check List* No. 300.

tūk (Esquimo).[1] Probably the first name given it by the early white men in New England was "wood hen." Today it is commonly called "partridge," "patridge," or "birch partridge" in New England, although it is not actually a partridge at all. In the southern Appalachians it is referred to as the "pheasant," but it is not a true pheasant either.[2] Other names include "mountain pheasant," "fool hen," "drumming pheasant," "wood-pilequarker," "drumming grouse," "drumming partridge," "drummer," "shoulder-knot grouse," "ruffed heath-cock," "moor fowl," "tippet grouse," "carpenter-bird," "white-flesher," "hazel hen," "red-tail," "gray-tail," "silver-tail," and just plain "grouse."

DESCRIPTION

Adults. The grouse is a symphony of rich browns, sometimes with a grayish tendency, sometimes rufous, with plump form, medium-proportioned beak, legs and tail, and a neck ruff of varying prominence. Length varies from fifteen to nineteen inches, wing spread twenty-two to twenty-five, tail four and one-half to seven and one-half, and weight from sixteen to twenty-eight ounces.

The head is topped with erectile feathers that are raised into a crest when the bird is excited. The crown is crossed with numerous lines or dabs of black and buff that gives the brown ground color a mottled appearance. There is a quite prominent buff eye-line from the base of the beak to the back of the head and a buff chin patch. The ruff feathers, which form a somewhat triangular patch on each side of the neck, are generally black with a green and purple iridescence. Occasionally on a very reddish bird the ruff is a rich reddish brown. The ruff is carried obscurely beneath the brownish neck feathers until erected into prominence by some excitement.

The browns of the neck, back, upper wings, and rump have varying patterns composed by the different characters of black, buff, and white. The neck is rather prominently marked with whitish, the back and rump mottled with long, black-edged spots along the feather

[1] I am indebted to W. L. McAtee of the U. S. Fish and Wildlife Service for most of the Indian names.

[2] The "true partridges" and the pheasants belong to the family Phasianidae, natives of the Old World. The European ("Hungarian") Partridge (*Perdix perdix*) and the ring-necked pheasant (*Phasianus colchicus torquatus*) are well established in northern U. S. and parts of Canada.

shafts; the rump is somewhat more rufous than the back; the wings usually show less rufous in the browns than the other upper parts, the primaries are quite dark with buff to whitish markings along the

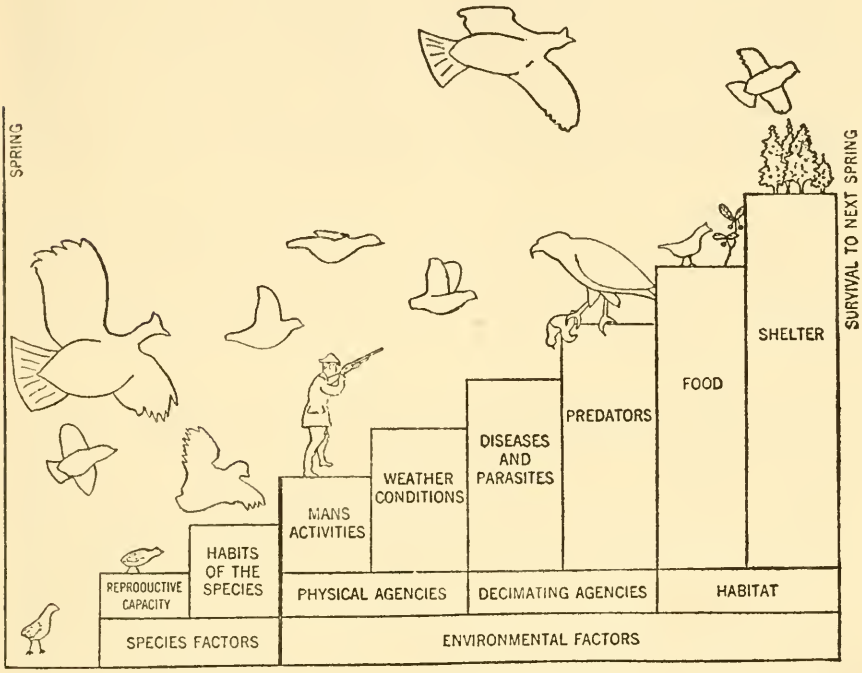

FIG. 1. The twelve grouse shown represent parents and a brood of grouse. We assume that the parents survived the winter on an area that has a carrying capacity of but two grouse. Therefore ten of this group must die by next spring if they remain in the area under the same conditions. The birds are illustrated as meeting the elements that may reduce their numbers. The higher the element, the greater the toll it may possibly take. The highest element, here shown as shelter, is the limiting factor. Only two grouse, in this instance one youngster and one parent, are able to surmount it. The reduction or elimination of any of the other seven lower elements would not result in a greater survival but merely a delayed mortality, since the shelter will permit the maintenance of only two grouse. Under different circumstances the eight factors might assume any order of importance, and any one might be the limiting factor.

narrow outer vanes; and the secondaries and coverts are bordered with buff or whitish with occasional black spotting.

The ground color of the eighteen[1] tail feathers (rectrices) is a

[1] A few specimens having twenty rectrices have been examined, usually males, and a few with only sixteen, usually females.

clear rufous brown transversed by a series of from six to eleven thin black bars. The tip of the tail is gray, but there is a broad black subterminal band that shows clearly in flight. The band is often broken with gray on the center feathers, especially in the females.

The lower parts vary from whitish to grayish or buffy white, tending mostly toward buff on the lower neck and upper breast. Numerous short bars of brown or blackish, darkest along the sides and fading toward the center, break up the gray background. The under wings and under tail coverts are predominantly an even gray or buff.

The beak is dark brown, the iris hazel, and the feet dark horn color. The tarsi are sparsely feathered above, naked below. During the winter months lateral pectinations appear on the toes, commonly and aptly known as "snowshoes." When spring comes these appendages are shed.

Plumage Differences Between the Sexes. The full-grown male is consistently larger and heavier than the full-grown female, although large females may match small males in these respects. The rectrices of the male are from six to seven and one-half inches long, while those of the female are from four and one-half to six and one-quarter, thus giving the male a distinctly longer tail. The ruff is relatively prominent on the male as compared with the female, always continuous across the breast where that of the female fades. The broad, black subterminal tail band is always broken with gray in the female, but is usually continuous in the male. The colors of the female are generally more subdued than those of the male and there is usually a slight pinkish wash to the brown of the forebreast. During the breeding season the male has a bright reddish naked patch over the eye that is not developed in the female.

With a bird in the hand, the sex is readily perceptible in almost all cases because of one or more of these characters, even though they are not each always constant. In the field the length of tail is a safe indicator most of the time, while ruff and tail band will often aid in making the sex identification. Sex identity in the wild may also be aided by actions characteristic of males or females, such as broodiness, drumming or strutting.

Color Phases. For most parts of its range, the grouse exhibits wide variation in basic ground color. Those birds with a rufous cast are

called the "red" phase, while grayish birds are "gray" phase. Every gradation between the extremes of dichromatism may be found.

Subspecies. Six subspecies are recognized by the 1931 *American Ornithologists' Union Check List.* The originally named form *B. umbellus umbellus,* has been described above. *B. umbellus togata* (Linn.), the Canada ruffed grouse, or northern ruffed grouse (A.O.U. No. 300a), is essentially like *B. u. umbellus,* but seems to average a little larger and heavier. A very large male will sometimes scale over thirty ounces. While this subspecies has a red and gray phase, it never attains the fullness of rufous or cinnamon color of the more southern subspecies. In *B. u. togata* the tail is generally grayer, the upper parts are a darker and more chestnut brown, and the under parts are more heavily barred. The feathers on the tarsus are somewhat longer than in *B. u. umbellus.*

B. umbellus thayeri (Bangs), the Nova Scotia ruffed grouse (A.O.U. No. 300d), is similar to *togata* in being two-phased but is darker gray, dusky or sooty, on the upper parts. Banding of under parts is regular and prominently dusky and more sharply contrasting against the background color. The bill is somewhat longer than in *B. u. umbellus.* The color phases are both very dark and not markedly different.

B. umbellus umbelloides (Douglas), the gray ruffed grouse (A.O.U. No. 300b), is usually a gray-to-slatish colored bird with very little brown on the upper parts, although red ruffs and brown tails occur occasionally. From mid-back to the top of the tail it is very slate gray, the arrow-head spots on the back feathers are gray with black edging, and the tail delicately vermiculated with black. Beneath it is whitish with a tawny caste. There are several brownish crossbars on each feather, largest and most sharply defined on the sides. The flank and vent feathers are nearly clear white and the foreneck and scapulars are a varied mixture of grays, browns, whites and rufous shades. The wing covert feathers generally have white shaft lines. The female is inclined to be more rufous than the male. The feathers on the tarsus are long, sometimes extending to the base of the toes.

B. umbellus sabini (Douglas), the Oregon (or red) ruffed grouse (A.O.U. No. 300c), is a large dark race. There is more blackish to the brown and the browns often are a marked chestnut shade. Ac-

cording to Coues (1903), this subspecies was discovered by Lewis and Clark in 1805–06 and first named *Tetrao fusca* by Ord (Guthrie's *Geography,* 2nd Am. ed. ii, 1815, pp. 317). "In strictness . . . this bird should be called *B. u. fusca* Coues," but he waives the point in favor of *B. u. sabini* as redescribed by Douglas.

B. umbellus yukonensis (Grinnell), the Yukon ruffed grouse (A.O.U. No. 300e), is the largest and grayest of the subspecies, similar to *B. u. umbelloides* but the light colors are more ashy and the dark markings finer.

While the six subspecies just described are all that were recognized officially in the 1931 edition of the *A.O.U. Check List of North American Birds,* several others have been described since this check list was printed.[1] One, from Vancouver Island, named *B. u. brunnescens* by Conover (1935), has since been accepted for the *A.O.U. Check List* (Auk Vol. 61, No. 3, July 1944). It is described as being most closely related to *sabini* but with a browner (less reddish) upper surface except for the tail. The tail is either a dull ochraceous umber instead of ferruginous in the red phase, or a clear gray without reddish cast and without double crossbarring in the gray phase. It is much darker brown on the upper parts than either *umbelloides* or *yukonensis,* and is more buffy below with more brown barring. It is thought to be restricted to Vancouver Island and islands adjacent to British Columbia and the mainland from Vancouver to Malaspina Inlet.

Three additional subspecies are described by Todd (1940) as follows: *B. u. monticola,* Appalachian ruffed grouse, "similar to *B. u. umbellus* but general coloration darker; the under parts more regularly and more heavily barred and more strongly suffused with buff." This subspecies is ascribed to the Appalachian mountain region from West Virginia southward. According to Wetmore (1941), birds from this area are indistinguishable from *B. u. togata.*

The second new subspecies described by Todd is *B. u. medianus,* Minnesota ruffed grouse, "Similar to *B. u. umbelloides,* but the upper parts are less grayish, more rufescent, and the under parts are more albescent and less heavily barred." Its range is given as the "Transition Zone from Alberta to southeastern Minnesota (and probably farther east)."

Third of Todd's new subspecies is *B. u. canescens,* northern ruffed

[1] A subspecies, called *B. u. Jobsii,* was described in 1871 by Jaycox from birds taken near Ithaca, N. Y. It was not accepted for the check list, however.

grouse. "Similar to *B. u. togata,* but the upper parts in general are grayer, less brownish, and thus lighter in tone, particularly on the secondaries, scapulars, rump, and upper tail-coverts. The under parts are also lighter colored on the average, and the dark barring is less intense. Similar to *B. u. medianus,* but the upper parts are generally darker, more grayish and less rufescent, and the tail is obviously darker gray; the buff of the under parts as a rule is not so rich and deep. The general coloration is lighter than *B. u. umbelloides.*" Its range is described as "from Labrador west to James Bay and thence to eastern Manitoba."

While Todd is proposing the addition of three new subspecies of *Bonasa umbellus* he suggests that the subspecies *B. u. thayeri,* accepted by the *A.O.U. Check List* as authentic, is actually identical with *B. u. togata.* He also indicates his belief that *B. u. brunnescens,* proposed by Conover, is adequately covered by *B. u. sabini.* In summary, Todd would recognize eight subspecies, although he says frankly, "A number of problems concerning distribution and systematics are necessarily left unsettled."

This is apparently the case, for only a year later Bailey (1941) describes another subspecies from Long Island, N. Y. Proposed as *B. u. helmei,* it is described: "A small ruffed grouse . . . very light buffy throat and a light-colored upper mandible . . . more whitish belly than any of the other races, heavily barred below with blackish; dark-breasted, but with more buffy breast than *togata;* neck ruffs and subterminal tail band black . . . gray-tailed type with few exceptions."

Recently, a complete taxonomic revision of the species was proposed by Aldrich and Friedmann (1943). They did not simplify the matter, but did provide sound ecological basis for their oganization. Twelve subspecies are recognized, eight previously described and four new ones. Three of those discussed above are discarded. Those substantiated are: *umbellus, togata, umbelloides, sabini, yukonensis, brunnescens, monticola, medianus.* Discarded are: *thayeri,* recognized in the *A.O.U. Check List* but considered by these authors to be the same as *togata; canescens,* described by Todd but here included with *umbelloides;* and *helmei,* which is covered by the type form *B. u. umbellus.* The four new subspecies described are *castaneus, affinis, phaios,* and *incanus.* These are distinguished as follows:

The Olympic ruffed grouse, *B. u. castaneus,* is the "darkest and

most richly colored of all the predominantly brown races of the species . . . darker than *sabini* and more reddish than *brunnescens;* brown of upper parts deep chestnut to dark auburn with no grayish mixture . . ." No gray phase is known. Its range is western Washington from Puget Sound to Oregon, south of the range of *brunnescens* and north and west of *sabini.*

The Columbian ruffed grouse, *B. u. affinis,* is described in both the gray and brown phases, the gray being the more prevalent. The gray birds are in ". . . general appearance intermediate between the gray phase of *umbellus* and that of *sabini* . . ." Brown-phase birds are "closest to the brown phase of *togata,* but have the black markings less extensive." The range extends from east-central Oregon and southwestern Idaho northward east of the Cascades through most of eastern Washington and the interior of British Columbia, to Hazleton.

The Idaho ruffed grouse, *B. u. phaios,* occurs in both color phases. In both it is most similar to *B. u. umbellus.* The gray birds are grayer, much darker, less brownish than the like phase of *umbellus,* while brown-phase birds of *phaios* are ". . . much darker, less rufescent, more brownish (more like corresponding phase of *brunnescens,* but with more grayish or dusky) . . ." than their *umbellus* counterpart. It is found on the west slopes of the Rocky Mountains in Idaho, and in portions of northeastern Oregon, southeastern Washington, and northeastern Washington.

The hoary ruffed grouse, *B. u. incanus,* in its brown phase, is ". . . a very ashy bird, similar not to brown but to gray phase of *B. u. umbellus,* but paler and, except for tail, less brownish, more like that of *B. u. umbelloides* but paler and less brownish on interscapulars, back, and upper surface of wings . . ." The gray phase is ". . . similar to brown phase but with tail feathers smoke gray with no buffy tone; ventral barrings duskier—light brownish olive darkening to sepia on the sides and flanks." It is found ". . . from west-central and central-northern Utah, southeastern Idaho and central-western Wyoming, northeastward across Wyoming and the Dakotas to northeastern North Dakota . . ."

It is well to note that Aldrich and Friedmann indicate in many instances that the subspecific characters grade from one to another along the boundaries of their ranges. Thus the delineation of the ranges of subspecies is somewhat arbitrary and the number recog-

nized is dependent upon the degree of variation one requires for such distinction.

I lay no claim to being an authority on the taxonomy of the ruffed grouse. Even so, having examined many hundreds of specimens of all ages and at all seasons from the northeastern states, I am thoroughly impressed with the unending variety in pattern and coloration of this remarkable bird. I have also seen birds of different subspecific pattern in single broods. How we view the question of subspecies depends upon whether we subscribe to the beliefs of the "lumpers" or the "splitters." I go along with the lumpers, for the sake of simplicity. My inclination is to go along with Todd in abandoning *B. u. thayeri* and *B. u. brunnescens*. But I am equally unsympathetic to the eight new subspecies suggested by Todd, Bailey and Aldrich and Friedmann. If the authorities reconsider the subspecies of *Bonasa umbellus* for the next edition of the *Check List*, I would cast my vote for simplification to four—corresponding to the present subspecies *umbellus, togata, sabini,* and *umbelloides*. However, for the sake of those who find merit in taxonomic detail, I commend the revision of Aldrich and Friedmann.

Immature. The juvenile plumage is similar to that of the adult but with less of contrasting blacks and whites, more of a pattern of somber browns. The ruffs are inconspicuous and the sexes are identical. The shape of the primaries and secondaries is less attenuate than in the adult, due to the greater width of the outer vane and the more blunt tips. The upper throat and chin are whitish.

The downy young are brownish buff on the upper parts mottled with pale buff, and yellowish buff below. There is a prominent black line extending behind the eye, occasionally broken.

PTERYLOGRAPHY

The fact that the feathers on a bird do not grow out of the skin evenly over the body, as does hair on a mammal, comes as a surprise to the average person. As every bird student soon learns, there are bare areas on the bird from which no feathers arise, and the areas from which the feathers do grow are called feather tracts. The extent and arrangement of these tracts (which vary greatly among birds) is called pterylosis and their study is called pterylography—the geography of feathers.

Ptilosis—Types of feathers and their characteristics.[1] Before discussing the feather tracts and spaces, let us consider the character and texture of the feathers themselves. This is known as ptilosis, or plumage:

Neossoptiles make up the natal down, distinguishable from similar feathers in the adult by the presence of pigment. They are the tips of the barbs of the succeeding juvenile feathers, sometimes called mesoptiles. Their length varies from six millimeters in the capital and dorsal cervical tracts to thirteen millimeters in the sternal and femoral.

Filoplumes are degenerate feathers, appearing almost like hairs. They arise from the skin elevations from which come also the teleoptiles and semiplumes. From zero to four may arise from these skin elevations. They range from half to three-quarters the length of the larger feathers.

Plumulae are adult down feathers, similar to neossoptiles but without pigment. They differ from semiplumes in the absence of a rachis. Strictly speaking there are no plumulae in the grouse, but those feathers resembling plumulae but having slight pigmentation have been called by this name.

Semiplumes are between plumulae and teleoptiles in character. They are always covered with other feathers, are downy, but possess a rachis. Large semiplumes, for all purposes merely downy teleoptiles, are found on the sides of the abdomen. Smaller ones occur in the posterior part of the spinal tract, in the cervical spaces, beside the primaries and many of the secondaries, and just above and below the bases of the inner rectrices.

Teleoptiles are the typical feathers of the adult—rectrices, remiges, coverts, contour feathers, and others. They vary widely according to modifications for various functions from the highly developed, almost completely pennaceous (i.e. not downy) rectrices and remiges to others difficult to distinguish from semiplumes. Some extremely modified teleoptiles are those of the eyelid, the oil gland, the ear, and the anus. Some, as those of the eyelid and oil gland, are probably functional and are small and modified of necessity; the others are likely only vestigial. In these modified feathers the barbicels are usually absent, the rachis (oil gland) is sometimes missing;

[1] For good photographs of several types of bird feathers, see *Life* magazine for July 17, 1944, pp. 8–11.

the barbs and barbules are few and stiff in the auriculars to allow free passage of sound; and in the anal feathers and those of the oil gland the aftershaft is practically gone.

The aftershaft is well developed in the ruffed grouse in all teleoptiles except the rectrices and functional remiges; in the anal and oil gland feathers, as noted above, it is often not distinguishable; it is rather poorly developed on the alula quills, axillaries, and the auriculars. It is always plumulaceous (*i.e.*, downy or fuzzy) and pigmented only at the tips of the longest barbs.

Sexual Variations in Feathers. Variations in the pterylosis between the sexes are minor. The number of feathers modified to compose the ruff is greater in the male. There is a tendency for the male to have more feathers than the female, possibly due to his larger size. The size of some of the feathers, as the rectrices, is larger in the male.

Snowshoes. These are cuticular outgrowths along the edges of the toes that grow in the fall and shed in the spring. Their purpose is to assist the bird in walking on snow by widening the toe area—hence the name snowshoes. Normal length is about two millimeters but in the northern subspecies tend to grow a little longer.

Moult. The ruffed grouse has a single moult each year. With the immature birds this takes place in August and September when the juvenile plumage is replaced by the first adult feathers. There is some evidence that the outer primary in this first adult plumage is shorter than in subsequent years.

The adults begin their annual moult in late July and continue into September. There is a period when many of the flight feathers have been dropped and the new ones are not well developed that the birds have some difficulty with flight. At this time it is not uncommon to see a "tailless" grouse.

It has been believed by some that a restricted pre-nuptial moult takes place in the ruffed grouse. This was originally based on two specimens of *B. u. sabini* described by Dwight (1900), which were collected in British Columbia in 1889, one on May 20 and the other on June 2. These specimens have been re-examined by Trainer who likewise found a few growing feathers on the head and throat regions (letter, January, 1942). He says, however, that the evidence indicates that these two birds are unusual and that the normal thing

in the ruffed grouse is a complete absence of moulting in the spring of the year. None of the thirty birds Trainer examined in the Cornell University collection that might have shown this moult did so.

Pterylosis—Feather tracts and spaces. The area of skin on the ruffed grouse may be divided into ten feather tracts which are separated by twelve bare areas, or spaces (see Fig. 2). These may be described as follows (Trainer, 1938): [1]

The Capital Tract includes all feathers on the head except those on the under center portion. Several isolated spaces, noted later, are found here. The feathers in this tract are all small, all point backward. Longest are the erectile crest feathers. Some of the feathers around the eyes are among the smallest on the body, being about two millimeters long. The feathers in this tract are divided into ten regions, named according to the part of the head: frontal, coronal, occipital, superciliary, loral, rictal, ocular, malar, auricular, and post-auricular.

The Spinal Tract covers the upper surface of the body proper, from the capital tract to the caudal tract. It is divided into three regions: cervical, interscapular, and posterior.

The Oil Gland Tract is at the posterior end of the spinal tract and consists of eight little (three and four-tenths millimeters) feathers arranged in a circle on the tip of the gland.

The Caudal Tract consists of the rectrices (tail feathers) with their upper and under coverts and the feathers around the anus. There are normally eighteen rectrices, although occasionally birds are found with twenty (usually males) or sixteen (usually females).

The Ventral Tract includes the whole under side of the body from the mental angle to the anal region. The foremedian portion is divided into the interramal region from the chin to below the eyes, the submalar region and the cervical region; the posterior median portion is called the abdominal region, and the lateral portions are divided into the sternal and axillar regions on each side.

Most notable feathers in the cervical region are the five rows which compose the ruff. They are situated near the middle of the length of the neck. The length of the male ruff feathers increases in size from sixteen millimeters to about seventy millimeters and then

[1] The descriptions of feather tracts and spaces are derived entirely from Trainer's work.

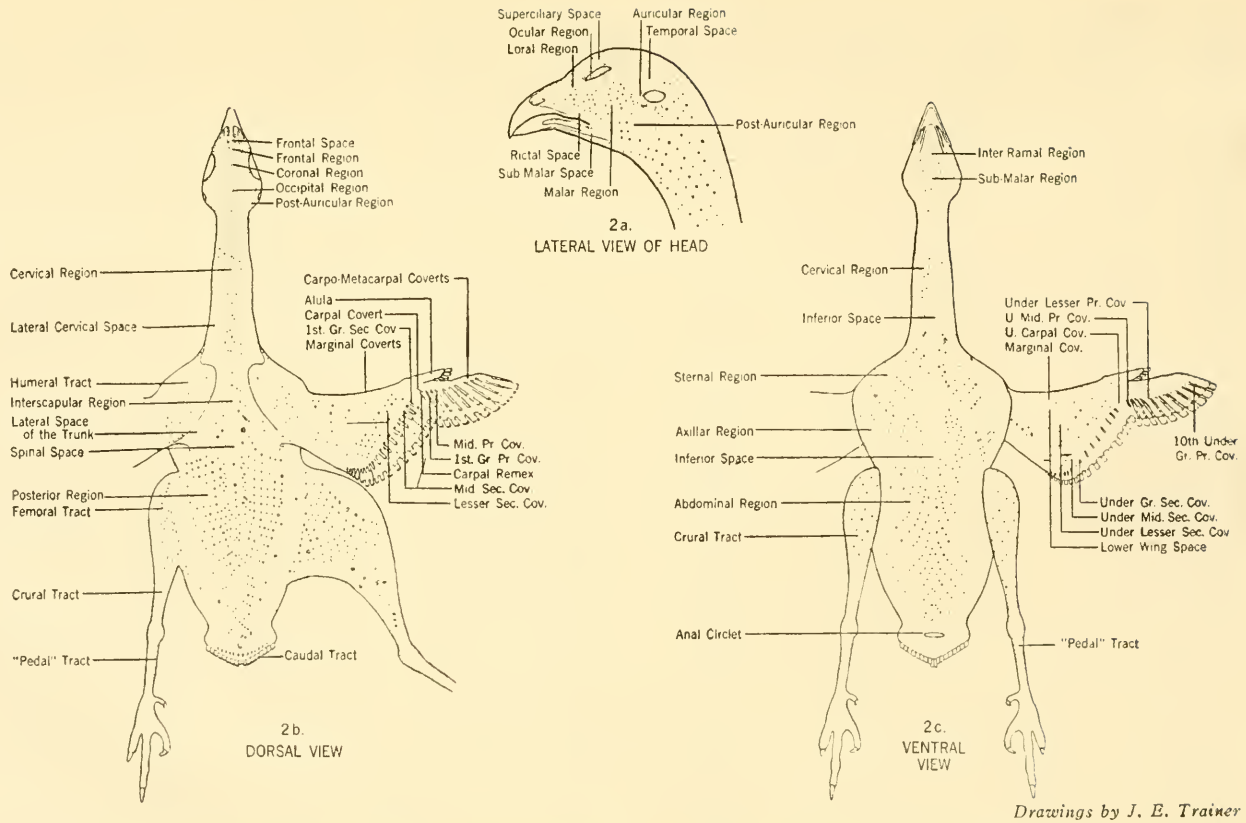

FIG. 2. Feather Tracts and Spaces of the Ruffed Grouse. A. Lateral View of Head. B. Dorsal View. C. Ventral View.

decreases to fifty millimeters at the back row; the female ruff feathers average shorter. All of the ruff feathers have truncated ends made by the exceptionally long proximal barbs.

The Humeral Tract bears the scapular feathers, which consist of a band of large feathers extending obliquely across the humerus. Beginning at the lower end of the neck they extend to the back edge of the upper arm.

The Alar Tract consists of all the wing feathers other than those of the humeral tract. Many of these wing feathers are identifiable as individuals and hence are significant taxonomically. The tract is composed of primaries, greater primary coverts, middle primary coverts, secondaries, greater secondary coverts, middle secondary coverts, carpal remex, carpal remex coverts, lesser secondary coverts, marginal coverts, alula, alula coverts, carpo-metacarpal coverts, under greater primary coverts, under middle primary coverts, under lesser primary coverts, under greater secondary coverts, under middle secondary coverts, under lesser secondary coverts, and under carpal covert.

The Femoral Tract covers most of the sides of the thighs with the rows radiating posteriorly from an apex at the anterior end, and the more posterior row curving somewhat dorsally.

The Crural Tract is divided into two regions, internal and external, covering the lower leg. The feathers are rather sparse, soft and hairlike, with a plumulaceous aftershaft extending about half their length.

The Pedal Tract is a continuation of the crural tract onto the tarsus. The feathers are also similar to the crural feathers, and are even more modified in the same direction. The rachis and calamus are almost entirely gone, and the plumulaceous aftershaft is short.

The spaces, or bare areas, separating these tracts are described as follows:

Capital Spaces: The temporal space, in front of and above the ear, is covered by the feathers of the ocular and upper auricular regions of the capital tract. The superciliary space above the eye is covered by the feathers above it, while the rictal space posterior to the nostril is covered by feathers from the rictal region above it. Over the ramus of the lower mandible is the submalar space, covered by the adjacent feathers of the submalar and interramal regions, while behind the culmen the bare frontal space is located.

The Lateral Cervical Space extends along each side of the neck from a point in front of the middle of the neck back to a point opposite the humeral tract. Occupying about one-sixth of the circumference on each side, this space lies predominantly above the median line.

The Lateral Trunk Space includes all the several spaces around the wings and legs. At the front it is continuous with the lateral cervical space above the wing; farther back it separates the femoral tract and the posterior part of the spinal tract, and then curves medially in front of the upper tail coverts to meet its other lateral half at the oil gland. It is covered by the feathers of the back part of the spinal tract and on the sides by some of the femoral tract. It is also connected with the inferior space by narrow bands extending between the sternal-axillar and abdominal regions on the ventral side.

The Spinal Space is found along the median line of the spinal tract from the middle of the interscapular region to a point opposite the middle of the femoral tract. It is covered by the adjacent feathers of the interscapular region.

The Inferior Space lies between the two halves of the ventral tract along the medio-ventral line, beginning on the neck just in front of the ruff and extending back to within about fifteen millimeters of the end of the sternum. It is covered by feathers of the lateral cervical, sternal and abdominal regions.

The Upper Wing Space is the area distal to the humeral tract, bounded by the marginal feathers of the shoulder, the secondary coverts and the feathers on the posterior edge of the upper arm. It is very irregular in shape and is covered by the marginal feathers of the shoulder, the proximal lesser secondary coverts, and the distal scapulars.

The Lower Wing Space is continuous with the lateral space of the trunk and extends to the underwing surface irregularly to the base of the first primary. It is mainly covered with the feathers anterior to it but next to the body the adjacent body feathers cover it.

The Crural Space separates the femoral tract from the lower leg plumage. It is a very small naked ring on the outer surface of the upper tibial region, continuous with the lateral trunk space.

These spaces vary from being entirely bare to having a sparse covering of plumulae. Their function is to facilitate movement or

position, as flying or walking, or fitting one part of the body into another, as in roosting, and probably economy of weight.

The Brood Spot: The female bird plucks the feathers from her abdominal region during incubation in order to make proper body contact with the large clutch of eggs. This bared area is called the brood spot. Normally all of the feathers on this spot are plucked except the filoplumes. Most of the abdominal region is plucked, as well as adjacent portions of the sternal and axillar regions and the femoral tract.

The Numbers of Feathers on a bird may vary considerably. Some indication of the number of feathers (teleoptiles and semiplumes) in the various tracts may be gained from the figures of Trainer obtained by plucking a female weighing five hundred thirty-nine and seven-tenths grams, collected April 27, 1937. He points out that the distinction between certain tracts is indefinite owing to the indefiniteness of some of the tract boundaries.

Tract	*Number of Feathers (both sides)*
Capital	776
Spinal	
Anterior	197
Posterior	360
Oil gland	8
Caudal	164
Ventral	
Cervical, submalar, interramal	241
Sternal, axillar	158
Abdominal	196
Humeral	144
Alar	1104
Femoral	284
Crural and Pedal	710
Total	4342

Range. The ruffed grouse in its six subspecies is found over most of the wooded areas of the United States and Canada. *B. u. umbellus* ranges from the Appalachian Mountains in northern Georgia, northern Alabama, and the Carolinas, through western Virginia and Maryland, Tennessee and Kentucky, southern Ohio, Pennsylvania and northern New Jersey, and northward approximately to a latitudinal line through the center of Minnesota, Wisconsin, Michigan, New York and northern Massachusetts. Here it blends into *B. u.*

togata. Scattered outposts remain in eastern Kansas, Missouri (?), Iowa, Illinois, and Indiana.

B. u. togata ranges northward from the Minnesota-Massachusetts line referred to above through Ontario, Quebec, and New Brunswick provinces, practically to the limit of trees in northern Ontario and Quebec.[1]

B. u. umbelloides is found from Alberta and west-central Mackenzie south to northern Utah, northern Colorado, and western South Dakota, including the whole of British Columbia east of the Coast and Cascade ranges (*A.O.U. Check List*, 1931).

B. u. sabini ranges from Vancouver Island and the adjacent mainland coast of British Columbia south to Humboldt County, Calif. (op. cit.).

B. u. thayeri is restricted to Nova Scotia and probably eastern New Brunswick (op. cit.).

B. u. yukonensis is found in the interior of Yukon Territory and Alaska (op. cit.).

Eggs. The eggs of the ruffed grouse are oval to short ovate in shape, broad and blunt at one end and more pointed at the other. The color is grayish-white to buffy, and only occasionally speckled. After a period of incubation and exposure they often become quite stained. The size averages about thirty-eight and five-tenths by thirty millimeters. Extremes of size of the eggs examined by Smythe (1925) were: largest, forty by thirty-two millimeters; smallest, thirty-three by twenty-five millimeters.

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2

Chronicle of the Ruffed Grouse in Eastern United States

During Indian times the *papahcogh* was an important item in the economic life of the Amerindians of the Northeast. How long this relationship had existed before the advent of the white man is not recorded, but it probably went back to an era when the aborigines were far more primitive than when first observed by the Pilgrims in 1620. It may have begun when the people first moved in from the West to settle what is now the northeastern United States. The grouse, or at least a bird very closely related to our modern species, has been recorded in remains from the Pleistocene period (circa 25,000 years ago) from areas in both the eastern and western parts of the country.

It is highly probable that the native birds and mammals were fairly stable elements in the environment of those times. At least we find no evidence that the Indians either exterminated or seriously threatened any species. Even though the grouse was a staple item of food, the proportion of game to the sparse population of humans was such that hunting was not a serious threat to it. The grouse and its natural enemies, including man, lived in a rather harmonious balance. There is evidence, however, that there were years when game was scarce, and presumably grouse were included. Indian lore tells of winters of famine, and Longfellow refers to them in his "Hiawatha." It should be stated again, though, that such temporary periods of scarcity were not likely due to overhunting.

The White Men Come. When the Pilgrims came to Massachusetts they found a land abounding in game. Of course there were not many of them at that time, but still the hunting was wonderful for the few that there were. Many of the old prints of the Pilgrim days show the grouse, along with the deer and the turkey being brought

home, as the prize of the hunt, to the log cabin as the fitting larder for a pioneer family.

It is to be expected that such a creature would quickly find its way into the writings of the time. Probably the first printed record is that of Morton in 1632, just twelve years after the initial white settlement. He was greatly impressed with the abundance of the bird, having seen as many as forty in a single tree at one time. Baron de Lahontan, in 1703, wrote of the great abundance and "comical" stupidity of the "wood hen," as he termed it. This "fool hen" characteristic did not detract from the high regard in which the bird was held as a table delicacy. Audubon, writing in 1856, considered it second only to the wild turkey among the upland game birds as a delectable food.

A Change of Character and Economics. The journals of the early American ornithologists contain many notes on the distribution, abundance, and habits of the species. From Wilson (1812) in Pennsylvania and Nuttall (1832) in New England to Bartram (1751) in Georgia, and Swainson and Richardson (1831) in Saskatchewan, the story developed until by 1849 Audubon determined that its range was the whole breadth of the continent. As the settlers advanced into the wilderness, the grouse continued to play an important part in the home diet.

With the forests being cleared to make way for agricultural lands, grouse range was vastly restricted. In the process, the range was temporarily improved by the vast development of edges[1] through the extensive woods, but ultimately the clearing reached such proportions that the species was eliminated from large areas and confined to a small fraction of the former range in others. Throughout the eighteenth and nineteenth centuries this process continued. Concurrently, as farming intensified and communications developed, cities sprang up all over the nation and the grouse ceased to be of great importance as a staple food. An era of commercialization developed, with professional hunters and trappers replacing the scattered pioneers. Along with the passenger pigeon and other game birds, the grouse were mostly shipped to the big city markets. The birds became scarce in the vicinity of big cities as this traffic

[1] "Edge," as used in wild-life management, refers to the boundaries between dissimilar types of cover, as for example hay field and woodland. It is so significant in animal ecology that game is sometimes said to be a product of edges.

developed. As early as 1812, Wilson records the retreat to the interior of the species away from the vicinity of Philadelphia.

The abundance apparently fluctuated considerably in different parts of the Northeast and the market price varied accordingly. From twenty-five cents a brace (Boston 1831, Cincinnati 1820) in the first third of the 1800's prices ranged to as high as two dollars a bird in New York later in the century.

Even when civilization pushed the species back from the cities, hope was held out for its recovery, as witness the item in the *U. S. Gazette* of November 18, 1832: "We are glad to perceive that the citizens of Bucks County [near Philadelphia] are giving heed to the preservation of game. . . . Few of that fine species of bird [the grouse] are to be seen. . . . Let us encourage their growth and we shall be repaid by purchasing them a few seasons hence at fifty cents per dozen."

During the last two decades before 1900, the importance of the grouse in commercial channels waned with the diminishing supply, and at the same time interest in hunting as a sport was growing rapidly. Demands for the legal elimination of commercial hunting became more and more vociferous until one after another the states enacted the needed restrictive legislation early in the present century. New York's law prohibiting sale of grouse was passed in 1903, Pennsylvania's was enacted in 1897.

The emphasis on grouse hunting as a sport and form of recreation has increased by leaps and bounds since the passing of the era of exploitation. Today he is called "the king of game birds" by most hunters familiar with him. In Pennsylvania it is the official state bird. That the grouse should attain such importance in the sporting field is a tribute not only to the wisdom of creating and enforcing adequate conservation laws but even more to the ability of the species to adjust itself to changing environment.

Reference has already been made to the "fool hen" characteristic of the bird that so amused de Lahontan. One early author told of hunting grouse with dogs—the more mongrel and yappy the better—wherein the trick was to first flush a covey. They would alight in a near-by tree and watch the dogs as they gathered at the base of the tree and ran around in circles, all the while making a great noise. The hunter then picked off the birds with his rifle. So long as he was careful to pick the lowest bird each time, so that its falling did not

disturb the others, he would get them all without any flying. While I have never witnessed a phenomenon like this, I have shot grouse in the deep Adirondacks with a high-powered rifle by taking their heads off, and within the past ten years. However, this is a far cry from the sporty bird of most of our Northeastern coverts today. Even those in remote mountainous areas are seldom the "fool hen" type.

The ability of the grouse to make this change is truly remarkable. Instead of a dumb biddy sitting on a limb awaiting its execution, today the normal grouse flushes so fast that a hunter hardly has time to get his gun braced to his shoulder in time to shoot, let alone to take aim. How amazing is this transformation of character may be judged by comparing it with the record of its near relative, the Canada spruce grouse (*Canachites canadensis canace*). This grouse was unable to meet the adjustment necessary for survival. It remained a fool hen, and today is exterminated from all of its former range except where an area of wilderness has remained beyond the hand of man.

Cycles and Surveys. When the transition from market produce to game bird extraordinary was completed, the grouse assumed a status of far greater importance to man. It is natural then that the sporting fraternity and nature lovers as well would become greatly concerned when sudden scarcity seemed to threaten the species with extinction. Then, as each crisis passed and was followed by a resurging abundance, the alternating periods of scarcity and plenitude appeared to possess an inexorable rhythm. Thus came the concept of the population cycle. The baffling nature of the cause of this cyclic phenomenon led many observers to the conclusion that some inscrutable, all-pervading force must be guiding it. This led naturally to the suggestion that the cause must be ethereal, probably emanating from the sun. Concurrent investigations indicating cycles in solar conditions abetted this theory. This being the case, these cycles must have been going on from time immemorial. And so the search for records began; records that would substantiate the existence of periods of scarcity prior to those that had been fully documented. They were not hard to find.

The Indian lore telling of winters of game scarcity are probably the earliest indication of the then unrecognized cycle. It did not take the white man long, however, to register the occurrence of grouse

depletion. Nuttall, in 1832, in New Hampshire, an article in the *U. S. Gazette* for November 18, 1832, and an anonymous editor in New York the same year, called attention to the disappearance of the birds in the winter of 1830–31 where they had been abundant the year before. Simple explanations were offered: migrated southward and hard winter respectively. They had not learned enough of the problem to make it complicated.

Written records reveal a few more so-called disappearances in the nineteenth century. The most definite records of scarcity are for a few years after the Civil War in eastern New York, for 1866 in Vermont (but abundant in Massachusetts that year), 1877 in New York, 1883 in Ontario, and 1896–97 in Pennsylvania. After the turn of the 1900's, when the interest in sport had greatly increased, the story is far more complete.

An exceedingly hard winter in 1903–04 seemed to have resulted in serious grouse losses in the Northeast. Following this, Forbush undertook the first of several questionnaire studies by sending out an inquiry to several hundred naturalists and sportsmen in Massachusetts. When the very severe scarcity of 1906–07 came it was quite generally recognized throughout the Northeast. It was feared that the end of the grouse was at hand. So alarmed was the Forest, Fish and Game Commission of New York that an investigation was ordered. The questionnaire survey which resulted (Woodruff, 1907), in addition to the four standard explanations—disease, bad weather, predators, hunting—added five more to the growing list of possibilities. He concluded that it probably was caused by an unhappy combination of the first three of these four.

While the meeting of the minds brought about by the 1907 survey resulted in the concept that a combination of factors may have impelled this grouse decline, the survey covering the next great decline disclosed just how complicated the problem can become when more attention is given to it. Following the 1914–16 period of decline, the New York State Conservation Department, this time in cooperation with the American Game Protective Association, again sponsored a questionnaire survey (Stoddart, 1918) in an attempt to ferret out the cause of the decline. No less than forty-five contributing causes are listed, the most prominent being foxes, bad nesting seasons, and hawks. Great emphasis is laid on predation; there are eighteen factors within this classification. Among the also-rans are: driven out

by pheasants, shooting from autos, pasturing of cattle in woods, and summer boarders and foreigners without licenses. It is interesting to note that disease was given relatively little importance in this inquiry, whereas it had been considered very important in the 1907 study. The note of new stock needed is the first mention we find of the inbreeding factor, destined to be highly ballyhooed a few years hence.

In 1924 an out-of-step decline seemed of sufficient severity to institute another investigation. At the American Game Conference that year Dr. A. A. Allen, who had been investigating the artificial propagation of grouse since 1919, reported the discovery of the stomach worm (*Dispharynx spiralis*) of such severity in New York grouse as to assume epidemic proportions. He suggested that it might be the cause of grouse cycles. At the instigation of Senator Walcott a national grouse investigation was created, with the late John B. Burnham as chairman of the committee. The work of this committee, directed by Dr. A. A. Allen, was concentrated largely on a study of grouse diseases. Specimens were received from all parts of the Northeast. Allen meanwhile continued his studies on methods of raising grouse in captivity. The next year the New England portion of the work was continued independently by Dr. A. O. Gross under the New England Ruffed Grouse Investigation sponsored by the Massachusetts Fish and Game Association, and Allen continued his work in New York, examining birds from Minnesota, Michigan, Pennsylvania, and New Jersey, as well as New York.

The 1924 decline was short-lived in most parts of New York and the birds were again plentiful in 1925. But the gains were not held for long. Indications of decline were noted in 1926 and by 1927 the species had declined to the lowest levels known. Hunting seasons were completely closed in New York and most other near-by states for a year or more. Both Allen and Gross examined hundreds of specimens sent in by interested sportsmen and scientists from all over the Northeast. In 1929 Gross reported: "Work on all phases of the life history of the ruffed grouse will be continued, but this fall we will give special emphasis to an intensive study of *Dispharynx* which has been found to be the most important parasite affecting the grouse. . . ." Altogether, seven progress reports of these investigations were made, two by the committee of the American Game Conference and five by the New England Investigation.

Chafing under the repression of two successive closed seasons on grouse in New York, leading sportsmen of the state met to consider what might be done to remedy the alarming situation. They requested Dr. Allen and Herbert Stoddard to draw up a comprehensive plan for a thorough investigation of the grouse in New York State, the proposed study to be financed by the New York State Conservation Department. As a result of their recommendations the Conservation Department in 1930 entered upon a thorough scientific study of the whole problem.

From 1930 to 1932 the grouse in the Northeast recovered from the depression of 1927–29. From 1932 to 1944, the population had numerous moderate ups and downs from a general plateau of moderate to great abundance, none of which can be compared in intensity with the 1927 crash or probably with some of the high populations of previous periods of abundance. The declines that have been observed in the East during the 1930's have been very spotty geographically, and usually quite local. In 1945 the number of grouse in the Northeast again declined to a low level. Owing to war, no studies were in process at the time.

Concurrently with the modern New York Investigation, a study of the ruffed grouse was being made in Minnesota under the leadership of Dr. Ralph T. King. Begun in 1929, these studies reached a climax in 1934 when the observers witnessed a very severe grouse decline. As a result of his studies, Dr. King came to the conclusion that the cyclic decline was precipitated by an upset in the reproductive functions of the female followed by an almost complete loss of young birds of the year. The underlying force causing this condition appeared to be beyond the control of man.

In the 1930's there were a number of smaller studies of the grouse, some confined to limited phases of the broad problem. C. H. D. Clarke in Ontario (1932–36), L. W. Fisher, F. W. Baumgartner and others in Michigan (1932–39), studied many of the factors governing populations. Other studies were made in Pennsylvania, Connecticut, Maine, Ohio, Virginia, New Hampshire, Wisconsin, and Massachusetts.

And so, with scientists of all classes sitting on the sidelines waiting to examine every aspect of the long overdue cyclic decline—theoretically to have occurred in 1937 in the Northeast—we find that apparently the phenomenon wasn't what it was thought to be after all.

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3

Biography

April Showers and May Flowers. Each dawn arrived a little sooner than the day before and each dusk delayed a little longer. The sun, when it shone, became warmer day by day. The winter snow had disappeared except for a few residual patches on the cool north slopes. These changes brought new experiences and sensations to the grouse that had been born and raised on the other side of the woodlot the summer before. They had not witnessed such changes and sensations before. It was thrilling.

All winter long they had lived along the hemlock ravine. They had several other companions off and on since autumn but they had not seen any of them for several weeks. One day the female felt more and more the need of solitude. The deep shelter of the ravine did not seem to fit the new feeling in the air. And so she wandered off—over near the little slash where first she had seen the light of day. There she encountered another grouse and, still wanting a place all her own, she decided to press on farther.

Just beyond the slashing was a woodland of young maples and beech. A logging road traversed this woods from the slashing, and wound its way down over the hill to the farmstead in the valley below. As the young hen bird leisurely picked at fresh spring greens and jumped for the first insects of the season, the sun came up higher through the lower tree branches and the old trail with its grassy edges seemed very homy. She was nervous. Something within tugged at her emotions. There was an increasing urge to respond to an unknown need. And it was not long in coming. A strange sound rent the air. Hardly had the first few beats of its thumping passed before she was tingling with anxiety to the tip of every nerve. Surely this was what she had been seeking, all unknowingly.

Slowly she made her way back towards the edge of the slashing—the direction from which this strange sound had come. Stealthily she chose her footsteps so as not to expose her presence. In just a

few minutes the thrilling beats started again—slowly at first, then at an increasing tempo, until at the end they blended into an indefinite whir—as though the speed had so increased as to have passed the field of audible vibrations. The hen bird's heart was in her throat as she came closer. Then suddenly, as she peered around the end of an old windfall, she beheld the object of her search. It was the grandest grouse she had ever seen. She froze in her tracks.

The Courtship. Apparently the old cock bird had spied her the instant she saw him. Facing her with his head turned slightly sideways he stood erect on a huge old fallen log. His tail was held high and spread into a huge fan; his wings drooped deliberately at his side, while the head was drawn stiffly back into an encircling black ruff, raised high (see Plate 2B). His sharp eyes held her attention steadfastly, as though he were attempting hypnosis. Slowly and carefully he took a stiff step forward—then another, and another. For several feet along the old log he thus slowly strutted towards her. Then he broke his gait and quickly jumped down from the log, and just as quickly regained the strutting pose again. After a moment he reached quickly down with his head and pretended to peck at each of a couple of leaves in front of him. In an almost continuous gesture, he began shaking his head forward and somewhat downward and sideways, first on one side and then on the other, and with each shake emitting a most peculiar sound. With each headshake he made a double hiss—something like "shh—ushh," the first half with an exhale and the second with an inhale. After a few preliminary, evenly spaced hisses, the headshakes gradually became more rapid and the hisses speeded up with an increasing crescendo, finally reaching the point where it became physically impossible to shake the head any faster. A final, long, letting-off-steam hiss following the finish of the headshaking was accompanied by a quick little forward run toward the hen bird during which every muscle in his body relaxed in a convulsive quiver.

By this time the female was so overcome with emotion at this devastating exhibition that she squatted, limp, on the ground. But when the male suddenly set upon her and struck her vicious blows about the head, she quickly regained her senses and beat a hurried retreat.

This performance Allen (1934) has called the "intimidation dis-

play" and apparently, insofar as the male is concerned, has little relation to mating. If the intruding bird had been another male, the same events would have taken place except that a fight might well have ensued. In this case the winner would remain in the territory and the loser would seek another location at some distance.

Both the drumming and intimidation display performances are acquired by instinct. The drumming takes a little time and practice to attain proficiency—the wings make only a swishing noise until the bird learns to make the drum sound, but it needs no guidance to know what to do. Allen (1934) had a captivity raised male learn to drum, never having seen or heard another grouse.

The hissing performance is a fascinating display. The whole action takes almost fifty seconds, the first thirty seconds being devoted to the slow, evenly timed double-hisses, about a second or slightly less apart; then about the same number of hisses again, thirty to forty, in fifteen seconds at a rapidly increasing tempo, and finally about twenty or more hisses at top speed for about five seconds culminating in the last hiss and run act. In all, the bird makes about ninety double-hisses in each display, with the beak held wider and wider open as it progresses, and the final long hiss is emitted with the beak nearly closed.

The Mating. Each day thereafter, the cock bird could be heard drumming on his log near the edge of the little slashing. From before dawn till after sun-up he was most ambitious, drumming every few minutes. Then he would slacken off and little would be heard from him until along toward nightfall. In other directions, but farther away, the hen bird could hear other grouse drumming too—inviting any and all grouse to combat, as she learned to her sorrow. She wanted to seek them out too, but her first experience had taught her the wisdom of caution. After a few days had passed, she could no longer control her emotions; so off she went to meet her adversary once more. Again, as he discovered her presence, he ceased his drumming, paused for a brief moment, then slowly descended from his log. This time his tail was held low and compact, all the feathers were depressed, and the look in his eye was one of appealing gentleness, not of fiery defiance. He walked toward her slowly, in a somewhat circuitous route, shaking his head a little, pecking at a leaf now and then.

To the hen this new advance was even more convincing than the first. His appeal was simply irresistible. He pecked gently at the base of her bill, then, placing first one foot and then the other upon her back he mounted for coition. She responded with slightly raised tail, spread wings, and body flat to the ground.

Probably the most peculiar aspect of the sexual relations in the grouse (and possibly in most birds) is the apparent lack of recognition of sex, as such. Differences between birds seem to be exemplified as relative strength or weakness, audacity or timidity. Not only will a strong male attempt coition with any subjugated bird, whether male or female, but timid males may actually accept such advances. In captivity, and possibly in the wild, this exhibiting of physical superiority is not confined to sexual activity. Once a bird is decisively beaten, regardless of sex or by what sex, it attains an inferiority complex, and from then on is easily drubbed by any other bird in the pen. If not removed, it will be killed but, if placed in isolation for a time, it often will regain its self-confidence.

Sex Rhythm. Why should the male bird have challenged his visitor to a duel upon the first meeting, and received her as a mate upon the second? The explanation lies in the phenomenon called by Allen (op. cit.) "sex rhythm." Both sexes have a short, restricted mating period, which may recur several times during the spring season. Only when both birds are in the mating phase of their physiological cycles will mating take place. At other times, without this synchronization, and regardless of whether either bird alone is in oestrus, mating will not take place. In these periods fighting—the working of the law that only the fittest can survive—is the order of the day.

Displays that appear superficially to be courtship or mating performances may take place at any time of year, by birds of either sex or any age. These are primarily the manifestation of the continuous urge to show superiority. Coition is often attempted, by either sex with either sex or by chicks as young as a single week old, but these exhibitions of male behavior are in reality an attempted demonstration of individual physical superiority.

Drumming. The truest exhibit of the male character is in his drumming. At once a challenge to other males or an invitation to receptive

females, it is the one display that sets him definitely apart from his sisters. Grouse have been known to drum during every month of the year and during every hour of the day and night. The period of really intensive drumming, however, is the early spring during late March and April. The amount of drumming begins to increase in early March and tapers off in early May. There is also a short period in midautumn when this activity increases for a few weeks. Apart from these periods drumming is only occasional and spasmodic.

The act is usually performed on a log, but in the absence of appropriate, prostrate logs, mossy mounds or boulders, stone walls, rail fences, or similar objects are sometimes used for the stage. The log, or logs, selected are usually of considerable diameter, averaging around twenty inches. They may vary greatly in length but usually are not less than ten feet, and are almost invariably long-fallen and moss-covered. Drumming always takes place at one spot. Since the same log is often used many years, this spot becomes well worn, even below the moss covering and the bark. The bird roosts at various places on the log most of the nights of the spring mating season and hence a well-used log will have many droppings piled on it. Considerable drumming-log roosting is also done through the fall and winter months, and the identity of a drumming log is most easily made by the presence of piles of droppings and the telltale worn spot.

Anyone who lives in grouse country can hardly be considered an experienced woodland naturalist if he has not witnessed a wild drumming grouse. It is one of those supreme thrills that makes life so surely worth living in a world full of sadness and strife. A careful stalker may approach a bird guided by the sound of the drumming if there are enough low-hanging evergreens or other cover to obscure the approach. However, the surest way is to locate a log in regular use, then sleep near it overnight. By building a screen of evergreen boughs in front of the blanket roll, about twenty or thirty feet from the log, the thrilling sight may be observed with comparative ease. Any movement must be made with the greatest of caution, for the slightest disturbance and the grouse will be gone in a flash.

Before a cold April dawn in the spring of 1931 I doubled my "frozen" feet under me in the sleeping bag with slow, soundless movement so as not to disturb the cock grouse sleeping on his drum-

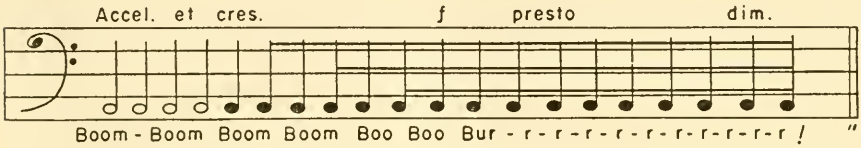
ming log only about fifteen feet away. I had hoped to photograph this bird and had rigged a little hemlock blind in which the camera was ready for action. This particular log was a very old, well-rotted, mossy granddad of a log, and had been used for drumming for many years, judging by the deeply worn drumming spot. The drumming spot was quite near one end of the log, where it hung suspended a few inches off the ground. And it so happened that at this particular moment the log broke off, right at the drumming spot, and the free end fell to the ground. Of course the cock left the place in a hurry. I figured that my chance of getting a photograph, or even of seeing the grouse again at that place, was remote, although at the moment I was not sure just what had happened.

Before completing this episode, I must note that there was a small mossy mound right next to the foot of my sleeping bag, and I went back to sleep. The next I knew I awoke suddenly just as dawn was breaking to hear the bird drumming so close it seemed to be almost on top of me. And truly, he almost was, for I could feel the wing beats against my feet at the side of the bag—he had selected the little mossy mound to drum on after having his regular log broken. To say that I thrilled to the tips of my hair is putting it mildly.

In drumming, the bird stands crosswise of the log, braces himself back on his tail, and brings the wings forward and upward with quick strokes like the beats of a well-trained crew (see Plate 2A). Slowly at first, then with increasing speed, the beats roll on until finally ending in a rapid whir. The quality of the drums may best be called a dull, hollow thumping. They possess a peculiar ventriloqual quality, often deceiving one as to the direction from which they come. They are also deceiving as to distance, drumming a quarter of a mile away sounding practically as loud as if only a hundred yards off.

The mechanics of the sound was long in dispute. Some held that the wings struck together behind the back, others that they came together in front; it was believed by still others that the wings struck the breast, or the log. It remained for Allen to prove by slow-motion movies that it actually results from the cupped wings striking the air. Mathews (1904) places the pitch of the sound at from A flat to B flat. Smythe (1925) says: " . . . the first tones are staccato and widely separated but the last are run together in a rapid roll . . ." (see musical expression on next page).

The drumming characteristic has been used in bygone days by hunters to lure the birds to their destruction. By beating on drums made of an inflated bladder, market hunters were able to shoot or net them. In more recent times numerous observers have noted that grouse are attracted by the sound of wood chopping.



Some male grouse apparently do not drum at all, nor do these birds establish drumming logs. Possibly there are one of two reasons for this apparently abnormal behavior. Most likely is the condition, demonstrated in captive birds, of having the need for drumming short-circuited by the ready presence of one or more female birds. The second condition might be an abnormal physiological deficiency. Many males use more than one log, but in these cases there is usually one primary log, and one or more secondary logs which are used more or less irregularly. Some birds use the same log year after year. On an average, there are about one and one-half active drumming logs per male grouse.

Location of Drumming Log. As has already been noted, the log selected for drumming must have certain characteristics of size and condition. The log is selected to a considerable extent on the basis of its location and surroundings. It is almost invariably inside the woods, not in the open nor on the very edge. It is also almost always very near to an edge of some type of opening, usually within two hundred feet. Very rarely is a log used that is deep in a woodland, far from a clearing. Preference seems to be for a young, second growth woodland, predominantly hardwood but with a fair scattering of conifers, especially young conifers. Mature woodlands, solid coniferous stands, open slashings, and brushland seem to be avoided.

The immediate location preferred is one well exposed to the sun on one side, preferably the side with a warm, morning sun. At the same time, one end on one side at least should have good escape shelter immediately at hand. This shelter is usually a clump of low hanging conifers, most often hemlock in the transition zone, spruce or balsam in the Canadian zone.

Nesting. When last we left our young hen grouse she had just received the male in coition. Following her first mating experience she made her way back to the sunny woods road in the near-by hardwoods. As she walked easily along, no doubt daydreaming of the wonderful new world unfolding to her, she would pick up dead leaves and toss them over her shoulder in careless abandon. She definitely was in a homemaking mood. The sunlight shining along the north side of the logging trail made it a delightful spot in the cool morning hours. There were several trees and old stumps close to the trail that offered protection for a home and she determined that she would build somewhere in this area. After looking over the various possibilities she chose an old yellow birch tree about twelve inches through. On the south side, next to the trail, a few sprigs of dead hemlock brush hung about a foot off the ground, the butt end braced on the ground near by. She would build her nest up against the trunk beneath this extra little sprig of camouflage, and so provide additional protection for her coming family.

Scratching in the leaves, twigs and humus she dug a little hollow about eight inches in diameter and this she lined with dead leaves. Simple as it was, it would serve as home for about five or six weeks to come (see Plate 3).

After completing her handiwork she went about the ordinary business of living—eating, sunning, resting, roosting—for several days. She never strayed far from her new headquarters, except for the occasion when she returned the few hundred yards to the edge of the slashing where the old cock grouse lived. As the days wore on it was apparent that a great change was taking place in her body. The region back of the legs became enlarged, and after about a week following nest making, she stayed close by the homesite, finally laying her first egg. After the egg was deposited she carefully covered it with dead leaves. Rarely did she stray from the near vicinity. Successive eggs were laid at intervals of about a day and a half. On one occasion, feeling in an adventurous mood, she harkened to the drum of another cock grouse, and set off to visit him about a quarter mile away near the opposite end of her own woods. This visit added new zest to her exciting new experiences. In a little over two weeks, eleven eggs were laid and the urge subsided. No longer did she have the desire to consort with the cock grouse, no longer did she want to add to the potential family she had already created. Now

she wanted to take care of her eggs, to mother them on to hatching. She was broody.

Incubation. Although the duty of setting on her clutch for twenty-three or twenty-four long days was bound to be somewhat of an ordeal, her devotion to the job was great enough to overcome any notion of giving up. As the days wore on, her determination to complete the incubation, regardless of any dangers that might arise, increased with each slowly passing hour.

She had hardly begun setting when it was apparent that she could not get all eleven eggs snugly close to her body for even warmth. So she plucked the feathers from a large part of her lower abdomen, using the feathers to make a softer lining for the nest, forming a large brood spot that enabled her to cover all the eggs evenly.

Early each morning she would leave the nest soon after dawn, being careful to cover the eggs with dead leaves, to get food and exercise. Habitually she went around behind the birch tree and off down the hill. Just as regularly she returned by way of a little draw on the opposite side of the woods trail. Being anxious not to allow the eggs to chill she would take only twenty or thirty minutes for her meal and toilet. And before settling on the eggs once more she would carefully turn each one over.

Late each afternoon the young hen again took time off from her duties to eat and relax. But apart from these two periods each day, her life was an unending and almost motionless vigil. Life continued as usual all around her. The ovenbird and the hermit thrush sang to their mates, who were also incubating nests of eggs among the dead leaves on the ground near by. In the trees above, the black-throated green warblers and the red-eyed vireos sang the whole day long. Squirrels and chipmunks scampered about, scolding at any other creature that came their way. Mice and shrews ran cautiously through the ground litter. Life was good. A feeling of freshness and new vitality was in the air, and it was manifest in the actions of all the woodland folk. When dusk fell, the activity of the day went too. But new creatures were abroad, many of whom she knew instinctively were not her friends. Now and then a waddling old skunk would amble by, seemingly not yet fully awake from his long winter sleep. And though he occupied himself in digging for grubs and small rodents in the humus of the forest floor, she would automati-

cally draw herself in rigidly if he happened to wander near to her abode. In the distance a horned owl hooted, and occasionally she would spy a fox sneaking stealthily along the lumber road. But she knew she was fairly safe if she remained motionless.

She had not seen another grouse since she last visited a drumming log, and in recent days the reassuring drumming of the cock birds had almost ceased. While feeling quite alone, she became more and more anxious for the fateful time when she could leave the woods road with her own precious little family. As the days became weeks, the dangers seemed to mount. She would often see sharp-shinned hawks darting through the trees, and soaring red-tails high in the sky renting the soft air with their screams. Then, what should come up over the hill along the road but a team of horses with a wagon. A man, queer creature she had never seen before, was on the wagon and a dog ran along beside. As they approached, her nervousness increased and she tightened her feathers against her body. Closer and closer they approached; the dog headed straight for the place where she lay. When it seemed certain that the dog would step on her the next instant, she rose from the nest with a terrific whir of wings and flurry of leaves. Luckily—or by design—the rush of wind behind her drew a flood of leaves which settled over the nest, obscuring the eggs from view. The dog was startled, and after turning to chase her a moment, wagged his tail in delight at the excitement and followed his master down the road.

The experience was terrifying to the grouse, but she was immensely relieved upon returning a half hour later to find her nest all safe. Life became routine again until suddenly, just a bit over three weeks from the time she started incubating, she felt the first little pecking within the eggs. This signal that hatching was only two days off made her all the more anxious, and her mother love for the little chicks that she could not yet see surged to new heights. But her troubles were not yet over for, just as the dawn of her twenty-third day of setting broke and she was about to go off to forage for a little food, she heard soft footsteps approaching. When it came into view it proved to be a fox. She had seen several foxes before and so she sat tight, as she always had, waiting for it to pass on. But as luck would have it, his course of travel came straight toward her as he wandered off the trail to look for mice, or a rabbit—or a grouse. At the last moment before the animal would surely grab her she de-

cided to make her escape. But realizing that other lives than her own were now at stake she had to be more resourceful than to merely flush quickly to her own safety. She must also draw the intruder away from her pipping eggs.

Jumping off the nest and behind the birch, she ran, lamelike and with wings dragging as though mortally wounded, all the while squealing as if in terrible pain. The fox lunged at her but was just too short, and she kept on with her broken-wing performance. Again and again he sprang upon her and each time she would just barely elude him until finally, having drawn him well away from the nest, she flew away to safety. She remained away for a quarter of an hour —a lifetime it seemed—and then returned home with the greatest of apprehension. But the eggs were there untouched, and they now began to show the chipping of the egg teeth of the chicks. She was lucky—lucky that the particular fox she encountered was not wise to the ways of hen grouse and the nests full of delicious food they sometimes leave behind them.

A Family Is Born. The next day dawned bright and warm. This was fortunate, for many early June days are rainy and rain is apt to be lethal to tender young grouselets. All night long the nest had been a beehive of activity. The new mother tolerantly and tenderly shifted her weight, first one way and then another, to make room for the hatching chicks. One after another, the ring around the large end of each egg was chipped complete and the downy, wet little creature within pushed the cap back to enable it to shove its way free of its prenatal tomb. There was a continual, pathetic sort of peeping—in fact there had been peeping for a couple of days if one were to place his ear close to the eggs to hear it—as the whole family extricated themselves from the shells. Some of the shells got pushed clear out of the nest to make room for the expansion. The mother hovered them carefully for several hours until about noon they had become well dried.

She raised herself clear of the nest for the first time since returning from the encounter with the fox, the sun shone in on her precious brood, and they first saw the light of day. Stepping just a few inches away, she clucked softly for them to follow. In this, their first language lesson, the chicks learned quickly for they were aided by a mysterious and unerring instinct to react to such sounds. With a

little necessary physical encouragement to a few, all were finally gathered about two feet out of their one and only home. As this was their first physical effort, they naturally tired easily; so the mother gathered them into a compact group beneath her sheltering body and hovered them for their first rest. Thus they left their home only a few short hours after birth, never to return. For such is the way of precocial birds.

The First Few Weeks Are the Hardest. Birds cannot count very well, and it's probably fortunate they can't. This grouse was no exception to the rule, for if she had been able to take stock of numbers, she might well have been concerned over the egg that still remained whole in the nest. For some reason, possibly because it had been out at the edge of the clutch for much of the time and was a bit retarded from too much chilling, this chick was about a day behind the others in its development. Another dawn and it would have emerged from its shell, possibly as healthy as the rest. But no, it was left to die; deliberately abandoned by a mother who was following blindly those inexorable laws of nature that only the fittest survive; and the species is what counts, not the individual. Thus, even before it embarked upon its journey into the world, this family had suffered its first casualty. This was only the beginning of unending trials and tribulations destined to reduce the number in the family again and again.

With a half hour's brooding, the hen again led her young hopefuls on, away from the homesite that held memories of two narrow escapes. They went off toward the edge of the little slashing, for there the insects would be especially plentiful and escape cover always close by. Progress was slow and the mother spent anxious and busy minutes keeping her charges from straying too far off, teaching them to obey instructions, and showing them how to catch insects. Every little while she would gather them together for brooding, but each time the space between broodings increased. By dusk they had reached the slashing, having covered the three hundred yards more or less in seven hours. Here they hovered together under their mother's protecting coat of warm feathers for their first night away from home, this time beside a tuft of grasses beneath a low hanging hemlock branch.

They were up and away with the dawn, searching industriously

for insects—almost any kind of crawling or flying insects that they could catch; scratching a little in the leaf litter on the ground, picking them off the lowgrowing vegetation, or jumping for them in the air. Eating insects was mainly a question of taking those kinds that were most available and easiest to catch—flies, ants, beetles and many other insects and related forms. Only a few species, such as some lightning bugs (*Lampyridae*) and lady bird beetles (*Coccinellidae*), are definitely avoided by some birds, apparently due to their offensive taste. While insects and other arthropods constitute almost the entire food of the chicks for a period after hatching, they soon learn to add a little fruit to their diet. A few strawberries and similar early season, soft-bodied fruits are eaten almost from the start.

After the morning meal was over the brood hovered for a short time before setting forth again. Straying chicks would call a plaintive "tsee-tsee-tsee-eee" in a rising pitch (Sawyer, 1923). More practice in discipline was then in order, particularly in responding to warning calls of danger, for all grouse soon have to learn ever to be on the alert for the many forms of sudden death that may strike at any time. They quickly learn to scatter and "freeze" among the dead leaves at the first warning signal.

It was not long before they had their first opportunity to test their skill in dead earnest. The alert mother spied a shadow darting through the trees in their direction. A quiet, stern "freeze" signal, a sort of low "pe-e-e-e-e-u-u-r-r-r" (Sawyer, 1923) was quickly given and the whole family squatted motionless instantly. It was too late. The female sharp-shin had spotted some movement and she plied her speed and dove earthward in what seemed to be a suicide plunge. As soon as the grouse mother realized that the attack was on she gave the violent scatter call, and herself flushed in a broken-wing act in an attempt to draw the accipiter from her young ones. But the hawk had concentrated its whole attention on the one chick whose movement it had first seen and the kill was made with little trouble. During the excitement the others had made good their escape and were perfectly concealed in the ground litter in a space about thirty feet across while the mother hung near by continuing her keep quiet instructions with mewing squeals and sharp "quit-quit" clucks. By this time the hawk had carried its prey to its habitual butchering log where it picked the little grouse before taking it to its young in their nest high in a near-by hemlock.

When the danger appeared to be past the grouse hen returned to their midst and gave the all-clear signal, a low "puk-puk-puk." Instantly, as if by magic, nine little fluffy brown chicks arose from their shelter and, peeping joyously, quickly gathered beside their mother. Off they went at a quickened pace, with no thought on the part of the parent to check to see if all were present. She had her family safe through the first skirmish and she was both thankful and anxious to put distance between them and the source of their trouble.

That day and the next they traveled across their home woodland to the edge along the fields that sloped down to the farm home in the valley below. Lots of shrubs and briars grew along this margin, and it provided both plenty of food, many tangles and small hemlock clumps for escape shelter. On the way over, during one of their foraging periods when the chicks had spread quite widely, one little fellow strayed beyond the mother's call. When it realized its predicament it cheeped wildly and pathetically, running first this way and then that, in an effort to locate the brood. That night it had no warm mother's breast to keep it warm, and nowhere near enough feathers of its own yet to do the job. So passed the third member of the original eleven. In but a few hours its tiny carcass disappeared into the ground as the scavenger beetles dug beneath to lower it to their advantage.

A week passed. The weather had been very kind, there having been only one light shower one afternoon. The chicks easily kept dry during that time beneath their mother's wings and breast. Several times predators had been sighted but attack had been avoided by freezing. The wing-flight feathers were developing rapidly and the chicks were enjoying a new half-running, half-flying type of exercise. By the middle of June, at twelve days of age, they could actually fly twenty or thirty feet if an occasion warranted real exertion.

Life Without Father. The wind began to whine through the tops of the near-by hemlocks. It was still several hours before dawn, and the brood were hovered under the edge of a briar and grape thicket along the woodland border. In the distance flashes of lightning were visible and the far-off rumble of thunder gave warning of the approach of a storm. It was not long in arriving. The wind whipped the trees savagely as the rain came down in sheets. The temperature had dropped to the vicinity of the lower fifties Fahrenheit. Such a turn

of the weather is very dangerous to young grouse during the early weeks of their lives. A single wet chilling, if not followed soon by a warm sunning, is apt to be fatal. In violent storms like this some chicks may be seriously soaked and chilled in spite of the hen's best efforts. Any abnormal exposure would lead to almost certain trouble. It was calamitous that upon such an occasion a water-soaked old skunk, caught away from his den by the storm, blundered through this particular thicket on his way home and scattered the grouse family. As quickly as possible the mother recalled her chicks and hovered them again, but the damage was done. Although the day came along bright and cheerful, three of the family failed to respond to the breakfast call. If they had been picked up by a man and taken to a game pathologist for autopsy, his report would probably read "cause of death unknown."

It was soon after the encounter with the storm that proved so disastrous that the family met another grouse, an old cock bird. This was the first of their kind other than their mother that the chicks had ever seen. The hen had not encountered another grouse since her last visit to a drumming log before starting incubation. The chicks stayed close to the mother's side, for they were not quite certain whether the newcomer was friend or foe. The cock bird, for his part, was completely nonchalant, paying scant attention. Soon the family were on their way, the male bird following a short distance behind for a few minutes, and then disappearing. He might have been their father (or one of their fathers) but if so he showed no paternal interest or sense of duty. While famed for his magnificent courtship, the male grouse is not a good parent. Among hundreds of grouse broods observed, only about one in fifteen had the benefit of a father's presence near by, and it is doubtful if many of these associations were anything but accidental. Further, it is probable that most of the relationships of male to the brood did not involve the actual father anyway. There is little inclination on the part of the male bird to associate with the brood at any time, but what solicitude does exist is stronger during the early weeks than during the last half of the summer. About one in ten broods up to six weeks of age are likely to be found with a male adult near by (within two hundred feet), whereas with older broods the ratio is only about five per cent.

Each day that the ground was dry considerable time was spent in

taking dust baths. Following their mother's example, each chick would wiggle and scratch a little hollow in the dry dust of an open spot or rotted wood of an old log, whichever was most convenient at the time (see Plate 2C). They would lie in their bath, first on the belly, then one side, then the other, all the while scratching and rubbing dust with the feathers. Among them all, they kicked up quite a smoke screen.

Dusting was a regular and necessary event. When handy they would use the same baths over again. It serves primarily to stimulate proper growth of the feathers, although it may help to get rid of external parasites too.

The little grouse grew rapidly. At three weeks they had become proficient flyers; at four weeks the feather coat was well enough developed to make hovering by the mother no longer necessary under average conditions. By six weeks the full juvenile plumage was attained, and the young grouse looked very much like miniature replicas of the adult. By this time the family was spending its nights roosting in trees, usually hemlocks or other evergreens. It had experienced many critical moments when natural enemies or the elements had threatened, but no additional casualties had resulted. Every one of the five remaining youngsters was now very proficient in making its escape from running or flying predators, and had grown hardy to the vicissitudes of the weather. But they still depended very much on the mother for leadership and warnings of danger.

Revolt in the Ranks. Almost as soon as the youngsters had left the nest, family squabbles began. The assertion of physical superiority, or at least equality, is a prime essential for successful survival in a grouse family or group. Often the affirmation of strength led to fights, but more often a chick would satisfy his ego by strutting to amuse or antagonize his brethren. Always the mother bird maintained control over these trivialities, though this control became more difficult as the chicks grew older. As the summer progressed to the dog days of late July and August, a surging of insubordination was noticeable on the part of the chicks. They were now half grown and were beginning to feel a need for freedom, and resented parental control. They would stray quite far apart in foraging for raspberries and the other summer fruits which now furnished a good proportion of their diet. They would fly off, chasing each other as their

rivalries became increasingly belligerent. In spite of the sometimes frantic orders from the mother, they would not heed her warning of impending dangers. So it was natural that the probability of additional mortality in the family would rise at this time.

One day a Cooper's hawk sat waiting on its perch in a dead chestnut tree as two chicks raced recklessly up the near-by draw. In a flash the hawk plummeted earthward as they approached and with a quick sideward surge grasped the second of the chicks. Thus the family was reduced to four youngsters—only thirty-six per cent of the number in the little nest at the base of the birch tree two months before.

The Family Grows Up with a Change of Clothes. The youngsters soon learned the dangers of independence and became more alert to observe dangers for themselves. Mother was more cautious than ever now because she was losing feathers and flight was not as powerful or accurate as usual. In the course of a few weeks she completed her moult and had a full new set of feathers. No longer were her tail and wing feathers ragged at the tips; every one was as fresh as a new leaf in the spring. Before she was through with her moult, the chicks began losing their juvenile plumage. By mid-September their first adult plumage was almost complete and they could hardly be distinguished from the mother. Two of them had very rufous tails, one was mottled rufous and gray like the mother, the fourth proved to be a gray-phase bird. The family allegiance became very loose, and the mother no longer concerned herself with her children's safety. It was every one for himself now, and they were found by themselves as often as they were together.

Crazy Flight and the Fall Shuffle. As the calendar turned to October, there was a new tang in the air. Many new fruits were ripening so that the grouse were to be found along woodland edges, in brush lots and even out along hedge-rows where the hawthorns, dogwoods, viburnums and other preferred fall foods were to be found. The youngsters attained their sexual maturity with an accompanying resurgence of quarreling, more vicious than ever before. Now when one of the brood was chased by another the victim was not likely to return. There was a definite antagonism on the part of most of the birds for all other grouse. It was not exactly an exhibition of territorial behavior as in the spring, but operated simi-

larly and arose from similar physiological causes. This dispersal of the family groups is called the fall shuffle.

When a bird is driven from its family group it seeks its *lebensraum* (living room) elsewhere. However, it may soon encounter another grouse or brood of grouse, and is then more than ever likely to be driven out again. With each failure to find a fall territory it can defend, the bird becomes more nervous, and more desperate as a result of its growing inferiority complex. It is alone in a strange and unfriendly world for the first time. Although it was brought up in an area of only forty or fifty acres and had never traveled over a half mile before, it may now find itself many miles from its summer home. Under such circumstances, a grouse often will fly far out of its normal coverts and many times come to a sudden end by flying into obstacles such as buildings.[1] This phenomenon has been termed crazy flight. Various explanations have been given for these actions, such as a nervousness brought on by the leaves falling, or irritation caused by internal parasites. While the falling of the leaves may well add to the nervousness of the birds, the crazy flight is merely an aberration of the normal fall shuffle—a social phenomenon that likely occurs with most sedentary species of birds and is well known in the bobwhite quail.

A-Hunting We Must Go. If we may assume that the young grouse in our biography did not reside on a survey area of some ruffed grouse study, it is quite probable that they have never encountered that most formidable of adversaries, man, up to this time—mid-October. Then comes a day, according to the calendar and the laws of the state, when the status of the grouse changes from a protected bird to fair game: the hunters, who have been chafing in their anxiety for weeks, swarm over fields and woods as the hand of the clock passes the fateful point.

Since our grouse family has now dispersed into four different coverts, with only two of them remaining together, we find it convenient to continue the life story through the experiences of only

[1] These escapades often result in human interest stories; for example, the March 27, 1942, issue of *The Boston Herald* headlined: "Shipyard Worker Keeps Bird Flying," then recounted: "The supper which William Catterall, Fall River shipyard worker, was enjoying . . . last night, was interrupted when a grouse entered the kitchen amid a shower of broken glass. Catterall, unperturbed, patched the bird's cuts . . . and released it. . . ."

a part of them. Let us take the two that have remained together —the mother and one young one.

Not far down the hill from their home woodland toward the farm in the valley below, was an old apple orchard. Between it and the woods ran an overgrown fence-row, with gray dogwood, wild apple, thornapple, black cherry and wild grape growing in tangled profusion. This was just the place for the grouse to be feeding this crisp, sunny October morning—either along the woods edge, in the orchard, or in the hedge-row between. An experienced grouse hunter would recognize this almost as well as a grouse. So it was not surprising when two hunters, well bedecked in their red plaid hunting garments, came up the hill from the farm, straight toward the orchard. Three beats across the orchard convinced them that no grouse were there. One of the hunters was particularly slow and deliberate, examining carefully each likely bit of cover for fresh sign. They turned up the hill again, one on each side of the hedge-row, working carefully towards the woods.

Just about fifty feet along the fence-row was a clump of thornapple loaded with fruit, and it was here that the two grouse had been feeding. They saw the two tall creatures coming and, true to their instincts and experience, crouched motionless on the ground until they should go away. But these were not ordinary adversaries. Just as they were about to pass the birds, one of the men gave a kick at the low-hanging thorn branches. With a terrific whir of wings, the startled birds burst into the air. Swinging out of the obstructing hedge-row on the side opposite the hunter who had flushed them, they made a splendid shot for his companion. The gun blazed twice, and one of the birds crumpled to the ground. The other, having experienced one hunting season before, had cut sharply back to the top of the hedge and on into the woods just at the critical moment, causing the shot to go wild. She flew far out of sight into the woods, coming to rest high in a clump of protecting hemlocks. From past experience, this was the safest place to avoid a repetition of the death-dealing flight of lead.

With each escape from the hunters' bullets the grouse becomes more wary and more able to make a successful getaway. This ability to dodge shot and baffle hunters has been developed in a relatively short time. Wilderness grouse even today sometimes exhibit the fool-hen characteristics that most grouse possessed when the white

men first introduced them to guns. But in coverts frequented by man, the grouse is well able to hold its own, given reasonable laws, good cover, and not too great a hunting pressure. Its ability to change direction in flight, to put trees between itself and the hunter, to outwit the hunter by flushing behind him are some of the characteristics that endear the grouse to millions of sportsmen and earn it the title "king of the game birds."

The four remaining grouse of our original brood, each in its own covert, met and evaded many hunters during the remainder of the open season. As the hunters' guns became a memory the season rapidly changed, and with it the coverts changed too. The leaves fell from all but the evergreens, making the hardwood areas quite bare of cover. The berries on most of the fruit-bearing trees and bushes were dropping rapidly, and although much fruit remained available, the birds' diet included more and more of tender buds; insects were practically gone now.

Winter Comes. As the wind swung around to the northwest and the skies assumed a leaden color, the temperature dropped below freezing and snow began to fill the air. There had been a few snow flurries earlier in the fall but this time it looked like more serious business. Winter had come. To many grouse this meant a change in their habitual coverts, a move to the shelter of the coniferous woodland. The hen bird returned to the hemlock ravine where she had spent the previous winter. Several other grouse had settled there too, and they banded together much of the time to form a covey. Gone was the antagonism of the early fall; no longer did each bird look upon the others as competitors. They settled down for the winter in an area particularly adapted for winter use; and since such areas were not over plentiful or too large, it was somewhat of a necessity for them to get along together if many were to survive.

Snow-Roosting. The birds roosted mainly in the thick hemlocks but sometimes, when the nights were bitter cold and the wind high, they would roost in the deep snow. If it were snowing at the time, a bird might simply squat deeply into the snow and then allow the weather to cover it up. On other occasions they would dive into a deep snowbank from the air. If the weather stayed bad, they might remain in a snow roost for several days. Occasionally it is reported that grouse are trapped in snow roosts by a quick freezing

crust but this I have never observed. Knowing the ability of the bird to go without food for days on end, it is doubtful if this is ever a very serious matter, although it is possible that it may actually happen.

Snow roosts do make the birds quite vulnerable to attack, especially by foxes. There is always a little breather hole from the birds' heads to the outside of the snow that is often easy to spot. Grouse tracks that end in a slight mound of snow are a sure indication of the birds' exact position. Even a man, if he is skillful, can catch the birds by hand under these conditions. There is good evidence that some foxes learn to catch on to these signs too.

The proportion of winter roosting beneath the snow varies in different years and also with the period of the winter. Winters with little snow will prevent the use of snow roosts to a considerable extent, but other than this limitation of opportunity the degree of snow-roosting depends upon the prevalence of abnormally severe weather, low temperatures and high winds. The first severe storms of the season always induce more snow-roosting than later ones. This appears to be due to the relatively greater change from late fall weather, whereas in the later storms the change in conditions is not as marked and the birds have then become accustomed to the hibernal extremes.

Gregariousness. The ruffed grouse is not a gregarious bird in the full sense of the word: living in flocks. However, it does exhibit varying degrees of cohabitation with those of its kind. It has already been noted that in the early spring there is a shuffle from the winter groupings to the male and female breeding territories. Thus, in the spring there is an almost complete loss of the gregarious tendency. We have noted two females nesting concurrently within fifty feet of each other on occasion. Two females occasionally lay in the same nest although, so far as we have been able to ascertain, only one bird does the incubating. Aside from these definitely abnormal associations, we may say that the species is solitary throughout the spring period.

During the summer two males are quite often found together, or a male and female that has no brood. It has already been noted that a male is occasionally found associating with a brood, although this is hardly an example of flocking. Several cases were observed of

two grouse broods consociating but most of these were not regular associations. In one case two broods stayed together throughout the summer. This seems to have been a true example of brood communism.

It is interesting to recall the clear distinctness of the brood identities in these associations. Upon one occasion of making a brood count, the observers were confused both by a poor count and an apparent extra female. One of the observers climbed a tree to await the regathering of the family (the chicks could not fly yet) while the other observers proceeded on out of sight. Soon one female reappeared and, finding the danger past, called her brood from the surrounding vegetation. Out they trooped in perfect order, assembled their skirmish line, and off they went. A few moments later the second hen returned and she too called out her brood. From the same terrain as the first appeared another whole family with just as unerring discipline, and they trooped off in another direction. It was clear that, even though only a week old, these chicks knew the call of their own mother as compared to other grouse and responded only to her. On some occasions, usually with birds just after hatching, there does occur some confusion in brood reassembling.

The groups of grouse that are occasionally found together during the fall are usually the remnants of a family and hence are not gregarious. But the regrouping of birds in the late fall and winter is the one strong period of communal activity they have. The usual groups run from three to six birds, the commonest numbers being in order from the lowest. Groups of from seven up to twelve or fourteen or even more are occasionally encountered, but not commonly. The period of greatest group activity is late fall to February. In late February and March the groups begin to break up to seek out their spring territories.

The Annual Wheel of Fortune Is Completed. When last we left the grouse family, one of the young ones had fallen before a hunter's gun. There were left only four, the mother and three offspring, each in a different area of coverts. If we may add an adult male to make the full complement of our original reproductive unit, we have now carried five of the original thirteen into the winter. We have shown some of the problems faced by them as a result of the change of seasons. Now we may see what happens to these five birds as the

winter progresses and the story returns to the time of beginning, early spring.

With each change of season the cover types used have shifted, and likewise the food habits are altered. As fall gave way to winter, the diet gradually changed from a predominance of fruits to a predominance of buds. Throughout the winter some fruit is eaten, an occasional insect and a little green leaf material. But the fare is largely buds, mostly those of trees found in association with the conifers or near by—birches, hophornbeam, soft maple, popple, cherry, and others. Traveling through the woods in winter one can readily understand why the grouse resort to budding, for food in other forms is mighty scarce indeed. Yet they are very skillful in locating available fruit. Even with a deep blanket of snow on the ground, grouse will find a few cherries, dogwood fruits, and similar fare when ordinary man is entirely unable to find them.

Food is not usually an important factor in limiting or reducing winter grouse numbers in coverts that are otherwise satisfactory. Shelter is very often a delimiting factor, according to the extent, type, and distribution of coniferous types and dense slashings. The winter season does bring on problems of survival in relation to the elements and to predators. While it is rare for ruffed grouse to be killed directly by freezing or exposure, the rigors of the season do increase their vulnerability to predation. Snow-roosting, the lack of protecting leaves on deciduous plants, telltale tracks in the snow, the bare snow ground cover, all contribute to this problem. Toward the end of the winter the arrival of the courtship activities greatly increases the danger of predation.

So it was that in February one of our five grouse was picked out of a snow roost by a fox and early in March another was taken from its tree perch in the dead of night by a great horned owl. The three remaining birds, one the old male, the other two a young male and a young female, left the shelter of their hemlock winter homes to locate new homes for the spring. The old male reestablished his territory of the previous year and once more boomed his defiance of the rest of the grouse world from his favorite drumming log. The young female set forth to find a suitable nesting territory from which she could seek out desirable males for mating. Possibly she would return to the part of the woodland where she was born, now left vacant by her mother's death.

Her brother (or half brother) also looked for an opportune drumming territory. Several times he was challenged by other males whose established territory he invaded and each time moved on until he finally located a desirable log that no other grouse immediately claimed. This he successfully defended against later comers and displayed his superiority with all the vigor and arrogance of his father before him. One dawn while he drummed his challenge to the world and paraded his wares on his mossy stage, a little thin, mottled brown and white, hunchbacked animal crept slowly toward him through the near-by hemlocks. The weasel was unappreciative of the fine points of the grouse's art; to it this creature was just another opportunity for a full belly. With a final spring from behind the log the weasel sank its teeth into the grouse's neck. A hectic struggle among flying feathers lasted but a few minutes.

As we complete the wheel of fortune of our grouse for the year, we note that of thirteen grouse early in June—a father, mother, and eleven youngsters—only two remain, a male and a female. Thus, although eighty-five per cent of the birds have succumbed, we have as many as we started with. The species carries on as plentiful as before. What more can we ask?

In recounting the biography of a grouse family around the seasons, I have attempted to cover the life history and habits of the species. Inevitably there would be some items that would not fit easily into this story. These are given below in several subheadings.

Territory. The term territory has been used several times, and in two different senses. In connection with the breeding season the male bird establishes an area centering around his favorite drumming log, from which he will drive out all other grouse. Thus he considers this his own backyard and, except for the reception of females when he is in the mating cycle, will permit no competition therein from his own species. Nice (1941) calls this the "mating station only" type of territory, one of six types recognized. The size of this territory is difficult to ascertain and undoubtedly varies greatly, depending upon the population density and the characteristics of the habitat. The maximum average size may be derived by dividing the available covert area by the number of male territories. This is no doubt too large for a true average, since much of the area, and notably the nesting localities, are often not frequented

by the male birds. Observations show these maximum averages in various coverts to run from about ten to over a hundred acres. Certainly no male bird ever tried to defend a hundred-acre territory, but what the limits of a bird's ambition would be when given full freedom to take as much territory as he wished is a matter of conjecture. Also, some males have gotten along with considerably less than ten acres. It is my judgment that when the spacing of male territories is such that less than twenty acres are available to each bird, the pressure between them becomes continuously active.

The second concept of territory is that area that an individual, or a brood, or a group, requires and uses in its year-round or seasonal activity. There is less connotation of conflict or of exclusive rights in this type of territory, although at times conflict does occur. The fall shuffle is the main occasion for this type of territorial activity. Evidence is that an average of four acres per bird is the minimum requirement. It will be noted that this figure corresponds to maximum carrying capacity (saturation point) and roughly corresponds to the minimum average figure for male spring territories (ten acres —or five per grouse if sexes were equally divided). This type of territory establishment does not mean a separation of area for each bird or group; rather it is the area utilized by them as a unit and only during the fall shuffle may it result in the exclusion of other birds from overlapping. An average of eight acres per bird for a group of six would indicate a forty-eight-acre territory for that season.

Territory on the part of the brood is simply the area they cover during the summer. No interbrood conflict is involved and territories often overlap—even occasionally are practically concurrent. The area required to raise a brood also varies—generally twenty to forty acres is utilized. Cases have been observed of broods living the entire summer in an area of about ten acres while other cases have involved in excess of a hundred acres. The latter cases are usually the result of abnormal movements resulting from disturbance.

Daily and Seasonal Range. The spring range of the male corresponds to his territory, while the sum of the seasonal ranges of all grouse add up to their yearly territory. However, seasonal ranges vary considerably. The spring range of the female, during egg laying and incubation is very restricted, often as little as three or four

acres, with travels of only one or two hundred yards, except for occasional longer trips to a drumming log. During the summer the range of the female covers the same territory as the brood, often extending half a mile or more, while males and broodless females are more restricted, often remaining within ten acres or less and traveling only two or three hundred yards in distance.

During the fall the greatest distances are traveled. Extremes are almost always birds of the year seeking new territories. Distances exceeding two miles are not uncommon, and fairly authentic records have been made of birds traveling up to twenty-two miles. Territories are large and daily travels are greater than at any other time. When winter arrives the territory is more restricted. Except for occasional warm, sunny days when they may wander afield in search of berries, they remain close to the winter shelter areas. Two or three hundred yards would be a normal range on an active day and it would not greatly exceed this for the season.

Daily range also varies widely, with the season, the weather, and the type of activity. Normally, the day's travels consume only one to three hundred yards, but if flushed and reflushed the bird may extend to a half mile or more. Occasionally a single flight will carry them a quarter of a mile. Females nesting far from a drumming male travel up to half a mile on their visits for mating.

Year around range normally adds up to about three-quarters of a mile, outside measurements.

Characteristics of Flight. Having short, rounded wings and powerful muscles for rapid wing movement, the grouse is a powerful and accurate flyer. Its ability to dodge obstacles and change its course at full speed are famed. However, its accuracy in flight is sometimes exceeded by its recklessness. A grouse flushed at night will often fly off as quickly as if it were daytime, unmindful of the branches hit along the way. Occasionally one hits a tree, fence or other obstacle and closes its career with a broken neck.

Probably the most marked characteristic of the grouse's flight in the mind of the average observer is the whirring, sometimes terrifying noise that accompanies it. Springing from the ground near by, it puts all its power into a quick getaway with the resulting loud whir. Even the most experienced woodsman will on occasion be so taken unawares by a grouse as to be scared nearly out of his wits.

Few people have the opportunity of observing an unflushed grouse taking flight at its leisure. When it takes the time to do so it can fly as silently as an owl.

Duration of flight varies but never very greatly. Assuming that it may make its own choice of satisfactory cover to alight in, the average flight from flushing is between three hundred and six hundred feet. Flights made for its own purposes usually are shorter. If the same bird is flushed about three or four times in quick succession it can be picked up by hand, exhausted. About half a mile is the limit of power flight (not counting long coasting) without recuperation of the muscles.

Speed of flight varies with the cover. In woodland with an average number of trees to dodge, it will be from thirty to forty-five miles per hour according to the strength of the bird, its anxiety to escape, and the amount of dodging required. In the open it can fly considerably faster. I timed one bird across an open field, using a stop watch, at fifty-one miles per hour, measured from the time it left the ground on one side of the field to the time it entered the woods on the other.

Relation of Nest Location to Drumming Logs. The positional relation of a female nesting site to the nearest active drumming log is normally negative. If the female has a definite thought in selecting her nest site with regard to the location of the male it is to get the nest as far away from him as practical. I have observed one drumming log fifteen feet from a nest but I was unable to check whether or not the log was used after the nest was made. Allen (1934) says that the distance between log and nest is sometimes as low as fifty feet and sometimes as far as half to three-quarters of a mile. The closest I have observed both nest and log in use at once was seventy-five feet. In this case these two birds habitually roosted in a hemlock tree over the drumming log prior to the incubation period. This is not usual, however.

In numerous cases nests have been observed half a mile from the nearest known drumming log in areas where we believed we knew the location of all active logs. The average distance is approximately one-quarter mile.

Nest Desertion and Renesting. Desertion of the nest is rare in the ruffed grouse. The few cases observed that appeared to be deser-

tion (as contrasted to the cases where the hen is killed away from the nest) have all been in the early stages of incubation or before egg-laying was completed. It is rarely possible conclusively to prove willful desertion since it is usually conceivable that the hen may have been killed and her remains not located. It is true, however, that the will to stay with a nest is weakest at the beginning and strengthens rapidly. It never is absolutely complete. If the setting bird is disturbed enough she may desert at any time. In our experience in trapping and marking setting females about a week before hatching time about one bird in twenty would not return to the nest after release.

Renesting is the building of a new nest and laying of a second clutch of eggs after the first nest has been destroyed. If the nest is broken up before two weeks of incubation the probability of renesting is fairly good. If the nest is broken up after two weeks of incubation, and most destroyed nests are, there is practically no possibility of a second nest. This is due to the loss of the urge to breed so late, by both sexes. Explained in terms of the sex rhythm, the probability of both hen and cock reaching the mating stage of the sexual cycle together after about the third week of May is almost none. Second nests that are made following early season nest losses are always in a new location, have fewer eggs than first nests and a higher proportion of infertility. In most cases the later the second nesting, the smaller will be the clutch, and the higher the number of infertile eggs.

Dust Bathing. Dust bathing by the brood has already been discussed. This practice is just as necessary for the adults as it is for the chicks, for it seems to be a requisite for proper maintenance of the feather coat as well as for normal feather growth. Grouse grown or held in captivity without benefit of dusting facilities usually develop a ragged coat. Dusting is done mostly from spring to fall with the greatest activity in the summer. Little dusting is done in the winter for lack of opportunity, but if the ground allows them to do so they will dust all year round. The increase in dust bathing in the summer lends weight to the supplementary theory of need for elimination of ectoparasites, although whether this is a primary reason for dusting is doubtful. The same bath is used repeatedly although one bird may have several in different places.

Relations of Grouse to Other Animals. Except for those animals that are recognized as enemies, grouse pay little attention to their woodland cousins. Other birds, as well as the small rodents and insectivores are taken for granted most of the time. Occasionally if a squirrel or chipmunk comes too close to a brood of young chicks the mother will drive off the intruder with a whirlwind attack. Sometimes jays will scold at grouse, apparently for their own amusement. Ring-necked pheasants will occasionally parasitize a grouse nest (see Plate 5C).

Grouse select their nest sites without regard for nests of other species. They occasionally will flaunt danger and locate the nest in the vicinity of an enemy. We watched one hen bring off a clutch successfully within fifty feet of an active red fox den. The fox pups had played within ten feet of the nest as evidenced by the "toys" (uneaten animal remains such as a bone or a piece of fur) left there. Another bird nested successfully almost beneath a sharp-shinned hawk's nest. Generally, however, they pay healthy respect to those creatures that they instinctively know to be dangerous.

Adaptability to Changing Environment. That the grouse is to be found within a few miles of New York City and is scattered in fair abundance throughout most of the highly populated northeastern states is a tribute to its ability to adapt itself to changing conditions. There is little question but that certain environmental conditions combine to make optimum survival of the species. But there is hardly a single one, or group, of these conditions that the bird cannot circumvent to maintain itself in reasonable numbers. In coverts throughout its range, it is constantly facing changes: lumbering, forest fires, grazing, changes in populations of predators and buffer species, in unending variety and combination. Grouse populations may go down as a result of changes in environment, in some extremes they are even extirpated, but as time wears on the species adapts itself and continues with surprising versatility.

Adaptability to Artificial Propagation. The story of man's attempts to raise ruffed grouse in captivity is even older than the profession of game breeding itself in America. As early as 1750 Bartram (In *Phil. Trans. Roy. Soc. London, 1754*) wrote a friend in England to the effect that the ruffed grouse could not be tamed or raised under hens. For over 150 years every other attempt met with the same

quick failure. The first faint hope of ultimate success came in 1903 when Professor Hodge of Massachusetts's Clark University succeeded in maturing several grouse from wild eggs. Two years later he passed another milestone with hatching of the first grouse from captivity-raised parents. From that time until 1916 Merrill and Torrey successively carried on the grouse raising experiments for the state of Massachusetts that Hodge had begun as a hobby. They proved conclusively the futility of trying to use wild-caught breeding stock; they succeeded in raising the first second-generation grouse, but finally became discouraged and released the seventeen birds remaining in the spring of 1916.

In 1912 the American Game Protective Association became interested in the problem and engaged Torrey to do their experiments. After he moved to the Massachusetts state game farm in 1914, the association encouraged other experiments. These, however, added little to the knowledge of the subject. In 1919 they persuaded Allen (1929) of Cornell to try his hand at the problem. Thus began the era of scientific fact finding in game breeding. In twelve years of alternating hope and despair, Allen proved that grouse could be raised in captivity with some success in small numbers. It was he who took the birds off the ground, placing them in wire-bottomed pens, thus partially solving the disease problem.[1] Allen uncovered the primary essentials of a breeding technique with the captive hens and cocks, so essential in obtaining a high fertility ratio and in preventing excessive mortality. And in many other aspects of grouse propagation, Allen developed the first satisfactory techniques.

In 1931, Bump took up the problem in connection with the New York Grouse Investigation and for several years Allen and Bump worked cooperatively, with Allen pursuing further definite research problems and Bump attempting to develop methods for practical large-scale propagation. In the ten years of work with grouse propagation, Bump raised nearly 2,000 grouse, including birds of the tenth generation. However, in spite of continually improving methods and a growing knowledge of the requirements of the species, grouse propagation is still not economical, dependable, or practical for restocking purposes.

The vital problems that still must be solved before the raising of

[1] Other breeders, with other species, developed the wire floor technique independently at about the same time.

grouse becomes a routine success are: increase in number of eggs laid by breeders (10.5 to 16.9 average per hen);[1] reduction of infertility in eggs (27.8 to 61.9 per cent a year);[1] increase in hatchability of fertile eggs (58.3 to 87.5 per cent);[1] increase in survival of hatched chicks (16.2 to 37.7 per cent).[1] In the latter case, the high mortality occurs mainly during the first two weeks after hatching.

There is little question that these problems will be solved in due time, but it will likely take many more years. The difficulties in producing grouse in confinement are to a considerable extent due to the relative unadaptability of the species to artificial propagation. The exacting conditions of the oestrus cycle, the vicious nature of the bird when not in the proper physiological condition for mating, its susceptibility to diseases and parasites of many kinds, and the natural fitness of the digestive system for insects almost exclusively in the early weeks of life, all contribute to make the grouse a difficult species to rear. On the other hand, the bird is very tractable in captivity, even more tame than the pheasant or bobwhite. It is potentially able to lay many eggs; one female examined during the egg-laying period proved to have 177 eggs visible to the naked eye, from pinhead size to one ready for laying.

In spite of its tameness in captivity, man-reared grouse readily revert to natural wildness when released in good coverts. The majority of game farm grouse restocked in New York became normally wild within a week after release. Some individuals do not lose their affinity for man so readily, however. I recall one bird in particular that ran up to greet a man as if he were a long lost brother, this in a woodland fairly remote from human habitation and about a month after the bird had been released.

Farm-reared birds appear to have little trouble in shifting from captivity food over to their natural diet but do experience considerable difficulty in avoiding predator attack. Probably this is as much due to unfamiliarity with the habitat as with a lack of wariness or ability.

[1] These figures are taken from *N. Y. S. Cons. Dept. Ann. Reports* for the five-year period prior to 1941.

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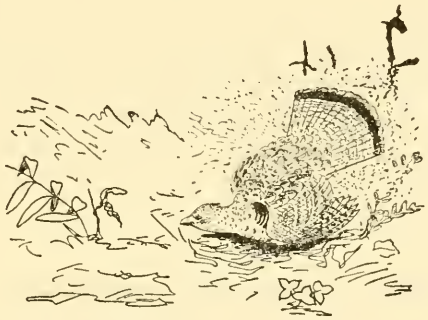


4

Shelter

TYPES OF GROUSE RANGE

Grouse range, in its broad sense, is the geographic area that the species inhabits. The types of grouse range, as used here, are the major subdivisions of the species range—divisions having common physiographic, climatic, ecologic, and temporal factors that affect grouse populations in an extensive way. Grouse range is a product of climate, soil, and time, the same as plant growth regions (Van-Dersal, 1938). On this basis, the grouse range in the northeastern states may logically be divided into three types—the northern New York-New England, northern Appalachian, and middle Appalachian. All three areas are humid and microthermal (having mean annual temperature between 14° and 0° centigrade). They differ primarily in the dominant plant associations, largely as regards woody plants, and character of land use as affecting the distribution of these associations.

Northern New York-New England Grouse Range. This, the most northern of the grouse range types in the eastern states, is naturally the coldest. It has the greatest amount of extensive forest range and is thus most nearly a wilderness habitat. Its topography varies from rugged mountains to level, wooded plateaus, all generally well watered. The winters are very severe, with low temperatures and heavy snows. The area was almost entirely glaciated during the last ice age, only the tops of the highest mountain peaks escaped the ice sheet. Most of this range is relatively uninhabited by man, although practically all the forest has been lumbered at least once. The sparsity of the human population has enabled the grouse in many of these coverts to remain today the fool-hen type of bird it formerly was everywhere.

The extensive areas of continuous forest in this northern habitat do not produce as high densities of grouse on an average as do the more southern ranges. The lack of cover type changes ("edges") well distributed over the range is without doubt one of the major factors that keeps down the grouse carrying capacity. The severe climate and the vegetative characteristics contribute importantly too.

The gross vegetative characteristics of a grouse range are closely allied with forest types and may best be briefly described by the tree species associations found therein. The most indicative forest types in this northern forest range are the spruce-fir group: red spruce-sugar maple-beech (17);[1] red spruce (18); red spruce-balsam fir (19); paper birch-red spruce-balsam fir (20); white spruce-balsam fir-paper birch (21); balsam fir (22); black spruce (23). The last is a wet soil type, the others are found on well-drained soils. The second very important group, though not as indicative of the range as the first, are the northern hardwoods types, the most prevalent of which are: sugar maple (14); yellow birch (15); yellow birch-red spruce (16); sugar maple-beech-yellow birch (12). Other common types are: aspen (4); paper birch (6); tamarack (25); and northern white cedar (24). Associated with these key species are many more tree species, many shrubs and herbs. Those of most importance to grouse are given in the cover type descriptions later in this chapter.

The prevalence of the above forest types in the northern range varies from area to area. Of great significance has been the changes in extent of types brought about by lumbering—mainly a change from a predominance of coniferous to hardwood types. This often resulted in the familiar pattern of hardwood ridges and coniferous bottoms.

The northern range, except that part extending into Canada, consists of the Adirondack region of New York, the Green Mountain range in Vermont, the White Mountains in New Hampshire, and all Maine but the most southern portion.

Northern Appalachian Grouse Range. This middle range extends through all New York and New England not covered by the northern

[1] These are the official Forest Cover Type numbers (Forest Cover Types of the United States; SAF Committee on Forest Types, *Journal of Forestry*, April, 1932). This reference gives associated tree species and variants.

range, except the coastal plain of Rhode Island and Connecticut, the majority of Pennsylvania and northern New Jersey, and a few localities in West Virginia and western Maryland at higher altitudes. It is fairly temperate in climate and has rather severe winters, with a dependable winter snow cover. Of the three ranges it is the most densely inhabited by man and, with some exceptions, the woodland is well broken up with farmland. Much of it was covered by glaciers during the last ice age. The best of the coverts in this range probably produce somewhat higher grouse densities than either the more northern or southern ranges. This is a result of good interspersion and desirable cover types and moderate climate.

The major forest types found in the northern Appalachian range include: hemlock (11); sugar maple-beech-yellow birch (12); a mixture of (11) and (12), which is very common; white pine (9); white pine-red oak-white ash (8); aspen (4); pin cherry (5); gray birch-red maple (7), and a mixture of (9) and (12).

To a considerable extent, this range is found on the more rugged lands, the poorly drained soils, or unproductive agricultural soils, which have been allowed to remain in woodland or to revert to woodland because of their impracticability for farming. In some areas, as in parts of northern Pennsylvania, and the Catskills of southeastern New York, this condition is so extensive as to allow almost continuous grouse coverts over many miles, resembling in this respect the more northern range.

Over much of this range, the change in forest composition as a result of cuttings for lumber and other wood products has followed a trend similar to that in the North—an extension of hardwood types at the expense of the hemlock and white pine. Other changes, as the growing predominance of beech in many woodlands, are also important as affecting the ruffed grouse.

Middle Appalachian Grouse Range. The southern range type of the northeastern states' grouse range extends southward from southern Pennsylvania and mid-New Jersey to include most of West Virginia, western Maryland and Virginia. There are a few small areas of the northern Appalachian type at higher altitudes in this zone and a few areas of the southern type in central Pennsylvania, Long Island, and southern New England.

For the most part this range type does not have a dependable

winter snow blanket, and consequently has a moderate climate compared with the more northern ranges. It is fairly densely inhabited by man and quite broken up with farm land, although less so than the northern Appalachian range type. There are some areas of rather extensive forest, as in western Virginia and eastern West Virginia. It was mostly untouched by the last glaciers. Its better grouse coverts are highly productive but, other factors being equal, probably are not quite as densely populated with grouse as are the middle range. The carrying capacity is generally somewhat higher than that of the most northern range.

The more important forest types included in the southern range are: southern red oak-scarlet oak (34); bear oak (35); chestnut oak (36); pitch pine (37); shortleaf pine (38); shortleaf pine-southern red oak-scarlet oak (40); shortleaf pine-Virginia pine (42); Virginia pine-southern red oak (43); Virginia pine (44); eastern red cedar (46); black locust (47); white oak-black oak-red oak (49); red oak-basswood-white ash (51); red oak (52); yellow poplar-white oak-red oak (55). It is clear that the dominant group in this part of the range are the oaks. These types, by themselves, are not very productive of grouse.[1] The conifers are primarily the hard pines. In middle age to maturity the forest is predominantly hardwood, as these pines are all short-lived, pioneer species.

The grouse range in the southern part of the Northeast, as with the middle area, is found mainly on the areas not suited to farming. To a greater degree than in New York and Pennsylvania, the ruffed grouse is found in the mountainous country which is often continuous forest except for the valleys. Forest fires and livestock grazing have been more prevalent in this region than farther north. Another commonly detrimental factor to grouse here, along with other game species, has been the prevalence of continuous hillbilly hunting.

COVER TYPES—CHARACTERISTICS AND COMPOSITION

There is abundant evidence that grouse react to differences between certain types of plant associations and between some age classes of a plant association. These constitute the cover types of

[1] T. E. Clark of Virginia told the author that on the George Washington National Forest ninety per cent of the grouse are on ten per cent of the range, almost none in the extensive oak types.

grouse range, from the point of view of the grouse, insofar as we can interpret their needs as expressed by their cover choices. The types most prominent in the northeastern range may be organized as follows:

Open land—predominantly herbaceous plants.
Overgrown fields—predominantly shrubs and saplings, succeeding from abandoned open fields.
Slashings—clearcut woodland, prior to reaching the pole stage of regeneration.
Hardwood woodlands—woods composed predominantly of hardwood species.
Mixed woodland—woods composed of a balance of hardwood and conifer species.
Coniferous woodland—woods composed predominantly of coniferous species.

Many subdivisions of these major types have some importance to the grouse. These types with the more important subtypes may be described as follows:

Open land: The great variety of open-field plant associations that are so vital to such species as the bobwhite quail and ring-necked pheasant make substantially one type for the grouse. They do not furnish satisfactory shelter. Some of them do furnish considerable food, particularly during the summer, but are not very important in this respect since other cover types furnish ample food of the same type and adequate shelter as well.

The greatest value of the open-land types is that they enhance the value of adjacent woody types by creating edges. The edges improve the fruiting capacity of woody plants, and many herbaceous plants from the fields will penetrate the woods edge to a short distance, thereby increasing the food supply. The abundance of shrubs is usually greater along an open field edge of a woods.

The edges of open fields are used some by grouse for feeding, sunning and dusting. Old fields of weeds and grasses are most desirable. Most crop fields are of practically no use to grouse. Buckwheat is sometimes used a little in early fall for food. In forest areas, roads, lakes, streams, marshes, and beaver meadows serve the functions of the open-field types.

Overgrown land: Fields abandoned from agricultural use will

normally succeed to woody vegetation. When enough of the land is covered with a sprinkling of bushes, saplings, briars and vines to attract grouse to use it regularly, it becomes overgrown land. This point of change between open land and brush is sharpest when about forty to fifty per cent of the ground is covered with woody plants of significant size, bush size or bigger. The land remains in this cover type until it develops into a pole-stage woodland, or is set back in its development by some external action.

The species that compose the overgrown land-plant association depends upon many factors: the type of soil, fertility and moisture characteristics of the site, the land use in recent years, presence of seed-producing plants near by, as well as climate and geographical location. Often a group of short-lived, light-demanding pioneers take over the area first—raspberries, poplars, "old field" pine, pin cherry, hardhack, and gray birch are examples. These are displaced in relatively few years by longer-lived shrubs and trees. On fields of good fertility, a good seeding of subclimax species will often result with the virtual elimination of the pioneer association stage. I recall an instance of a complete establishment of red pine the year following abandonment of a potato field. Many times one may observe similar stands of maple, ash, and other long-lived species.

The type of overgrown land is of considerable importance to grouse. For convenience it may be divided into three subtypes (see Plate 9). The first varies immensely but in each case is made up largely of a single species, usually a short-lived one. If the species is quaking aspen it is a high quality grouse cover type; if pin cherry, scrub oak, or alder it makes rather good cover too, but if it is gray birch or hardhack it is definitely inferior. The second type may be described as a mixture of hardwood shrubs and tree saplings, with few if any conifers. The last important subtype is the same as the second except that it contains considerable conifers in the mixture, one third or more of the total.

Among the more important plants found in the last two subtypes are: thornapples, hazelnut, sumacs, rose, brambles, blueberries, viburnums, grape, bayberry, huckleberry, and elder among the shrubs. White pine, red pine, and hemlock are best among the conifers while oaks, apple, cherry, and poplar are among the more useful trees—all, except the tree oaks, being useful as saplings. Among the more useful herbaceous plants found in these types are sedges

(*Carex*), strawberry, sheep sorrel, everlasting, asters, cinquefoil, buttercups, clovers, violets, and barren strawberry.

Slashings: Woodlands that have been lumbered in recent years by the clear-cutting method serve substantially the same purpose for grouse as do the overgrown-land types. These differ from overgrown land basically in origin, in that there is a regenerating woody plant association rather than a new seeding of woody plants in an herbaceous association. This results in a large proportion (except in coniferous stands) of coppice growth and a relatively small proportion of seedling plants. The species in a slashing association also normally vary widely from the overgrown-land groups. Both the woody species and herbaceous species in a slashing are to a considerable degree those that were present in the woodland before cutting. There are fewer shrubs and more tree saplings than in overgrown land. The newly seeded species often are quite different too. The use of fire in disposing of brush following the cutting frequently brings in a thick stand of *Rubus*, pin cherry, or other species that germinate well after burning. On the other hand, slashings have fewer of pioneer woody plants, grasses and field herbs than does overgrown land.

The prime characteristic of the slashing, therefore, is that it is a woody plant association with few, if any, trees. A woodland set back in its plant succession, the few trees that may remain are usually old gnarled stubs that were not worth taking out for wood products. Another characteristic of many slashings for a few years after cutting, is the presence of dead brush—the tops of the cut trees. This often results in a tangle of stumps, brush, and tree tops that furnishes very desirable shelter.

Slashings seem to be divided into two types, from the point of view of grouse use, primarily on the basis of age (see Plate 10). One we may call the briar-stage slashing, the other the sapling-stage. In the first instance the slashing operation removes the trees, releases many shrubs and herbs (which, however, may suffer from this release), and induces the germination of new species of herbs and shrubs. Various species of blackberry and raspberry are usually prominent in this stage, hence the term briar stage. Depending on several factors, mainly the composition of the original woodland, soil type, degree of burning, and aspect, this stage lasts from three to ten or more years. As hardwood saplings develop, either as cop-

pice or seedlings, they gradually displace the briars and herbs and finally become a thick stand of saplings. This is the second type. It is generally somewhat less useful to grouse than the first, especially for young birds. When the saplings grow into the pole stage, about three or four inches diameter at breast height (d.b.h.) the stand becomes a woodland again. This stage generally lasts from fifteen to thirty years after cutting.

The species that are prominent in slashings have already been indicated to some extent. Brambles, pin cherry, coppice of the former woodland hardwood species, and popple are among the commoner woody species. Grasses, ferns (especially bracken), fireweed, wild lettuce, and other rank-growing tall herbs may also be prominent. The conifers are usually absent. Unless the original stand had a coniferous mixture in the understory, the slashing is apt to be all hardwoods. In many northeastern woodland areas the native conifers do not seed in readily in clearcut areas. The deficiency in conifers following lumbering is among the most serious problems in both forestry and wild-life management.

Hardwood woodlands: Woodlands predominating in hardwood species constitute a high proportion of northeastern grouse range, particularly in the southern portion. To a degree, grouse need this type of cover in their year-round life, but as a general utility type it is seriously deficient in protective shelter—that is in conifers. Hence the vast extent of this type indicates one of the major faults with the northeastern range.

The hardwood woodland type may be divided into two or more major subtypes from the standpoint of grouse use; the main criterion is the age class. The mature hardwoods, averaging about twelve inches or more d.b.h., are distinguished also by the sparsity of the undergrowth. Second-growth hardwoods, those from pole stage up to the mature stands, constitute the second subtype. Here the understory is usually well balanced. Small openings scattered through make an improved subtype of either age class.

The density of hardwood types varies considerably. In the mature type, the stem density is usually sparse but the crown density close, unless selective cutting or windfalls have made some openings. The younger stands are progressively more dense in stems but usually more open in the crown. In either case, those with scattered glade-like openings are best. Corollary to the crown density, the herbaceous

ground cover is more luxuriant when the crown allows plenty of light to penetrate to the ground.

There are many other variations of the hardwood type, some of considerable importance to grouse. If the woods is pastured, the woody understory is likely to be absent; hence this factor may be important in grouse range. The species composition may be very important depending mainly upon the inclusion of staple food producers. Some of the more prevalent hardwood compositions in the Northeast are: northern hardwoods (birches, maple, serviceberries, poplar, black cherry, hophornbeam); northern Appalachian hardwoods (beech, birches, maples, cherries, poplars, serviceberries, oaks, hophornbeam, hornbeam); Appalachian hardwoods (oaks, hickories, gums, serviceberry, hophornbeam); mixed oaks. These are the more prominent tree species in the hardwood types that occur in plant growth zones from Canada to Virginia.

The shrubs found in the understory of these subtypes vary too. In the North, witchhobble (*V. alnifolium*), withe rod (*V. cassinoides*), nannyberry (*V. lentago*), are prominent; in the middle region, mapleleaf viburnum (*V. acerifolium*), poison ivy, blueberries, grape are among the commoner species; while to the south flowering dogwood, mountain laurel, greenbrier, blueberries, honeysuckle, poison ivy, and grapes are common. There are also minor differences in the ground cover. Bunchberry (*Cornus canadensis*), ferns, Canada mayflower, violet, wood sorrel, jewelweed, shinleaf, miterwort, false miterwort, skunk cabbage, and hepatica are significant in the North; while to the south the ferns, lespedezas, hepatica, alumroot, skunk cabbage, wood sorrel, and false miterwort are among the more important plants.

Mixed woodland: The difference between the mixed woods and the hardwood types lies primarily in the tree composition, and in the proportion of conifers in the mixture. From the standpoint of grouse needs, the hardwood types are deficient in conifers. Most of the areas of the hardwood type have no conifers at all, or but a scattered few. These areas are clearly conifer-deficient, but what about stands that have five per cent, ten per cent, fifteen per cent and so on, of conifers? Since we cannot interpret the reactions of grouse to shelter with such fine accuracy, and since these reactions will vary under different conditions, we have to be somewhat arbitrary in drawing the line between the two type groups. However, twenty per cent of conifers appears to be a proper proportion.

Of course, the value to grouse depends on the character of the coniferous element, too. Whether the conifers exist primarily in the understory as reproduction, primarily in the crown as mature trees, or in all age classes is of great significance; the latter is most satisfactory, the second class poorest (see Plate 13).

Just as we find it necessary to distinguish the line between hardwoods and mixed woods, so we must also define the point of change from mixed woods to coniferous woods. This criterion appears to be about seventy per cent of conifers. The mixed woods is thus a balanced stand containing hardwoods and from twenty per cent to seventy per cent conifers, based on area of crown coverage. It provides grouse with food and shelter for all seasons, although the cover in summer is imperfect.

The subtypes of mixed woodland follow the same general distinctions as the hardwood types: differences in age class, in prevalence of small openings, and in species composition. The mature and second-growth stands are distinguishable as in the hardwoods, the critical point being in the neighborhood of an average twelve inches d.b.h. The species associations follow the hardwood types with conifers added: in the North, spruce, red pine, and balsam fir grow in combination with the northern hardwoods; white pine, hemlock, and sometimes Banks' or other pines in combination with the beech-birch-maple group; the southern oak and hickory types contain some white pine and hemlock at higher altitudes, but, toward the south, include more of the hard pines, especially Virginia pine, pitch pine and shortleaf pine.

The shrub species are substantially those in the hardwood stands. In the ground cover we find some significant variations, notably the addition of partridgeberry, wintergreen, and club mosses (*Lycopodium*).

Coniferous woodland: Woodland, predominately coniferous trees (excepting tamarack), having less than about thirty per cent of its crown taken up by hardwoods, constitutes the last of the important northeastern type groups. In young stands, this type is usually very deficient in food though well provided with shelter, but in mature stands there is usually a hardwood understory of significance. Subtypes, as with the last two type groups, are based on age class and species composition (see Plate 15). In addition to the mature stands and the second-growth stage, it is sometimes desirable to add a third age-class subtype, the pure, one-species reproduction (or reforesta-

tion) stands after the stage when briars and other hardwoods are present and before it reaches the pole size. This subtype could be considered a phase of the overgrown-land type but since its function for grouse is more associated with the coniferous woodland group it is included here.

The important species subtypes are the same as given for the conifer element of the mixed woods subtypes, from the spruces and fir of the North to the hard pines of the South. The understory and ground cover of the coniferous types are generally quite different, however. Shrubs are usually sparse or absent, and limited in species when present. In mature stands the understory of shrubs and hardwood trees is more complete and also more varied in species. The ground cover is quite scanty, too, and varies markedly from that found in the hardwood types. Amongst a heavy ground litter of needles and leaves, we find wintergreen, some ferns, partridgeberry, some orchids, bunchberry, club mosses, blueberries, polygala, and a few others.

INTERSPERSION OF COVER TYPES

We have discussed the character and quality of the major types of grouse cover. But regardless of quality, an extensive area of any cover type is too much. And so it is with grouse cover. Large units of a single type are relatively unproductive of grouse, no matter what the type. That fact brings us to the importance of arrangement of types, and the need for interspersion. Interspersion as applied to cover types refers to the mixture of different types in small enough units so that the game species may conveniently make use of them day by day or season by season as needed. The need for two or more types within a short range is brought about by two basic facts in grouse ecology; the bird requires several different types for satisfactory year-round range and it prefers edges between woods and overgrown land or slashings, woods and open land, or between overgrown land or slashings and open land, rather than the deep interior of any cover types. These are basic requirements for most wild-life species.

It is clear then, that the consideration of the character and carrying capacity of any grouse range must give full weight to the arrangement of the cover types and their degree of interspersion. Likewise

management of grouse range must take cognizance of these principles.

PLANT SUCCESSION CHANGES COVER TYPES

Grouse range is an unstable, ever-changing complex. The plants change with the years, and as they mature, particularly the tree species, the character of the cover types gradually changes. Not only do the plants grow, and thereby alter the physical nature of the cover, some of them die and are replaced by new plants, often different species. Thus the composition of species in a cover type changes too. This phenomenon of plant succession follows definite laws. Grouse management must be based largely on these laws.

In order to understand the character of plant succession as it affects grouse habitat, let us consider the history of an abandoned farm field next to a woodland. To be specific, let it be a timothy meadow which has about run out due to lack of fertilizer and loss of topsoil by erosion. Many annual and perennial weeds have already replaced a part of the timothy at the time of abandonment. Upon going wild these weeds gradually displace most of the timothy and the field is taken over by goldenrod, daisies, devil's paintbrush, poverty grass, wild carrot, and associated plants. If the field had been recently ploughed before abandonment the weeds would be primarily annuals for a time, such as ragweed, foxtail, and smartweed, which would then be succeeded by the perennials.

The decline in fertility may continue for a time after abandonment and portions of the field may be so poor as to be barren of vegetation, or merely support mosses. But sooner or later the first woody pioneers begin to take hold—often dewberries and blackberries at first, or sometimes sweet fern, or plants like quaking aspen or fire cherry. Up to the time these woody plants attain some size and a fair density, the cover is essentially of one type so far as the grouse is concerned—open land. But as the brushy type takes over, the area becomes overgrown land, with an entirely different prospect for grouse.

The changes that take place during the overgrown stage depend upon the species that are initially established and, as in all stages of succession, upon the distribution of mature seeding plants in the vicinity (see Plate 17). Generally the composition gradually changes

to subclimax or climax [1] species while the pioneers are maturing and dying out or are being crowded out. Sometimes a mixture of moderately tolerant shrubs, like the dogwoods, viburnums, thornapples, alders, and others takes over as intermediate between the earliest woody plants and the later tree saplings. This stage is particularly useful to grouse, especially if some conifers too are in the mixture. Another alternative that occurs commonly in some portions of the Northeast is a dense stand of pine. This usually follows the weed stage, or sometimes the early shrubs.

As the long-lived tree species gain height and crown, the shrubs and pioneer trees are replaced to form a subclimax pole-size woodland. This is somewhere between twenty and forty years, or even more, along the path of change since the field was abandoned by man. This type is again quite different from the overgrown land as grouse cover. It may be any one of the three woodland types, hardwoods, mixed woods, or coniferous woods. The rate of change in type now slows down greatly. A new stage, except for age class change, may not develop for many decades. Oft times there is a gradual change in species composition, such as the replacement of hard pines with hardwoods, or the introduction of hemlock into a stand. Thus the woodland reaches its climax type. Changes then are brought about by the dying of large trees and the ensuing plant succession from the briar stage in the small openings formed.

Actually this unhampered trend of plant laws seldom runs a full course. Catastrophes occur that set back the successive stages and prevent the climax being reached. Fire, either natural or man-made, may sweep the woodland and bring the land cover back to an herb-briar stage somewhat different from that described above, one dominated by plants that germinate well following a burn. More commonly, man steps in with ax and saw, and reduces the woodland to a slashing or to a spotty, small-clearing pattern if he pursues selective cutting. In either case, the succession is set back many decades, often a century or more. If he follows clear cutting with stump pulling and ploughing, or if he grazes the cutover area with livestock, the stage is placed still farther back. Then too, grazing, even without lumbering, will materially alter the character of the

[1] Climax plant associations are those that complete the stages of plant succession for an area and, unless disturbed, maintain themselves indefinitely. Subclimax species are those in the stage preceding the climax.

woodland, eventually reducing it to grass or weeds if continued intensively beyond the lives of the crown trees.

This is just one story of plant succession, with some alternatives discussed. Many other similar trends of plant changes occur under other conditions. But whatever the conditions, the potentialities of ruffed grouse management are bound up in these principles. Thus sound management should be based upon the manipulation of plant succession by means of man's tools—axes, saws, planting irons, fire, fencing, livestock, and others.

RELATION OF SHELTER TO THE GROUSE NESTING

Cover Types Used for Nesting. Most hen grouse shift their scene of activity from a predominance of coniferous types in the winter and very early spring to a predominantly hardwood type in nesting season. This change to hardwood types on the part of nesting females is much more pronounced than the same trend by other grouse. The predominantly coniferous types—most important through the winter—are practically abandoned as nesting territory. Fewer than one grouse in twenty uses a conifer type for the nest location.

A medium-age stand of mixed hardwoods is the most commonly used nesting type in New York, usually with a scattering of conifers. Closely following is the medium-aged stand of mixed hardwoods and conifers. These types were selected for nesting in two thirds of the 1,270 instances observed (see Table 1) (Bump, 1938). When the records are weighted[1] to account for the variation in extent of the different cover types on the area, these types are still predominant but the slashing types also rise to prominence. From the ratios of nests to acres of types, we conclude that the three types—predominantly hardwoods, mixed woods, and slashings—are the best types for grouse nesting. The variation in acceptance between them is not significant. Open land is of no value for nesting, while the overgrown-land types and coniferous types are used only to a small extent, far less than their proportional existence.

Among the desirable hardwood types and mixed hardwood-conifer types, the middle-aged stands are superior as nesting cover over the mature stands by a very significant margin.

[1] Number of records is divided by acres of cover type to provide comparable data.

Table 1

Cover Types Selected by Grouse for Nesting (Based on 1,270 Nests in New York, 1930–36)

Cover Type	*Percentage of Nests Found in Each Type*	*Ratio of Nesting Use to Cover Type Prevalence* [1]
Open land	1.4	.002
Overgrown (brush) land	9.8	.05
Hardwood woodland	45.2	.12
Hardwood-conifer mixed woods	21.5	.13
Coniferous woodland	4.1	.07
Slashings	9.9	.13
Cover type not specified—8.1	[1] Norm, including open land	.09
	Norm, excluding open land	.11

Ratios based on Connecticut Hill cover type proportions.

Specific Location of Grouse Nests. Two thirds of the nests I have observed were located at the base of trees, with about two thirds of these being hardwoods and almost all trees of considerable size (see Plate 18). Of the other third, the majority were at the base of a tree stump, with a few located beside or under logs, bushes, or brush piles.

There appears to be no significant selection among tree species for nest location. The species chosen are those predominating in the woodland. These were mainly beech, maple, birch, hemlock, pine, chestnut (dead), oaks, etc. A somewhat disproportionate number of nests at the base of dead chestnuts seems to be due to the additional sunlight reaching the ground with the absence of the tree canopy rather than to the species of tree.

If we may presume to interpret the desires of a hen grouse for a nesting location on the basis of having observed several hundred of their choices, the selection appears to be a compromise between (1) a position protected from attack by enemies; (2) good visibility of the immediate terrain; (3) protection from the elements; (4) desire for direct sunlight; (5) proximity to edges; (6) lack of obstructions in the way of quick escape. The result is a fairly exposed situation with a solid backing, and near the edge of a prominent cover type. A spot at the base of a tree, or near a stump or log in a relatively open woodland, and near a road, field, or thicket seems to meet requirements.

The setting bird always faces outward with her tail raised against the tree. From this attitude she can view her surroundings in all directions except the rear, where the tree gives protection. Usually she chooses a tree or stump that has few, if any, bushes or saplings immediately in front for several feet—thus giving an open front yard —but often a very small sprig of living or dead brush will protrude a few inches above and in front of the nest to assist in obscuring her position. The desire for sunlight results in many nests placed along old woods roads, beside stumps where the canopy has been broken by the removal of a large tree, at the base of dead trees (notably chestnut), and in similar spots where the advantages of the woodland are combined with more than ordinary exposure to the sun.

Most grouse habitat is quite free from evidences of man's civilization. However, if its cover requirements are met, the grouse pays little attention to such intrusions. Sights, sounds, or movement of mechanical objects, as long as they are regular, cause no fear. Several grouse nests I have observed bear witness to this fact. One was located on the bank of a railroad right of way, protected only by a bracken fern, and within a few feet of the track. The nest was discovered by a keen-eyed railroad man who spotted the bird on the nest from the train. Another nest, in the oil well region of southwestern New York, was situated beneath the iron drive-rod that connects the powerhouse with the well. This rod, supported every little ways with tripods, was only about three inches above the bird's head. About four hours each day, when the wells were being pumped, this rod squeaked back and forth without causing the bird concern. Nests are occasionally found on the borders of public highways. The passing of speeding automobiles a few yards away does not seem to worry a grouse hen.

In selecting a nest site, the bird usually chooses one with a very open undergrowth, as has already been noted. The crown density of the nest sites observed also appears to average a little on the open side but generally about in proportion to what the woods contains. A very large majority of the nests I have seen were within a hundred feet of a coniferous type, or a clump of conifers, in spite of the relative unimportance of conifers to nesting. The presence of a significant amount of evergreen cover in the vicinity seems desirable for protection from the weather even though coniferous cover is little used for nesting and a thick growth of conifers around the nest is avoided.

Location of Nests with Respect to Openings. With the exception of slashings, which have as high a degree of nesting use as any type, the openings (cover types without crown cover) are little used for nest locations. However, they do determine the location of nests in other types to a considerable degree. The need for "edge" places most nests close to an opening. More than half the nests observed were within fifty feet of such an opening, and almost three quarters were within a hundred feet. Very few were located more than three hundred feet away from an open field, brushy area, slashing, or a significant road opening. Most of the nests are nearest to an open field or slashing type of opening, and the proportion placed in or near slashings is significant.

The occurrence of grouse nests close to roadway openings in the woodland, usually wagon roads, is notable. Nearly one third of all nests were within fifty feet of a road. Although it is not certain that the road location affected the nest site selection in all cases, it was the closest opening by a considerable distance for many of the nests. The woods road seemed to provide an adequate opening and still avoided the exposure of a wide open edge.

Effect of Slope on Nest Location. The only effect of degree of slope on choice of nesting sites is a relative avoidance of the very steep slopes (twenty per cent and over). Only about one half of the normal proportion of nests are found on steep slopes. The moderate slopes have a proportionally higher number of the nests while the flat land has its proportionate share.

The slight variations in proportions of nests on the various exposures are not significant.

Does Cover Affect Nest Mortality from Predators? The percentage of nests broken up varies slightly according to cover type, tending to be higher in slashings and conifers. Since these conclusions are based on relatively few observations, it is doubtful if they are dependable. It is interesting to note, though, that the seemingly safer cover types are generally the preferred types, and one type (conifers) with the higher mortality rate is used to a lesser degree. It is at least possible that the predation hazard may affect the choice of type of cover for nesting.

There also is a possible correlation between undergrowth density and nest loss, but here again the evidence is not abundant enough

to be fully reliable. The majority of nests are in cover with open understory and the mortality in these is average. The mortality in cases having a dense understory was very excessive. The possibility exists, and is logical, that a dense undergrowth tends to increase nest mortality. Again, the habit of the grouse in avoiding nest sites where the understory is dense may be conditioned by the predator hazard.

RELATION OF SHELTER TO GROUSE BROODS

Cover Type Preferences of Grouse Broods. Families of young grouse observed up to the end of September may be considered as broods. Since the location of the family and its activities are determined by the needs of the young birds, the mother bird is considered a part of the group. So many of the requirements of the young birds differ from those of the adults that it would be likely that their shelter requirements would differ; and since their food habits vary markedly from the old birds, the cover types chosen also may well vary considerably. What are the cover type preferences of the chicks as they grow up, and how do they vary from the cover chosen by adults by themselves in the summer? The records of 1,515 brood observations in New York from 1930–1936 are given in Table 2 (Bump, 1938).

TABLE 2

COVER TYPES SELECTED BY GROUSE BROODS IN NEW YORK, 1930–1936

Cover Type	*Percentage of Total Flushes*	*Flushes per Acre Reduced to Part of Most Used Type Taken as 1.00* [1]	
		Chicks	*Adults*
Overgrown land	44.7	1.00	.61
Slashings	12.4	.65	.72
Hardwood woods	25.5	.22	1.00
Coniferous woods	4.2	.22	.17
Mixed woods	10.4	.17	.25
Open land	2.9	.06	.03

It is clear that the tendencies in cover type use in summer by young and old birds is similar—a definite preference for the brushy types, primarily overgrown land, followed by slashings. This tend-

[1] Figures derived from Connecticut Hill data. See Bump, 1938.

ency is very much more pronounced with the broods, however. When the figures are corrected to a per acre basis, these two types prove to be far more intensively used than all others. Correspondingly, the use made of the woodland types is much lower than for adults.

The cover used by broods may be divided into two types of major significance, brushy cover and woodland. Differentiation in use of the several woodland types is of little significance. The greater preference for overgrown land as compared with slashings is of considerable significance. It is one of the major explanations of the greater grouse-carrying capacity of separated coverts as compared with continuous forest cover. The extensive forest has very little of this overgrown border cover, and the only approach that the forest has in this direction is their slashings and the occasional alder runs along stream courses. The need of brushy cover for broods also poses one of the biggest problems in grouse management,—and offers one of the biggest opportunities for raising the carrying capacity in many coverts.

A more detailed analysis of cover used by broods brings to light further interesting trends, all of them consistent with the principle that hardwood bushy cover is best for broods. Of the overgrown land subtypes, that which contains a high proportion of young conifers is used less, the mixed hardwoods and pure stands of popple prove to be used more than the type as a whole. Likewise, hardwood woods that have been "spot-lumbered" have a use rating nearly double that for the entire type group. As would be expected, the younger woodland stands are much more used by broods than are the mature woods. In hardwoods the comparison is about four to one for stands under twelve inches d.b.h. compared to older stands, while in mixed woods the use intensity for the younger stands is over twice that for mature woods.

Corollary to the predominant use of the brushy types by broods is the relation between the location of edges of brushy or open land for the broods that are actually found within woodland types. Most of them are found within fifty feet of such an edge and records of broods over a hundred feet from an edge definitely are unusual. Thus the interspersion of the more open types is of the greatest importance in determining the productivity of the range.

The changes in cover type use by broods from birth to the time

when they reach maturity are in accordance with the relations of brood cover to adult cover. The younger the brood, the more strongly is its tendency to adhere to brood-cover selection habits, and the older the brood the greater the chance that the cover types selected will follow adult habits. The high use intensity of overgrown land is most prominent in the first six weeks, and drops off rapidly after that time. Similarly, the use of the woodland types increases after midsummer, except for that of coniferous woods, which does not increase materially in use intensity until autumn. Slashings are used rather consistently at all ages by the chicks, as would be expected since the use intensity of slashings by the adults is about the same as it is for the broods.

CHANGES IN COVER TYPES UTILIZED AT DIFFERENT TIMES OF DAY

As is the case with the adults, the cover types used by the broods vary considerably at different hours of the day. These changes are the result of the needs of the birds for food, for roosting cover, for dusting, or for sunny spots, all of which vary from morning to night; and in many instances are the results of reactions to weather conditions which vary according to time of day, notably the cold at night and the heat at midday.

The most important brood-cover type, overgrown land, shows a marked increase in use intensity throughout the day, the use in early morning being a little below, and that in late afternoon correspondingly above, the mean. In slashings the tendency is toward highest use at midday and early afternoon, and lowest use at late afternoon. These trends in cover-type use by broods are at some variance with the habits of the adults (see page 92). The old birds use overgrown cover most in early morning, least at midday, and normally in the afternoon; and slashings least in the morning, highest at midday.

The use of hardwood woods increases from morning through mid-afternoon, then drops off at evening. The latter trend is opposite to the habit of adults of increasing the use of hardwoods towards evening. With mixed woods and conifers the trend is complementary to the rest, a higher use intensity in the early day and falling off later.

THE EFFECT OF SLOPE ON SELECTION OF COVER TYPE

Many factors enter into the choice of cover made by grouse broods. Under most conditions the steepness and aspect of the slope is probably less important than some other factors. However, slope is of some importance, directly or indirectly, in its relation to cover, plant species, and weather (see page 93). The effect of slope on brood-cover selection is essentially the same as for adults at the same season. Steep slopes are generally avoided, even more so than with adults.

COVER SELECTION IN RELATION TO OPENINGS

The great importance of open cover types and openings (open land, overgrown land, slashings, and roadways are classed as open types or openings) to grouse is most strongly shown by the young birds. While grouse are usually thought of as birds of the woodland, their need for openings and brushy cover is clearly indicated. Three quarters of all grouse broods are found in or within a few feet of an opening or open cover type, and almost all stay within fifty feet of openings.

Thus the young birds utilize a relatively small proportion of the cover in most areas, especially forest areas. The need for interspersion of the open types with woodland types is apparent if the range is to have a high grouse production capacity.

COVER TYPES CHOSEN AS AFFECTED BY WEATHER CONDITIONS

Cover-type selection by broods is somewhat more stable under varying weather conditions than is the case with the grown birds. The most important type used, overgrown land, does not vary significantly in use under any conditions of temperature, sky, or wind. It is thus an all-weather type for birds in summer, which is probably one of the factors bearing on its importance.

Changes in temperatures affect cover type selection the least of the three weather attributes. As usual the most significant changes occur in the use of coniferous woods. These are used much more than average on hot days, and correspondingly less on cold days. Although this relative preference for conifers as a place of escape

from the heat is significant from the standpoint of use of this type, it is of little importance to the birds, since the type is so little used.

Sky conditions produce no significant changes in brood cover selections in the types most used except for a pronounced avoidance of slashings in the rain. On the other hand, there is a very pronounced increase in the use of coniferous woods during rain. This indicates the need for heavy shelter during summer rains.

Differences in wind conditions produce several deviations in cover selections worthy of note, mainly in the use of conifers. Here we find the pines and hemlocks used primarily in windless weather, and used well below average under moderate and strong winds. The explanation probably lies in the association of windless weather with hot days in the summer, and breezy weather with cooler days. A reduction in use of slashings during strong winds and a high use intensity of hardwood woods on windless days are both significant.

Probably the two most important items in these weather relationships are (1) the indicated need of broods for coniferous cover, even in the summer, for escape from heat and rain; and (2) the weakness of the slashing type as an all-weather cover in comparison with overgrown land. It is notably less used during rain and strong winds.

RELATION OF SHELTER TO ADULT GROUSE

Cover Type Preferences of Adults. The cover types in which adult grouse were flushed in the several seasons of the year on Connecticut Hill for 13,553 records taken from 1930 to 1936 are shown in Fig. 3. These do not include females with broods in summer.

Let us first consider the preferences of grouse during each season. In order properly to evaluate the data it is necessary to weight them according to the availability of each of the cover types. Taking the winter (January to mid-March) records first, we find that the number of records per acre of each cover type, when reduced to parts of the major type taken as 1.0, are:

Coniferous woods	1.00
Mixed woods	.62
Hardwoods	.46
Overgrown land	.38
Slashings	.22
Open land	.02

The preference for coniferous woods during the winter is shown to be one of the outstanding grouse cover requirements. No other consideration at this season can compare with this need for heavy protection cover. The second preference, that of mixed woods over all hardwood types is also significant, and is merely a repetition of the need for conifers. The difference between the various hardwood types—the hardwood woodland, overgrown land, and slashings—is less important, except that slashings are even less useful than the others. The open land, as at all seasons, is not significant as a cover

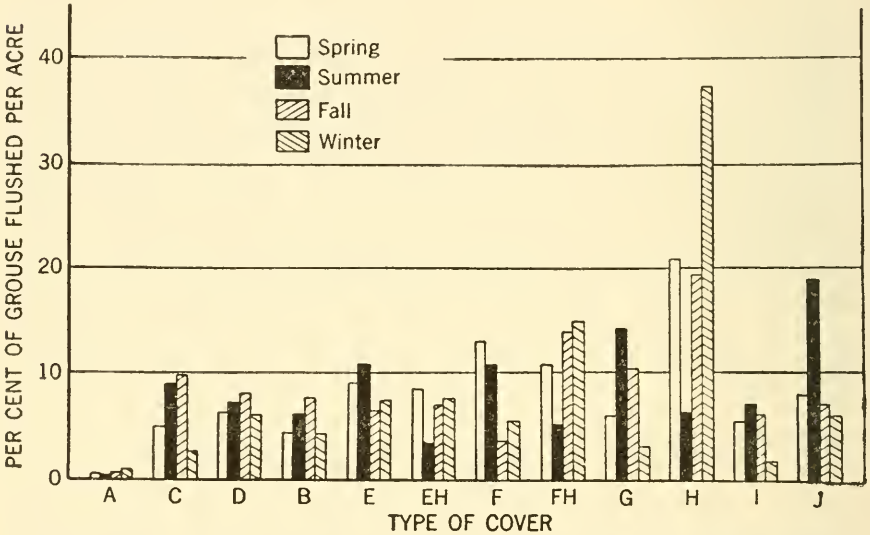


Fig. 3. *Analysis of Certain Cover Requirements of the Ruffed Grouse in New York State* (taken from G. Bump, 1938). Symbols used for type of cover are: A—open land; B—overgrown land, single species; C—overgrown land, mixed hardwoods; D—overgrown land, hardwoods and conifers; E—young hardwood woodland; F—mature hardwoods; G—spot-lumbered woodland; EH—young mixed hardwood-conifer woodland; FH—mature mixed hardwoods and conifers; H—coniferous woods; I—briar-stage slashing; J—sapling-stage slashing.

type although very important in improving adjacent types by producing edge. Thus, for the grouse, there are three distinctive winter cover types: First, and most vital, is the coniferous woodland; second in importance comes the mixed hardwoods and conifers; and thirdly the various types, brushy and woodland, that are predominantly hardwood. The latter are important in winter primarily in proportion to their proximity to coniferous or to mixed woods.

They are predominantly food-producing types in the winter and, except in the portions close to conifer shelter, are not used intensively at this season.

In the spring the choice of cover types is substantially the same as in winter except for the hardwoods type as we see from the following comparison of records. In addition to the predominant use of hardwoods, the great preference for coniferous woods, in proportion to mixed woods, is much reduced. The differences between the intensities of use of overgrown land and slashings is not significant.

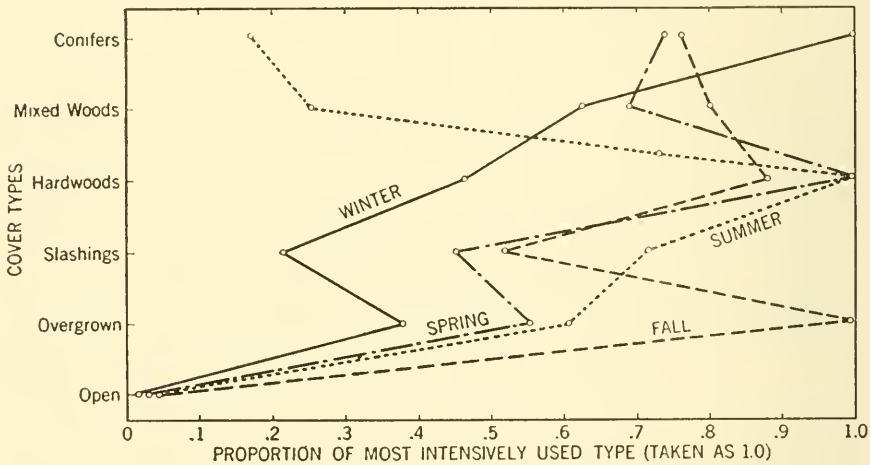
Hardwoods	1.00	Use intensity ratio when reduced to parts of major type taken as 1.0
Coniferous woods	.73	
Mixed woods	.69	
Overgrown land	.55	
Slashings	.45	
Open land	.03	

In comparison with the use made of the same type groups in winter, we see that both the mixed woodlands and the several hardwood types have greatly increased in use in proportion to conifers. The coniferous woods is now second to hardwoods as the most intensively used type and is used much less than during the winter. The use made of overgrown land and slashings is increased considerably as compared with the winter period and during the last half of the spring period assumes great importance. For the spring period we may summarize by saying that an approximately equal requirement exists for coniferous types and for hardwood types, and that mixed woods is extensively used as a compromise containing both of the required elements well balanced. As has been shown elsewhere in the discussion of nesting cover, the female definitely makes use of the hardwood types for the most part after the middle of April.

By the arrival of summer, the intensity of use of the various cover types has changed immensely. No longer is the coniferous element of great importance. In its place shrubby, brushy, sunny cover—the open types of overgrown land and slashings—is preferred. Conifers, while used less extensively than any other type group, except open land, are still used some, mainly to escape excessive sun heat and summer storms. The intensity of summer use of the type groups is as follows:

Hardwoods	1.00	Use intensity ratio when reduced to parts of the major type taken as 1.0
Slashings	.72	
Overgrown land	.61	
Mixed woods	.25	
Conifers	.17	
Open land	.03	

The significance of the difference in use intensity between slashings and overgrown land is questionable. Together they constitute the most important type of summer cover—the woody cover without a tree canopy or crown—although the hardwood type is most used as a single type. The difference in use made of mixed woods and conifers is probably not significant. It is worthy of note that in spite of the trend toward more open cover in the summer, the use of open land is less than at any other season.



(*From Connecticut Hill, N.Y. data*)

Fig. 4. Intensity of Use of Cover Types by Adult Grouse by Seasons.

In connection with all these summer records, it should be noted again that only males and broodless females are included. The brood mothers, whose choice of cover is presumably determined by the needs of the brood, are omitted. Since the brood records are even more predominantly in the overgrown-land and slashing types, the addition of these to the adult records given here would only further accentuate the trends shown. We may sum up the summer cover requirements of the adults by dividing them into two preference groups: the open types, slashings and overgrown lands, that are preferred under normal weather conditions; the crown types that

are used some for normal conditions (mainly hardwoods), and the mixed woods and coniferous types used particularly for escape from extremes of heat or storm conditions.

With the advent of autumn the choice of cover types begins the trend back toward winter conditions with a greatly increased use of coniferous and mixed woods. The slashing, with its abundance of brambles for summer food, wanes in importance but overgrown land reaches its highest degree of use due to the abundance of fall-fruiting shrubs in these types. Once more, as in spring, there is a significant increase in the use of open land although this never rises to a position of great importance. The use intensities of the cover types in the fall are:

Overgrown land	1.00	Use intensity ratio when reduced to parts of the major type taken as 1.0
Hardwoods	.88	
Mixed woods	.80	
Coniferous woods	.76	
Slashings	.52	
Open land	.04	

The great importance of coniferous cover at this season is probably a reflection that the last of the fall season as used here, all or most of December at least, is really winter so far as the grouse is concerned. The choice of cover in the early fall tends more to the hardwood groups, particularly overgrown land where such desirable fall foods as hawthorn are to be found.

It appears that the intensity of use of cover-type groups in the fall is significant from each other except between conifers and mixed woods. However, here as in all of the cover-type records, the use of hardwood woodlands probably ranks somewhat lower than is actually warranted. The fact that the hardwood stands were by a wide margin the most extensive stands on the Connecticut Hill area, coupled with the second fact that these several stands included the largest continuous blocks, results in a lower use intensity than the character of the type itself would warrant. As with all cover types, the edges are used most, hence the types having the greatest proportions of area far from edges will be used less, other things being equal. If the prevalence of the hardwood-woodland types in an area were small in comparison, let us say, to the coniferous or overgrown-land types, then the intensity of use of the hardwoods in relation to the others would rise markedly.

We have analyzed the shelter type selections of the adult grouse

during the four seasons and we find them to vary widely according to the season. These variations are exhibited graphically in Figure 4. The most marked contrast is in the summer type use intensities in comparison with the other three seasons. Now let us consider the same data from the standpoint of the variation in use made through the year of each major cover type group.

Coniferous Woods: It is rash to say that one type is more important than any other. The truth is that one type—any type—by itself loses much of its importance. The potential value of any type can only be attained when its quantity, quality, and distribution are in harmony with the same qualities of other important types of cover. It is likewise true that no type of cover is indispensable. Some grouse may exist within the geographical range of the species even if one type, however important, is completely absent. This is also true, but progressively less so, if two or more types are absent. Keeping these generalizations in mind, it is clear that coniferous woodland is the most intensively used type during the colder months and hence, with a reasonable balance of other types, the more important of the several type groups during the period from mid-fall through mid-spring. The marked preference for this type, especially in the winter months, was enhanced in the records given here by the moderate quantity and good distribution of this cover on the study area. This factor tends to widen the use intensity ratio between conifer cover and the mixed- and hardwood-woodland type groups because of the greater area and more extensive blocks of the latter. Thus, while coniferous woodland is an immensely important—almost vitally important—component type for satisfactory grouse range, it should be in moderate proportion and well distributed in order to be most effective.

There were two main coniferous types on the Connecticut Hill area, hemlock woods and pine (white and red) woods. The hemlock is definitely superior to the pine type. Over the northeastern range the coniferous-type group may conveniently be divided into four types, hemlock, spruce-fir, white and red pine, hard pine (pitch, banks, or Virginia). These are arranged in order of quality, with the hard pine type definitely inferior to the other three. The quality of shelter in each is affected greatly by the age class and by the amount of admixture of hardwood trees and shrubs. The highest quality is obtained in the stands having all ages of trees, including

a moderate proportion of young reproduction. It is also desirable to have a small proportion of hardwood species.

The variation in seasonal importance of coniferous types may be

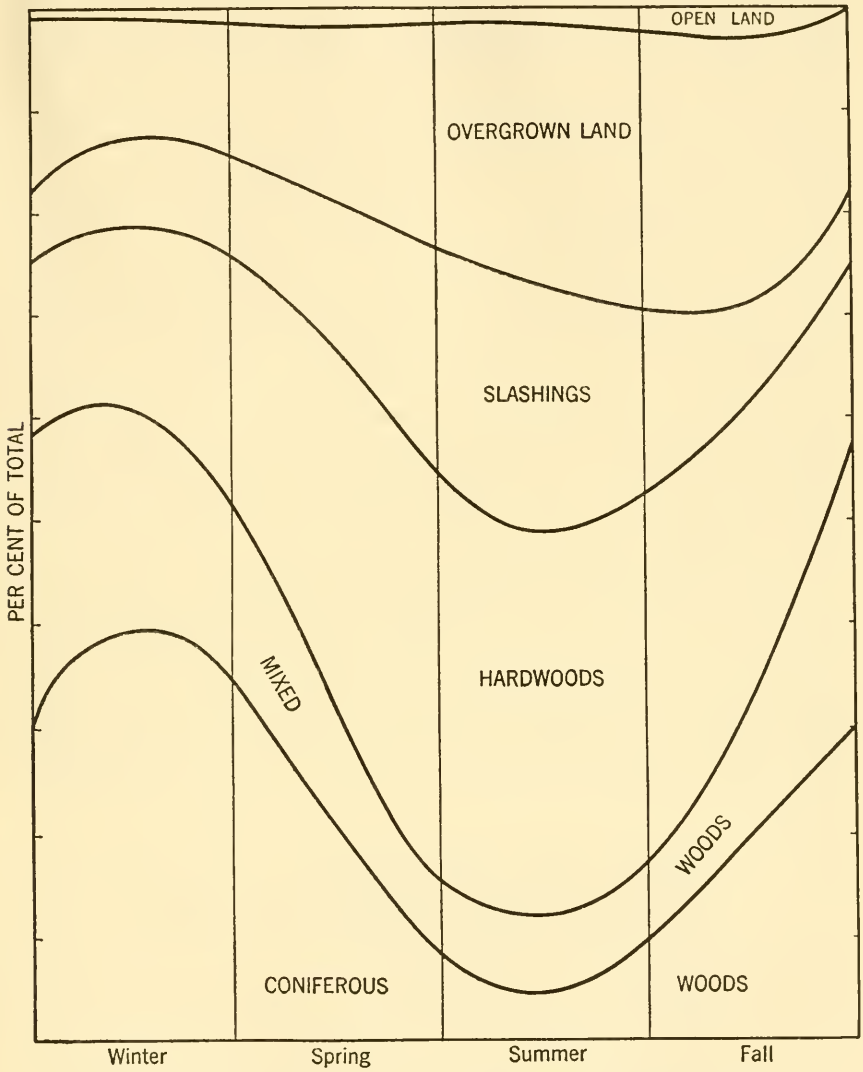


Fig. 5. Cover Types Used by Adult Grouse at Different Seasons.

noted from the percentages of total flushes per acre in these types in each season: winter, thirty-seven per cent; fall, nineteen per cent; spring, twenty-one per cent; summer, six per cent.

Mixed Conifer-Hardwood Woods. The mixed woods is an important year-round type providing a significant amount of conifer shelter interspersed with hardwoods that furnish food and serve other purposes. It is the one type group that, with interspersion of open land, can support a fair grouse population without the presence of the other major types. In winter it ranks second in use intensity only to coniferous woods, and in fall and spring it ranks third behind conifers and hardwoods. In the summer it is used less intensively than any of the other crown-type groups except conifers.

The primary subdivisions of the mixed-woods type on Connecticut Hill are distinguished by age class. Mature mixed woods has a high proportion of the trees in the twelve inches and above d.b.h. class, and a rather sparse understory. The submature mixed woods has a large majority of trees in the four inches to 12 inches d.b.h. class and the understory is usually well stocked. The latter is superior to the mature stands for grouse cover. The mature stands can usually be improved by selective cutting. When the density of mature trees is reduced so that reproduction of both conifers and hardwoods establishes a good understory, the stand is changed to the more desirable grouse cover type.

Over the northeastern states there are a number of subtypes of mixed woodland varying considerably in value as grouse cover. The subtypes are combinations of the two age classes just noted with the several types of conifer and hardwood associations that occur as mixtures. The most important subtypes, in approximate order of value, are as follows (each of these may occur as mature or submature stands):

Hemlock—beech, birch, maple
White pine, red pine—beech, birch, maple
Spruce, fir—northern hardwoods
White pine—oak, hickory
Hard pine—oak, hickory
Hard pine—oak

The seasonal use of mixed woodland varies little except in summer, varying from nine per cent of all flushes per acre in summer to twenty-three per cent in winter. The percentage of flushes for each season are: winter twenty-three per cent; spring, twenty per cent; fall, twenty per cent; summer, nine per cent.

Hardwood Woods: The various types of hardwood stands are rather mediocre grouse cover unless interspersed with one or both of the conifer or mixed-woods types. With this interspersion, the hardwoods are important as nesting cover in the spring, and as feeding cover most of the year. It is not good roosting cover, except as the birds sleep on nests and drumming logs in the spring. The hardwood types are most important in spring and summer, least important in the winter. The proportion of use for each season on Connecticut Hill was: summer, thirty-six per cent; spring, twenty-nine per cent; fall, twenty-two per cent; winter, seventeen per cent.

The hardwood group, apart from species composition, may conveniently be composed into three types, according to age class and density: mature hardwoods, with a high proportion of the trees over twelve inches d.b.h., and sparse understory; submature stands with few trees over twelve inches, and a good understory. Either of the former may have scattered large trees recently removed leaving small openings in the crown, usually with brambles filling in these spots. The latter may be called "spot-lumbered." The mature stands are definitely inferior to the other two as grouse cover and receive little use. Theoretically, owing to the small scattered openings, the spot-lumbered type should be superior to the subclimax hardwoods from spring to fall. This proves true in the fall, but for some reason fails in spring and summer. In the spring it proved to be less intensively used than the regular type. The explanation for the failure of the statistics to support logic may be inadequate data for the spot-lumbered type.

The hardwood type most prevalent on Connecticut Hill was the beech-birch-maple association. This seems to be the most satisfactory of the hardwood types for grouse. In order of their value, the other common hardwood types in northeastern grouse range are: northern hardwoods, oak-hickory, and oak. All these types may be subdivided according to age class and density. These hardwood types all exist extensively without appreciable conifer admixture, and as such are poor grouse range.

Slashings: Areas that have been clearcut in recent years furnish excellent cover for summer use. At all other seasons it is relatively unimportant as a cover type. Slashings have a second use, however, that may be even more important than its cover use, certainly so when considered apart from summer. Within wooded areas slashings serve to create openings, hence edges, and thus serve grouse range

in the same manner as open land does. Extensive areas of continuous woodland range may be greatly improved by the judicious creation of slashings in accordance with this principle.

As a cover type, slashings serve somewhat the same use as overgrown land, especially in the summer. Both have an abundance of summer food of berries, largely brambles, and insects. During this season it is an intensively used cover type. In fall, winter, and spring it is the least-used type excepting open land, largely due to poor food conditions. The percentage of flushes per acre found in slashings in each season were: summer, twenty-six per cent; fall, thirteen per cent; spring, thirteen per cent; winter, eight per cent.

Slashings may be conveniently divided into two subtypes as grouse cover, largely on the basis of length of time since cutting: areas cut over from five to ten years or less, depending upon rate of regeneration, that show considerable ground covered by herbaceous species, and that have many brambles and few saplings; areas cut over five to ten years or longer, depending upon rate of regeneration, that have little open herbaceous cover, and that have many saplings both from sprouts and seedlings and relatively fewer brambles than the first. A slashing grows from the first type into the second. As cover, the type is most valuable during the latter half of its first stage and for the first few years of its second stage. As an opening it is most valuable in its first stage. As the slashing grows toward the pole stage, toward becoming either a hardwood or mixed-woods type, its value as slashing cover gradually disappears.

Overgrown Land: Shrubby areas grown up from old fields are an important cover type group from spring through fall, but definitely most important in fall. At this season it serves as a feeding ground abounding in fruits and succulent greens. During the summer this type produces an abundant supply of berries and insects and is much used. In winter it is little used, for most of the fruit is gone and winter shelter is usually lacking. The percentage per acre of flushes in this type group by season was: fall, twenty-five per cent; summer, twenty-two per cent; spring, sixteen per cent; winter, fourteen per cent.

There are three primary subdivisions of this type group in the Northeast, all occurring on Connecticut Hill in significant quantities. These are: pure stands of temporary hardwood species; mixed

hardwoods, mainly climax and subclimax species; mixed hardwoods and conifers.

The first category were primarily popple (*P. tremuloides*) although areas of hawthorn were common and stands of alder and pin cherry also occurred. In all of these subtypes brambles were plentiful in the ground cover. The use of these three categories varied considerably both by type and seasons. Most intensively used year round were the pure stands of short-lived species, next the mixed hardwoods and lastly the mixed hardwoods and conifers. By seasons, the popple and hawthorn stands were used most intensively throughout the year, except in summer. During summer the mixed hardwoods showed a little the heaviest use. The overgrown lands with mixed conifers were used more intensively than mixed hardwoods only in the spring; at all other seasons this subtype was least used of the three. This relative unimportance of the coniferous mixture in overgrown-land types as compared with woodland types is interesting and reflects the use made of the several overgrown-land types—feeding rather than shelter. The significant superiority of the pure-temporary stands from fall through spring is probably due to the value of the hawthorn fruit in the fall and of the popple buds in winter and spring, but there may be a further explanation.

Open Land: Grouse are found in open-field cover most often in fall, and least in winter. However, open land is not an important cover type at any time for grouse. As already noted, its importance lies in creating edge, and raising the quality of adjacent coverts thereby, rather than in its own intrinsic value. A large proportion of the records of grouse actually flushed in open fields are due to the presence of a bushy fence-row, an isolated apple tree, or some similar attraction.

THE EFFECT OF OPENINGS ON COVER SELECTION

The grouse is well-known as a bird of the edges. We have already seen that in nesting, the grouse mother generally selects a location near the woods edge or an interior opening. Likewise the broods were found mainly in the open cover types or near the edges if in the woods. The same principle follows in the selection of cover by the old birds, although not so completely. I reported on the utilization of coniferous reforestation by grouse (Edminster, 1935) and

found a general limit of three hundred feet, beyond which the birds did not penetrate the solid coniferous stands. In this case, few grouse ventured more than two hundred feet from the outside edges. In ordinary range we find this three-hundred-foot distance to be a good rule of thumb for all woodland types, although most types are used regularly in the two-hundred-to-three-hundred-foot zone. Even the brushy cover types are relatively little used at a distance of more than three hundred feet from the edges when present in large uniform blocks.

We conclude that cover types should be so interspersed that no point is over three hundred feet from an edge (between open or brushy type and woodland type) if the range is to be fully and regularly used. The optimum zone of woods types is from the edge to a depth of two hundred feet.

VARIATION IN COVER TYPE PREFERENCE AT DIFFERENT TIMES OF DAY

There are numerous factors that combine to determine the type of cover selected by a grouse at any given time. We have just observed the marked variation in the different seasons. Less marked, but still highly significant, are the differences in cover needed at various hours of the day within the seasons. Seasonal requirements must be met within the limits of the bird's yearly range—a reasonably flexible limitation—but the hourly changes required must be available within the daily cruising radius.

During the fall and winter the most significant trends are: a high early-morning-use intensity of coniferous woods, hardwoods, slashings, and overgrown land, all generally declining in use intensity through the day; a low intensity in the early morning for mixed woods, which rises through the day. All these trends are logical, except that it would seem that the trend for use of coniferous woods should parallel that for mixed woods instead of the hardwood group. The fall and winter season use of the several deciduous types at early morning feeding time, most notable in the fall, are linked with the birds' feeding habits.

In spring the hourly cover-type-use trends shift somewhat from those of winter. The use of mixed woods rises from early morning until midafternoon as before, but then significantly drops again

toward evening. The variations in use of other types are less notable. A rise in use of conifers toward evening is contrary to the previous season's trend.

Summer adjustments complete the shifts in daily cover type use. Slashings show a notable increase in use intensity from morning to night. Mixed woods has a high use intensity at midday with markedly lower use in the early day and again towards evening. This is complementary to the trend in use of overgrown land, which is high in morning and evening and low at midday. In summer, the use of conifer woods is not important.

The reasons for these movements from one cover type to another during the day are linked with the birds' habits, although often conditioned by the weather. Thus the habit of feeding in early morning takes the bird from its night roost, usually conifers or mixed woods except in summer, into the types that furnish food, usually the deciduous types. However, if the weather is inclement, this normal habit will likely be altered temporarily; the bird either gets some food in its protection cover or delays feeding for some hours, or even days, until the weather is better. The requirements for sunning, dusting, drumming, and nesting similarly stimulate quick movements from one cover type to another for the purpose of the moment. To provide adequately for these varying needs within easy daily range, the range must provide not only the needed types of cover, but also have them interspersed intimately enough for ready accessibility. Upon these needs must be built any effective plan for range management.

THE EFFECT OF SLOPE ON SELECTION OF COVER BY ADULT GROUSE

Slope bears numerous relations to cover and to the acceptability of cover under various conditions. The steepness of a slope may impede the bird's mobility, or aid it. When on level ground, a grouse moves about on the basis of its horizontal flight capability. With increasing steepness of slope, it requires more power to go uphill and maintain speed and less power to go downhill; that is, it loses speed when ascending, and gets additional velocity when "power diving." Whether a bird desires to go uphill or down when on a given slope may depend considerably on the location of cover types.

Considering these factors, it is at least possible that grouse may choose to avoid areas because of their degree of slope.

Similarly, the direction of the slope may be important. A north slope, that is one sloping downward predominantly between northwest and northeast, is a cool slope, whereas the south and west slopes are comparatively warmer. Cover composition often varies considerably according to aspect, and may affect grouse distribution. For example, in south-central New York, mountain laurel is found only on south slopes. When winds come predominantly from certain directions, particularly winds accompanied by storms, opposite slopes are the most protected, other things being equal.

Substantially the same relationships among the slope-use intensities prevail at all seasons. Steep slopes are used much less than others. This partial avoidance of steep slopes—those in excess of twenty degrees—is probably due to a disinclination to climb up and down, even in flight. Just how steep a slope has to be before a grouse begins to shun it is not at all clear.

The other significant preference is for east and west slopes over flat (less than five degrees), south, and north slopes.

COVER TYPES CHOSEN AS AFFECTED BY WEATHER CONDITIONS

Every hunter of grouse knows that the birds will be found in different situations under varying weather conditions. It is natural that there should be differences in selection of cover with changes of temperature, sky conditions, wind, and possibly other elements. We ourselves seek the most protective abode in a storm, and are inclined to sun ourselves under clear, balmy skies. So why should not the grouse do likewise? And they do.

Effect of Temperature on Cover Used. Temperature is relative as it affects grouse behavior. Fifty degrees Fahrenheit in the summer would be cold, in the winter warm, and in spring or summer it would likely be about normal. Conceivably, it would be possible to record the temperature and precise measurements of other weather factors in the field as each grouse is flushed, but this is unnecessary. The temperature at the moment involved may be gauged as warm, normal, or cold, where normal means that it is within the

regularly anticipated range of temperature for the time of year, and the others indicate an abnormal extreme in one direction or the other. Analyzed on this basis we are able to discuss numerous effects of temperature on selection of cover by adult grouse, but it should be made clear here that temperature is less important as the determining element of the weather than either sky condition or wind.

During the fall and winter, especially in the winter, there are more shifts from the normal in cover type use as a result of temperature extremes than at any other season. Most significant are a high-use rate of overgrown land in warm weather and an avoidance of slashings, and an increased use of hardwood woodland and coniferous woods in cold weather. The increase in use of hardwood stands on cold days is mainly in the autumn, that of conifers in the winter. Also important are the complementary effects—an avoidance of brushland in cold weather, and of hardwoods and conifer woods in warm days.

In the spring, the tendency to deviate from average habits under extremes of temperatures is less pronounced than in the winter. Particularly significant at this season, however, is the marked avoidance of hardwood stands on cold days, and of coniferous woods when it is warm. Peculiarly enough, mixed woodlands are selected more than normal under both extremes, hot days and cold. Hardwood stands are used intensively in warm weather too, while slashings seem to attract most in cold weather, and less than normal in warm weather.

During the summer, deviations from average are less than at other seasons. Most important is a clear trend to the use of coniferous cover on hot days (the opposite trend is true in winter), and a corresponding avoidance of hardwood stands. Of some significance is the greater-than-average use of slashings in warm weather and of mixed woods when it is cold.

Thus, the other things being equal, the selection of cover type is considerably affected by temperatures. But it may be repeated that temperature is less important as a determining element than wind and sky conditions.

Relation of Sky Condition to Cover Used. The condition of the sky plays a very important part in determining what cover a grouse will

utilize. While there are endless variations that might be analyzed in relation to grouse habits, the major sky conditions are predominantly sunny, cloudy, rainy, and snowing.

Except for the spring, there are many marked variations in cover-type use according to atmospheric condition. In spring, the problems of courtship, mating, and incubation probably have a leavening effect on quick shifts in cover types used.

During fall and winter, the most notable deviation from average on sunny days is a marked increase in use of slashings and a decrease in use of coniferous cover. There is no significant shift from normal during cloudy weather at these seasons, but precipitation brings the most marked changes of all. In the autumn, rain brings a strong shift to overgrown land and slashings while the heavier woodland types are all used less, though the decreases are distributed evenly. In winter, sunny skies bring a very different shift, an immense increase in use of coniferous cover, and reduction below average in all other types. Thus there are many extremes in cover selection at these seasons according to the sky, more than at any other season. Generally the trend is to the more protected areas in stormy weather and to the more exposed (and food-producing) coverts in mild weather.

Spring is a season of more stable cover type use habits. The one really significant deviation from the norm is the great shift to coniferous cover during snowstorms, and a corresponding reduction in all other types. The only appreciable deviation in sunny weather is a shift in use of heavy cover from conifers to mixed woods. Under cloudy skies there is an increase in use of overgrown land and conifers and a decrease in use of mixed woods. In the rain there is a general reduction in use of all types from overgrown land to mixed woods in favor of coniferous cover.

During the summer the greatest deviations occur during rainstorms, and these are very pronounced; a great increase in use of mixed woodland (the heaviest protection of coniferous woods is apparently unnecessary at this season), and a large decrease in use of overgrown land and hardwood woods. There is also a notable shift to mixed woods and overgrown land in cloudy weather and a reduction in use of slashing cover, and evergreen woods. On sunny days the deviations are not so pronounced.

At all times of the year there is a generally increased rise in the

use of heavy shelter types in stormy weather and a greater use of the more open types in clear weather.

Cover Type Use as Affected by Wind. The strength of wind, without respect to direction, may be noted as either still, moderate, or strong. When the air is entirely quiet or with just an appreciable movement, it is called still; when gusty or an average light blow, it receives the designation of moderate; when the wind rises to stormy strength, probably exceeding twenty miles per hour, it is strong. The evidence shows clearly that a strong wind, as compared to a lack of wind, produces very significant differences in predominance of cover types selected. While it is not possible fully to separate the relative effects of the different elements of the weather, all acting at once as they do, it is probable that wind is nearly as important as sky condition in determining grouse use of cover types. Surely it is a more prominent factor than temperature at its extremes.

More than that of any other factor, the effect of wind is consistent throughout the year. Strong winds bring an increased use of overgrown land (particularly popple stands) at all seasons and of coniferous woods from fall through spring, and lessened utilization of mixed woodland at all seasons and other types at some seasons. In still weather, especially in summer, the most notable shift is to hardwoods.

In analyzing the effect of weather on cover type selection, we have separated the three most effective weather elements and considered them separately. This simplified the analysis but actually, of course, the weather factors all occur together, and hence we should consider what cover is used when the several factors occur in the various combinations. To do this would require long and relatively unproductive analysis. We have noted that sky condition appears to be the more dominating element, wind following closely, and temperature trailing. However, it is also true that extremes, whether of one factor or another, tend to be the determining element. Thus, on a clear, quiet, and hot summer day, the temperature may determine the cover a bird will select; or on a very windy day, with cloudy skies and normal temperatures, the wind will be the guiding element. When extremes of similar direction occur together, as a snowy, windy, cold day, it makes little difference which elements dominate the consideration since all bring the same result.

RELATION OF COVER TO GROUSE MORTALITY BY PREDATORS

It is generally recognized that cover conditions affect predation. Other things being equal, quality of shelter and loss from predation are inversely proportioned—the better the cover, the lower the mortality from this cause. It would logically follow then that different cover types, since they vary in their shelter quality, would produce different predation rates. Possibly other aspects of cover too may affect predation mortality. Let us consider this problem from the point of view of the locations where grouse are found killed.

In the first place we must make a hazardous assumption: That the locations where grouse remains are found are the places where they were killed; or at least the occasions of difference will balance. However, that assumption is invalid. Since a large number of grouse kills are picked up in open fields, it is quite certain that the majority were carried here by the predators from the location of the kill in some other cover type. And from the habits of many of the predatory species, especially in the spring of the year, we know that it is a common habit to carry a kill some distance before consuming it, and there leaving the waste parts.

While we cannot depend too much on the locations where grouse remains are found as an indication of cover type vulnerability, there are some fairly dependable conclusions that can be drawn when supported by field observations. Probably the most important correlations are the relatively low vulnerability of the birds in coniferous woodland and overgrown land, in both cases a reflection of high protective character of the cover types.

Shelter as a Limiting Factor. We have seen that the ruffed grouse has a rather complicated shelter requirement to satisfy its needs at all seasons, under various conditions of climate and other physical conditions and for all of its activities. Yet at the same time we are impressed repeatedly with the remarkable adaptability of the bird to different conditions and to the changes that bring about new environments. With all its flexibility in meeting successfully a variety of conditions, it is still limited very definitely by the shelter factor of the environment. Shelter is probably the limiting factor in the long run throughout most of the Northeast.

We may better understand the importance of shelter if we consider the two extremes: no appreciable shelter available; and a cover composed of too-complete shelter. In the first instance we may consider a large area of open farmland devoid of woodland or brush. It may be of any type of fields—hay, pasture, or farm crops—they are all alike to the grouse in that they are almost completely devoid of shelter of the kind required by these birds. Of course, this type of range produces no grouse, can maintain no grouse, even though many grouse foods (herbaceous ones) might be present in quantity, and other needs may be present. Without shelter, grouse cannot inhabit an area. On the other extreme we have the situation where shelter cover is so dense and extensive that little of it can be utilized by grouse. Extensive areas of pure stands of some conifers at certain age periods are in this condition. The birds are able to use only the exterior margins and very rarely will penetrate more than three hundred feet into such an area (Edminster, 1935). Here again shelter has proved to be a limiting factor for grouse, limiting by virtue of excluding other needed components of the range.

Between these two extremes we have all manner of variations in shelter conditions and in the degree of limiting effect it has on grouse populations. If shelter is excellent on a piece of grouse range, food conditions may well be good also, in which case some other factor would limit the numbers of grouse, possibly the saturation point of four acres per bird. Generally this ideal state will not prevail and the quality, quantity, and arrangement of the shelter components of the range will play a considerable part in determining the level of grouse abundance.

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5

Food and Water

Types of Food Utilized. Within the limits of its physical ability the ruffed grouse may be said to be practically omnivorous in its food habits. Vegetable foods of nearly all types are taken: leaves, buds, twigs, fruits, seeds, flowers. Its animal foods are more restricted in type due to the size and structure of the bird; insects and other related invertebrates are about the only forms it can readily catch and handle. Within these limitations almost any kind of insect, spider, or similar type is accepted.

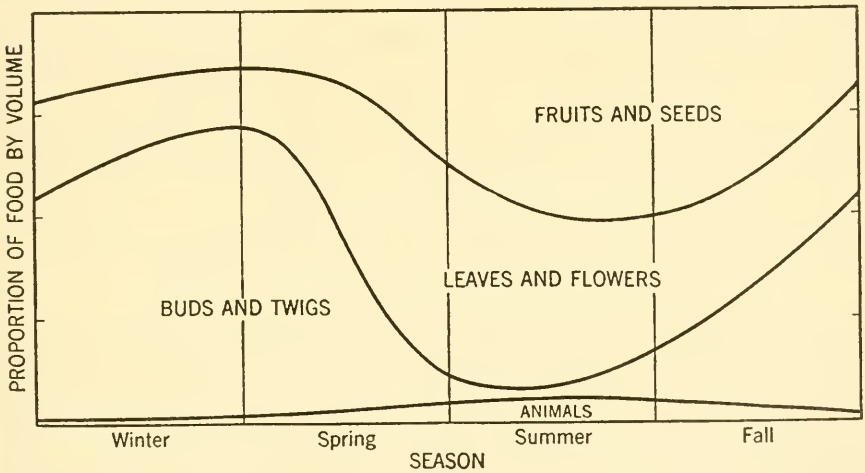


Fig. 6. Seasonal Utilization of Food by Adult Ruffed Grouse According to Type of Food (Northeastern States)

For purposes of simplification we may include all animal foods as one type, twigs and buds as another, flowers and leaves as the third, with seeds and fruits as the fourth. Thus arranged, the seasonal food habits of the adult grouse according to type of food are given graphically in Fig. 6.

This information applies to the northeastern states, from Virginia and West Virginia to Maine, and is of necessity somewhat idealized since records for all seasons for all parts of the region are not available in adequate quantity. Thus, the percentages at any exact time of the year for any specific area are not set forth as exactly correct. However, the diagram does indicate the trends in seasonal use of various types of food.

It is clear that animal food furnishes a significant proportion of the volume of adult food only during the summer. Leaves, including fern fronds, flower parts, and other vegetative parts except buds and twigs, are by a narrow margin the most staple type of food used throughout the year, increasing considerably in the spring and summer, but furnishing from fifteen per cent to forty-five per cent of the food at all times. Fruits and seeds furnish nearly as much, generally from fifteen per cent to fifty per cent, of the diet, with greatest use in summer and fall, while buds and twigs vary widely, from an almost negligible quantity in summer to nearly three quarters of all food in late winter.

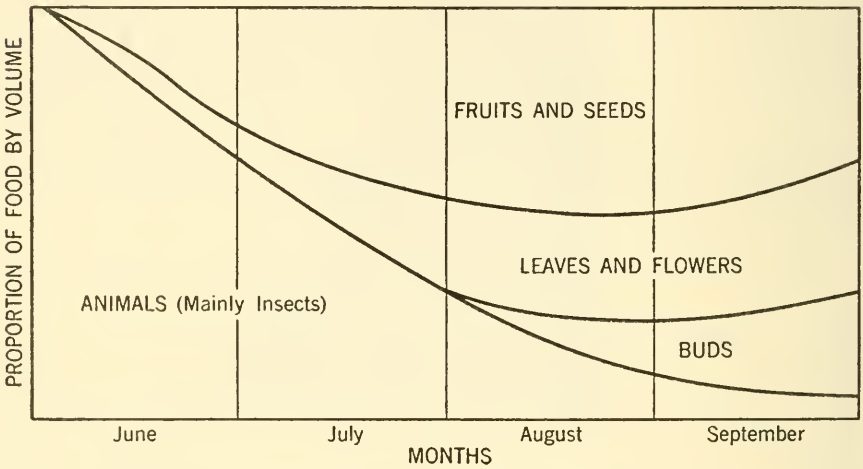


Fig. 7. Utilization of Food by Young Ruffed Grouse According to Types of Food (Northeastern States)

The types of food utilized by the immature grouse are widely at variance with the adult diet during the early summer but gradually change until by the end of the juvenile moult they agree with those taken by adults. These trends are illustrated in Fig. 7.

It will be noted that the chicks start off with a full insect diet, but soon add fruit to their fare. By the time they are a month old they are consuming green food and by midsummer insects make up less than half the diet. Toward the end of the summer, buds are added to the menu and the use of insects decreases rapidly. As with the case of the diagram of adult food types utilized by seasons, the trends in food habits of the young birds had to be interpolated freely in order to get a smooth trend. Except for occasional quick changes in food habits resulting from violent weather, or the sudden ripening of a certain fruit, trends through the months take place quite gradually and therefore properly appear in a graph as smooth curves.

Utilization of Food Species by Seasons. Compared with that of most wild creatures, the ruffed grouse's diet in the Northeast is well-known. The records given here and the conclusions drawn are based on around 4,000 stomach analyses of birds collected from Virginia and Ohio to Maine as well as upon many supplementary observations. However, because the majority of the specimens are obtained as a by-product of hunting, the records are largely from fall and early winter, and the late winter, spring, and summer material is relatively scant. The New York investigation made collections of adult birds throughout the year, except during the hunting season, in order to obtain the needed food habits information. Young birds as well as adults were collected through the summer. With a scattering of records from other sources, the year round food habits of the species are now pretty well established.

The diversity of foods taken by the grouse is indicated by the some 374 kinds of plants and 131 kinds of small animal life already known to be eaten by it in measurable quantities in the Northeast. And yet this list is without doubt far from complete. The author picked up a grouse (killed by a broken neck) in Sullivan County, Pennsylvania, in December, 1940 while deer hunting. Its crop contained several fruits of mountain holly (*Ilex montana*)—a species not previously recorded as eaten by grouse. But this normally rare plant happened to be common on this particular mountain, and the adaptable grouse appeared to be making good use of it.

The number of species of insects known to be taken by grouse is doubtless only a small fraction of those that the birds actually eat. Experiments conducted by the State Conservation Department at

Ithaca in 1936 with captive grouse chicks indicate they will take almost any kind of insect. The main limitation is their ability to locate the prey and then to capture it.

Even though grouse eat parts of plants of hundreds of species and in many cases two or more parts in different seasons, the bulk of their food at any one season comes from a relatively small number of species. The species that are predominantly represented in the food at any given time and place depend upon availability and the degree of preference by the grouse. There is wide variation between Virginia grouse food habits and those in New York, or between those in New York and those in Maine. But at the same time, insofar as staple food plants are available in each part of the range, they are consistently used.

The sources of food habits records given are mainly as follows:

Author	Year of Publication	No. of Analyses
Judd, Sylvester D.[1]	1905	208 adults, 18 chicks
Smyth, Thomas	1923 (unpublished thesis)	279 adults, 8 chicks
U. S. Biological Survey[1]	1933	111 adults
Kelso, Leon[1]	1935	80 adults
New York State Conservation Department's Annual Report[2]	1937	—
Gross, A. O.	1937	1055 adults
Hosley, Niel[1]	1938 (unpublished thesis)	925 adults
Nelson, A. L., Clarke, T. E., & Bailey, W. W.[1]	1938	185 adults
Van Dersal, W. R.	1938	—
Darrow, Robert W.[2]	1939	485 adults, 332 chicks
Kuhn, Tracy M.	1940	230 adults
Allen, A. A.	not published	321 adults
Kuhn, Tracy M.	1941	207 adults
MacGregor, Arthur E.	1941	102 adults (some chicks included)
Merritts, Helen V.	1943	112 adults
Gilfillan, M. C., & Bezdek, H.	1944	42 adults
	TOTAL	4300[1] adults, 358 chicks

[1] The records used in these studies overlap to a considerable extent; hence the totals of specimens used are not wholly original with each study after the first, and the grand total of analyses is larger than the actual number of birds involved.

[2] Darrow's records include all the specimens covered by the 1937 *N. Y. S. Cons. Dept. Ann. Rep.;* hence the number of specimens is omitted from the latter reference.

By seasons, the adult records were approximately: Fall—2,113; winter—392; spring—125; summer—85; fall and winter—1,318.

By area they were collected: Northeast (in general)—319; New England—1,818; New York—995; Pennsylvania—642; Virginia—205; Ohio—42.

The chicks were largely from New York.

WINTER FOODS

Insects are a negligible item of food during the winter months. The greatest proportion of winter food consists of buds and twigs, with fruits and mast taken as available, and a surprising amount of green leaves taken, considering the general difficulty in finding exposed ground vegetation. In the region from mid-Pennsylvania, northward, the buds of cherry, birch, apple, and popple are abundantly used, with those of hophornbeam vying with them in importance in New York. Fruits of dogwoods, apple, and grape are very important foods throughout the Northeast, while those of greenbriar, acorns, and laurel leaves are among the most important items of diet from Pennsylvania southward. Others indicated as of considerable importance by the leading food studies are the leaves of ferns, Canada mayflower, strawberry, sheep sorrel, and partridgeberry; fruits or seeds of sumac, rose, partridgeberry, hawthorn, and wintergreen; and buds of maple, blueberry, and blue beech. Beechnuts are used intensively when available but have not amounted to a primary item in any recent analysis (see under relation of food to cover types).

Taking the Northeast as a whole, the records show that from forty-seven to sixty-four per cent of the winter food normally comes from plants of twelve genera that average two per cent or more each in total volume of food taken.

The remainder is derived from plants of a large number of genera. In each individual study from ten to all twelve of these genera were recorded in significant quantities, and from six to nine were found to compose two per cent or more of the total food. These twelve genera and their contribution to the winter food are summarized in Table 3.

SPRING FOODS

Actual analyses of spring-collected grouse are confined to those made by the New York investigation and a scattering from the records of Smyth, Judd, and others. It is, therefore, necessary to interpret somewhat our knowledge of foods palatable and food available in order to present a broad summary of the birds' diet at this time of year for the whole Northeast. There is a gradual transition from staple bud and twig foods available all winter, regardless of snow,

Table 3

Primary Winter Foods of the Ruffed Grouse in the Northeast

Genus	Species Primarily Used	Area of Utilization in Northeast	Average Volume of Food	Maximum Volume of Food	Minimum Volume of Food
Populus (Popple)	*P. tremuloides* *P. grandidentata*	Pa. and northward	6.6%	14.0% [5]	0.0% [4]
Malus (Apple)	*M. malus*	Entire region, but little in South	6.2%	14.4% [1]	0.4% [4]
Smilax (Greenbriar)	*S. glauca* *S. rotundifolia*	Entire region, mainly in South	5.7%	16.3% [4]	1.0% app.[3]
Vitis (Wild grape)	*V. vulpina* *V. aestivalis* *V. labrusca* *V. cordifolia*	Entire region, but heaviest in South	5.0%	9.0% [4]	1.0% app.[3]
Betula (Birch)	*B. lutea* *B. lenta*	Entire region, but mainly North	4.8%	12.3% [3]	0.5% [2]
Quercus (Oak)	*Q. rubra; Q. alba* *Q. borealis* *Q. ilicifolia*	Entire region, mainly in South	4.8%	10.6% [4]	1.0% app.[3]
Prunus (Cherry)	*P. serotina* *P. pennsylvanicum* *P. virginiana*	Pa. and North	4.7%	9.8% [1]	0.0% [4]
Kalmia (Laurel)	*K. latifolia*	Entire region, but mainly from Pa. southward	4.4%	7.9% [4]	1.0% app.[3]
Ostrya (Hophornbeam)	*O. virginiana*	Entire region, but somewhat local	3.9%	14.7% [3]	0.0% [2]
Gaultheria (Wintergreen)	*G. procumbens*	Entire region	3.3%	6.1% [4]	0.5% app.[1]
Vaccinium (Blueberry)	*V. pennsylvanicum* *V. corymbosum*	Entire region	2.5%	4.2% [4]	1.0% app.[3]
Cornus (Dogwood)	*C. florida* *C. paniculata*	Entire region	2.5%	8.4% [5]	0.0% [1]

Reference numbers in last two columns: [1] BS—1297, 1933; [2] Smyth, 1923; [3] Kelso, 1935; [4] Nelson, et. al., 1938; [5] Gilfillan & Bezdek.

to a larger volume of succulent green-leaf food exposed by melting snow and newly sprouted with the advent of the new growing season. As spring merges into summer, buds practically disappear from the diet, fresh fruits become more important, and insects are taken to a significant extent. Flowers, particularly strawberry blossoms, are sometimes eaten in considerable quantity.

In point of volume, buds of poplar, birch, cherry, hophornbeam, and blueberry continue to furnish a large per cent of the food well into May. Leaves of ferns, grass-like plants (particularly *Carex*), strawberry, hawthorn, partridgeberry, sheep sorrel, wood sorrel, mountain laurel, Canada mayflower, and wintergreen are all of considerable importance. Owing to scarcity, relatively little fruit is eaten until the advent of summer brings on the strawberries. The fruits most commonly eaten during the spring are those of sumac (including poison ivy), rose, greenbriar, hawthorn, wintergreen, and partridgeberry.

SUMMER FOODS

The summer diet is composed mainly of fruits in season as they ripen, green leaves, and insects. For the adults the emphasis is on fruits, with green material a close second, and insects a poor third. For the chicks insects are predominant during June and part of July, with fruit second and leaves third. During the latter part of the summer the young gradually take the same proportions and types of foods as do the adults.

Outstanding among the fruits eaten by adults are strawberries, raspberries (including blackberries, dewberries, etc. of genus *Rubus*), cherries, sedges (seeds), and blueberries (see Plate 21). Most prominent of the plants providing green materials are poplar, touch-me-not, buttercup, apple, hawthorn, and partridgeberry. Fruits of Juneberry (*Amelanchier*) and some dogwoods are also eaten to a considerable extent in the summer, the former during the early part and the latter during August and September. Insects constitute from one per cent to three per cent of the total food. Orders of insects and related animals most commonly utilized by adult grouse in order are: *Hymenoptera* (mainly ants), *Coleoptera* (beetles), *Arachnida* (spiders), *Lepidoptera* (caterpillars), *Orthoptera* (largely grasshoppers), and *Opiliones* (harvestmen).

TABLE 4.

PRIMARY FALL FOODS OF THE RUFFED GROUSE IN THE NORTHEAST

Genus	*Species Primarily Used*	*Area of Utilization in Northeast*	*Average Vol. of Food*	*Maximum Vol. of Food*	*Minimum Vol. of Food*
Quercus (Oaks)	*Q. rubra, Q. borealis* *Q. alba, Q. ilicifolia*	Entire region, but less in N. Y.	7.1% [1] (10.3)	11.6% [1] (45.5–R.I.)	0.6%(2)
Crataegus (Hawthorn)	Various	Entire region, but mainly N. Y. and New England	7.0%	13.6%(2) [1] (6.5)	0.0 (1)
Prunus (Cherries)	*P. serotina, P. virginiana* *P. pennsylvanicum*	Entire region	5.7% [1] (4.5)	11.6%(1)	1.0%(2) [1] (0.9–Pa., R.I.)
Rumex (Sheep sorrel)	*R. acetosella*	Entire region, but less in New England	5.1%	11.5%(1)	0.9%(3)
Vitis (Grape)	*V. vulpina, V. labrusca* *V. aestivalis, V. bicolor*	Entire region	4.8% [1] (7.2)	5.7%(3) [1] (28.2–Conn.)	4.1%(1) [1] (0.0–Maine)
Malus (Apple)	*M. malus*	Entire region	4.5% [1] (4.5)	5.3% [1] (12.0–N.H.)	3.5%(2) [1] (0.0–R.I., Pa.)
Cornus (Dogwoods)	*C. canadensis, C. florida* *C. paniculata, C. amomum* *C. stolonifera*	Entire region	4.0% [1] (3.8)	5.2% [1] (10.1–Pa.)	2.0%(1) [1] (0.3–Vt.)
Populus (Popple)	*P. tremuloides* *P. grandidentata*	Entire region, less in south	3.9% [1] (3.6)	6.4% [1] (10.5–Vt.)	2.2%(2) [1] (0.0–R.I.)
Fagus (Beech)	*F. americana*	Mainly Pa. northward	3.0% [1] (3.0)	8.2% [1] (14.2–Pa.)	0.0 (1)
Betula (Birch)	*B. lutea, B. lenta*	Entire region, but less in South	2.8% [1] (4.0)	3.4%(1) [1] (10.0–N.Y.)	2.2%(3) [1] (0.3–Conn.)

Mitella (Miterwort)	*M. diphylla*	Entire region	2.5%	6.8%(2)	0.2%(1)
Smilax (Greenbriar)	*S. glauca* *S. rotundifolia*	Entire region, but mainly in South	2.4% [1] (1.5)	4.8%(1) [1] (6.3–R.I.)	0.3%(2) [1] (0.0–Maine)
Rhus (Sumac)	*R. copallina, R. glabra* *R. toxidodendron, R. typhina* *R. vernix*	Entire region	2.4% [1] (2.9)	2.8% [1] (6.4–Pa.)	1.7%(1) [1] (0.0–Vt.)
Tiarella (False miterwort)	*T. cordifolia*	Probably entire region, noted in quantity from N. Y. and Pa.	2.3%	4.7%(1)	0.0 (3)
Rubus (Raspberry, Blackberry)	*R. hispidus, R. villosus* *R. idaeus aculeatissimus* *R. allegheniensis*	Entire region	2.2% [1] (1.9)	4.1%(3) [1] (6.4–N.H.)	0.1%(2)

Reference numbers in last two columns: (1) Kuhn, 1940; (2) Smyth, 1923; (3) Gross, 1937.

[1] Records obtained by including Hosley's (1938) records separately by states, as well as other records. Hosley's summaries are tabulated only by separate states and include only woody plant records. Therefore, they were not used in obtaining the figures not marked with [1].

For the chicks, insects, spiders, etc. made up forty-six and eight-tenths per cent of the food in the Adirondacks, sixty-eight and three-tenths per cent in the Catskill part of New York and about sixty per cent over the rest of the state. In July the proportion of animal food in the diet has dropped to between ten and twenty per cent and in August it has further declined to from one and three-tenths per cent in the state outside the mountains to six and nine-tenths per cent in the Adirondacks. In records on eight stomachs, Smyth found sixty-six and nine-tenths per cent animal food in June, eleven per cent in July, ten per cent (one stomach) in August. Thus, the young birds change their food habits rapidly; from an almost one hundred per cent insect diet in the first week or two, they shift to only a small per cent of insect foods within three months. Other foods are similar to those of the adults.

Fruits eaten by the young birds are mainly the same as with the adults: raspberries, strawberries, Juneberries, and cherries. However, raspberries assume vastly more importance than with the adults, comprising over thirty per cent of the total summer food. Elderberries also are considerably used.

The young birds partake of a larger quantity of seeds in summer than do their parents. Seeds of maple, violet, jewelweed, and sedge are taken in considerable quantity, while leaves of sedge, buttercup, and sheep sorrel are staple foods.

Orders of insects used by the chicks in order of importance are: *Hymenoptera, Coleoptera, Lepidoptera, Opiliones, Hemiptera* (bugs), and *Diptera* (flies). Thus the insects and other invertebrates taken by the chicks come mainly from the same orders as with the adults and nearly in the same order of importance. With the chicks, the true bugs (*Hemiptera*) and flies (*Diptera*) were significant but not for the adults; for the adults grasshoppers (*Orthoptera*) and spiders (*Arachnida*) were taken in numbers but not by the chicks.

FALL FOODS

As summer gives way to autumn the quantities of fruits and green leaves in the diet gradually decrease, insects nearly disappear, and buds are taken in constantly increasing abundance. It is not until the arrival of winter, however, that buds become the dominant type of food. As long as fruits and tender leaves are available, they are pre-

ferred. Outstanding among the fall foods taken are acorns and haws. Fruits and buds of cherries, leaves of sheep sorrel, and wild grapes come next in general importance. From fifty-six to sixty-nine per cent of the total fall food normally is derived from plants of fifteen genera that each average two per cent or more of total fall food. These are summarized in Table 4.

While these fifteen genera of plants are listed in order of volume of food furnished by each, obtained by arithmetically averaging the records from the various studies of fall food habits, it is not safe to attach very much importance to the exact order. The relative volumes of food gleaned from plants of the various groups depends on availability as well as preference, and even in a given locality the availability of some species varies widely from year to year. Beechnuts are an excellent example—a primary and preferred fall food in a good crop year, but relatively unavailable during most years. It is also true that the averaging of the statistics from different studies is not a proper statistical procedure. However, if the order is not taken strictly, this procedure does seem to bring out the group of primary foods.

In certain areas, a food plant may be of great importance, and yet not be one of the fifteen groups listed above. For example, in the Adirondacks of northern New York wild raisin (*Viburnum*), wood ferns (*Thelypteris=Dryopteris*), violets (*Viola*), and Juneberries (*Amelanchier*) are among the ten most used fall foods—but all of these are not among the fifteen most important for the Northeast as a whole and do not average two per cent of the fall food over the Northeast.

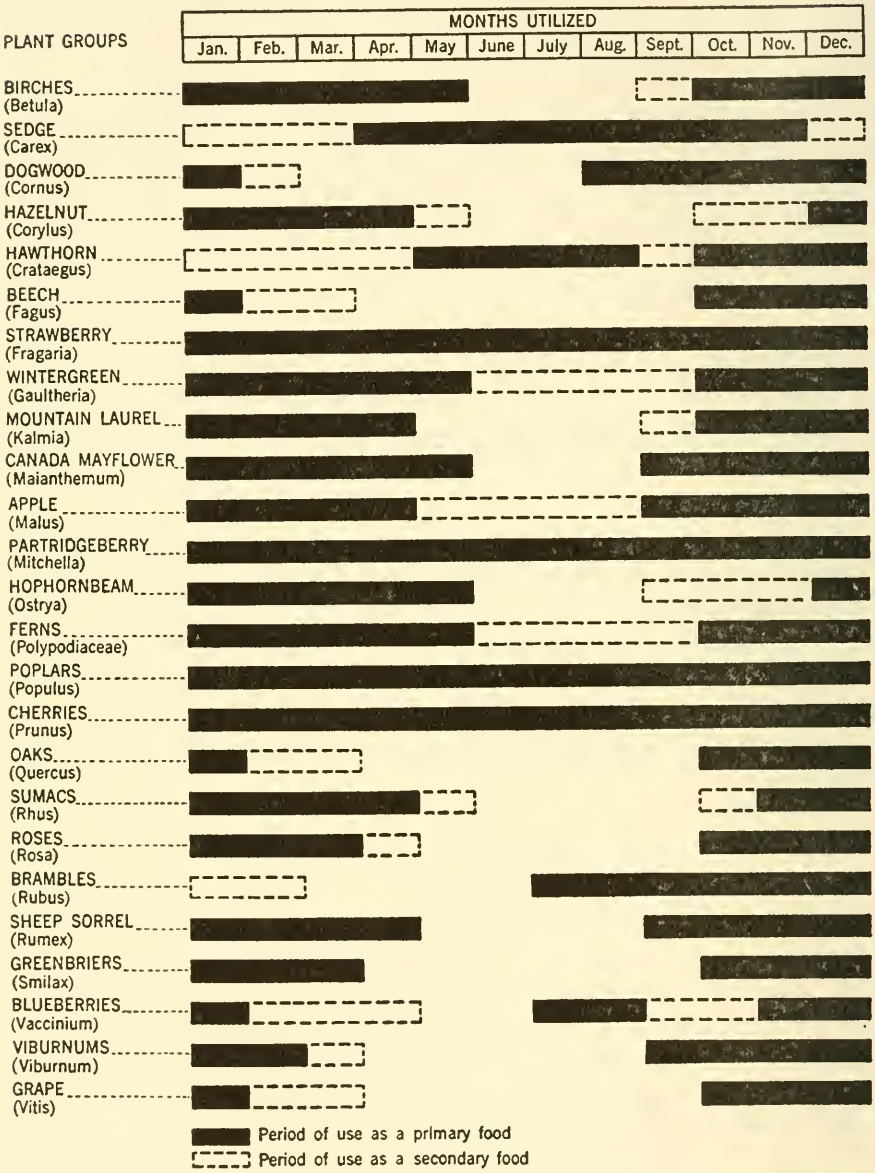
SUMMARY OF FOODS UTILIZED

Arbitrarily taking the twenty-five genera[1] of plants that furnish the most food to grouse in the Northeast year in and year out, we find that their contribution to the total food of the species is from sixty-five to eighty-eight per cent, varying with locality, year, and season. These we may consider to be the primary foods of the ruffed grouse in this region. No attempt is made at this point to say which of these twenty-five is first, second, third, etc.; there is too much

[1] One of the groups named is a family (*Polypodiaciae*), that of the ferns—an assemblage of genera, of which those most used are *Thelypteris* and *Polystichum*.

FIG. 8. TWENTY-FIVE MOST IMPORTANT FOOD PLANTS USED BY THE RUFFED GROUSE IN THE NORTHEAST

FROM 65% TO 88% OF THE FOOD OF THE ADULT GROUSE AT ANY TIME OF THE YEAR WILL USUALLY COME FROM THIS GROUP



variation in different areas to make such a ranking of much value. However, it is apparent that some are of greater utility than others.

The question of palatability is discussed later. Suffice it here to say that if adequate quantities of these twenty-five groups are readily available, the food situation on a grouse range is not likely to be a limiting factor. Figure 8 shows the months during which these foods are of primary importance (solid bar) and of secondary importance (dashed bar).

THE TWENTY-FIVE PRIMARY GROUSE FOODS IN THE NORTHEAST

The Birches (*Betula*)

Species utilized: yellow birch (*B. lutea*), black or sweet birch (*B. lenta*), paper birch (*B. papyrifera*), gray birch (*B. populifolia*), river birch (*B. nigra*), listed in approximate order of importance (see Plate 20C).

Seasonal importance: most important as a winter and early-spring food, reaching the height of utilization in February and March; taken in increasing quantities from late September on to the mid-winter peak, and in rapidly decreasing quantities after midspring.

Parts used: Almost entirely leaf buds; slight use of catkins and seeds.

Geographical importance: Northern New England, New York and Pennsylvania constitute the region of greatest use of birch. The range south of Pennsylvania and in southern New England provides little of the three more valuable birch species and reflects this deficiency in low utilization records. The gray birch, most prevalent in southern New England, is relatively unimportant as a source of grouse food.

The birches, particularly yellow, black, and paper, are one of the groups of trees and shrubs which through their readily available and palatable buds enable the grouse to survive the rigors of winter in the northern portions of its range without difficulty. Utilization within the genus is partly determined by availability, partly by selectivity. Yellow and black birches, and to a slightly lesser degree paper birch, are highly palatable. Their use by grouse is mainly determined by their abundance and distribution. Gray birch, and probably river

birch, are less palatable; the latter is not well distributed in good grouse range, and both are relatively of little importance.

The yellow, black, and paper birches are long-lived species. All three are found abundantly in the climax or subclimax types of woodland and forest, mainly in the Appalachian and St. Lawrence plant-growth regions of the Northeast.[1]

Paper birch finds its optimum conditions in the more northern St. Lawrence zone in association with the spruce-fir type, while black birch is more prevalent in the Appalachian area, particularly its northern portion. Yellow birch is an important species in the northern hardwoods type of the St. Lawrence region, and in the beech-birch-maple-hemlock type of the Appalachian area. These three birches practically never appear in pure stands, although paper birch sometimes constitutes a high percentage of the crown species mixture. They are all found in mixtures of both hardwoods and conifers. Gray birch is a temporary, short-lived species that pioneers on old field areas.

Paper birch seeds in abundantly following burns and is moisture loving but does not thrive in swamps. The yellow and black birches seed in readily in the understory of rich, well-drained, upland woodlands but do not tolerate swampy soils so well.

The birches are also used as food by the white-tailed deer, cottontail rabbit, beaver, moose, and snowshoe hare. Since these mammals all feed from the ground, the grouse receives no significant competition from them for the tree buds.

Chemical Composition:[2] Yellow birch—fresh buds: water—45.0 per cent; protein—5.2 per cent; fat—2.4 per cent; nitrogen-free extract—25.5 per cent; fiber—20.4 per cent; ash—1.5 per cent (Hosley, 1938).

Sedges (*Carex* spp.)

Species utilized: Many, including the following seven that have been specifically identified: *C. crinita; C. flexuosa; C. gracillima; C. intumescens; C. lupulina; C. plantaginia; C. tenella.* There is in-

[1] Van Dersal, 1938, gives a map of the plant growth regions.

[2] The significance of these analyses, given when available, presumably lies in showing nutritive values. Since little is known of the specific nutrition of the grouse, no attempt is made here to interpret the figures.

sufficient information concerning the use of the different species to warrant any comparisons of degree of use. Parts of these plants are usually identified only to genus.

Seasonal importance: Most important as a summer and fall food, reaching greatest use in summer by both adults and chicks. Utilization begins with the growth of the new leaves in the spring and continues until seeds are gone and leaves dried up in the fall.

Parts used: Seeds and leaves; leaves from spring through fall, seeds in summer and fall.

Geographical importance: Since the seeds and leaves of sedges are only important from spring to early fall, it is not surprising to find only small quantities recorded in the majority of food studies—those made of fall and winter specimens. However, records are available from Canada to Virginia, even in late fall stomachs. It seems likely that *Carex* is an important spring and summer food throughout the region as it is in New York, especially for the young birds.

Of more than two hundred recognized species of *Carex,* representations of only seven have been specifically identified, five in New England by Gross, one in New York by Smyth, and one by Judd. However, it is likely that many species are taken by grouse and that use is primarily dependent on size of seed, distribution, and abundance. Sedges are low-growing, perennial, grass-like herbaceous plants (see Plate 20B) found mainly in old fields, along woods edges, in marshes and clearings. Some species are found in open woodlands, still others in thickets. Many are particularly adapted to wet soils although some will grow in very dry situations.

The Dogwoods (*Cornus* spp.)

Species utilized: Flowering dogwood (*C. florida*); gray dogwood (*C. paniculata*); bunchberry (*C. canadensis*); red osier (*C. stolonifera*); roundleaf dogwood (*C. circinnata*); silky cornel (*C. amomum*); roughleaf cornel (*C. asperifolia*); blue cornel (*C. alternifolia*); in approximate order of importance.

Seasonal importance: Fruits of some species of dogwoods begin to ripen in midsummer and are taken by both adult and young grouse. Most species are primarily fall food producers but flowering dogwood fruits are also important as a winter food.

Parts used: Mainly the fruits although buds are taken to a slight degree.

Geographical importance: Dogwoods are an important fall grouse food throughout the region. *C. canadensis* is primarily important in the northern portions of New England and New York, *C. paniculata* from Pennsylvania northward. *C. florida* is important both in fall and winter from southern New England to Pennsylvania and Ohio southward. The Virginia dogwood records of Nelson et al. (1938), even if entirely *C. florida,* are low in volume although considerable in rate of incidence. However, many of Smyth's winter records were from Virginia and showed a high incidence of flowering dogwood, which indicates that the species is used where available. Gilfillan and Bezdek (1944) found flowering dogwood fruits favored highly in Ohio.

The dogwoods vary widely in type of plant and in their position in the habitat. Bunchberry is a small, almost herbaceous plant found in the ground cover of northern woodlands, usually in association with hemlock or spruce. Silky cornel and red osier (see Plate 23D) are medium-sized shrubs usually found on open streambanks or in damp swales. Gray dogwood, roundleaved dogwood and roughleaf cornel are medium-sized shrubs usually located in dry or well-drained thickets in old fields or along woodland borders. Flowering dogwood (see Plate 23C) and blue cornel are large shrubs or small trees found in the woodland understory, mainly along the edges.

The fruits of the dogwoods are eaten by many other birds including the quail, ring-necked pheasant, wild turkey, and numerous song birds, and by Virginia deer, gray fox, beaver, cottontail rabbit, eastern chipmunk, and gray squirrel. Since the available dogwood fruits are to a considerable extent exhausted each season, these animals compete with the grouse for this food. This competition may cause the grouse to shift to a greater proportion of less palatable foods, but is rarely an important factor in maintaining grouse numbers.

Chemical composition: Gray dogwood fruit: water—3.6 per cent; protein—10.1 per cent; fat—18.8 per cent; nitrogen-free extract—30.0 per cent; fiber—34.8 per cent; ash—2.8 per cent (Hosley, 1938).

Hazelnuts (*Corylus* spp.)

Species utilized: American hazelnut (*C. americana*), beaked hazelnut (*C. rostrata*), the former probably constituting the bulk of food produced by this genus in most areas. Selection between species is probably determined by availability.

Seasonal importance: Twigs and buds are taken mainly in winter and early spring, somewhat in late fall; the nuts are taken mostly in the fall.

Parts used: Twigs and leaf buds, mainly nuts, and catkins to some extent.

Geographical importance: Both species of hazelnut are used throughout the northeastern region apparently with no marked choice.

The hazelnuts are medium-height shrubs found in dry or well-drained thickets along woodland edges and in old fields. The nuts are eaten by many species of mammals, particularly gray squirrels, and by several of the larger birds. The browse is also eaten by deer. Competition for this food is of little importance to the grouse.

The Hawthorns (*Crataegus* spp.)

Species utilized: The species of *Crataegus*, of which over fifty are recognized in northeastern United States, are difficult to identify. So it is not surprising to find that the fruits and seeds in crops and stomachs of grouse are determined only to genus. Two species, *C. coccinea* (Judd, 1905), and *C. crus-galli* (Judd, 1905; Hosley, 1938) definitely have been recorded as used. It is probable that most species are taken as available. Those that hold their fruit on the branches well into the winter, and those whose fruit remains plump and firm on the ground until spring, are probably most useful. *C. crus-galli*, which occurs throughout the East, is one of the most widely distributed natives of the Northeast that holds its fruit well. *C. phaenopyrum* in Virginia, *C. canbyi* in Maryland and southern Pennsylvania, and *C. arnoldiana* in Massachusetts and Connecticut are of more limited range. There are others, introduced as well as native, that also are useful in winter and spring.

Seasonal importance: The fruits are primarily important in fall

and early winter, and to a lesser extent, as available, throughout the winter and early spring. The leaves are a staple food in the late spring and throughout the summer.

Parts used: Fruit and leaves, both very important.

Geographical importance: An important food in New York and New England, except possibly along the southern New England coast; of secondary importance from Pennsylvania southwards.

The hawthorns are tall shrubs found on old fields, along woodland borders, and in poor pastures, where they are often weeds. They are valuable as ornamentals for their flowers and fruits, but many species are subject to fungus diseases. The fruits are eaten by many species besides the grouse, including the bobwhite, ring-necked pheasant, at least thirty-six other species of birds, the gray fox, white-tailed deer, and cottontail. Their competition for this food, however, is unimportant to the ruffed grouse.

Chemical analysis: (Fresh fruit): water—75.8 per cent; protein—2.0 per cent; fat—0.6 per cent; nitrogen-free extract—20.8 per cent; fiber—2.1 per cent; ash—0.8 per cent (Hosley, 1938).

Beech (*Fagus grandifolia*)

Seasonal importance: Important only as a fall and early winter food but probably one of the most highly selected of all preferred foods of the grouse (see Fig. 28). Its importance, however, is weakened by its irregular availability. It also appears to be considerably less important in recent years than formerly due to the changed character of the beech composition of many farm woodlands (see "Effects on Food of Cultural Operations—Lumbering"). These points are well illustrated by Kuhn's (1940) records of grouse stomach contents from Bradford County, Pa., the first week of November, 1911, the first week of December, 1919, and November 2–9, 1938. The volume of beech nuts in the food was fifty and nine-tenths per cent, seventy-two per cent, and zero, respectively, for these years. There was a complete failure of the beechnut crop in 1938. The trend toward elimination of the "worthless" old beech "wolf" trees in woodlands has the effect of eliminating the only mast-producing trees of the species. Nevertheless, the beech remains a very important source of grouse food. Birds that have been feeding extensively on beechnuts have a superior flesh flavor.

Parts used: Nuts, and to a negligible extent buds and leaves.

Geographical importance: Ohio, Pennsylvania, New York, and Northern New England, in areas where the beech-birch-maple-hemlock woodland type is prevalent is the area of importance for beech.

The beech is a large tree of the northern-hardwoods association found mainly on slightly acid, loam soils in well-drained situations. Its tree associations are mainly maples, birches, hophornbeams, black cherry, hemlock, and white pine. It grows slowly, reaches a very old age and sprouts profusely after cutting. It is considered by many to be a forest weed because its wood is not as valuable as that of leading timber species.

The triangular nut is borne in a prickly bur. Trees do not ordinarily fruit until they are from forty to fifty years old and then very irregularly. It is eaten by at least fourteen species of birds in addition to the ruffed grouse, including the bobwhite, wild turkey, and ring-necked pheasant. It is also taken by many mammals, among them all the squirrels, foxes, raccoon, opossum, white-tailed deer, black bear, porcupine, and cottontail.

Chemical analysis: (entire nut: water—2.3 per cent; protein—13.0 per cent; fat—34.0 per cent; nitrogen-free extract—7.8 per cent; fiber—40.8 per cent; ash—2.1 per cent; calories per pound—1820 (Hosley, 1938).

Wild Strawberries (*Fragaria* spp.)

Species utilized: There are two species of wild strawberries in the Northeast, both of them common. Stomach analysis reports give all strawberry as *Fragaria* sp. No doubt both *F. virginiana,* and *F. vesca* var. *americana* are utilized although only the former has been identified.

Seasonal importance: The fruit is a major summer food of both adults and chicks. The leaves are eaten throughout the year, often constituting a significant item at any season for young and old. They are most important in summer, secondly, in winter.

Parts used: Fruit, leaves, and flowers.

Geographical importance: From the records there is some indication that the strawberry is less important in New England than in New York and Pennsylvania. This is probably not actually true,

since the New England grouse specimens were almost all taken in the fall when the prevalence of many fruits makes strawberry temporarily less important. The small quantity of strawberry leaves taken in Virginia in early winter, even though the incidence is fairly high, indicates that it may not be a highly important winter food there. It is probably more important in summer. We are quite safe in saying, however, that *Fragaria* is important throughout the region in summer, and from Pennsylvania northward throughout the year.

The strawberries are low trailing herbaceous plants found in old fields and in the ground cover of open woodlands. They flower in May, fruit in June and July, and the leaves remain somewhat succulent throughout the winter. Numerous birds and mammals partake of the ripe fruit but offer no serious competition to the grouse, since the abundance of the fruit at the season of ripeness almost always exceeds the demands upon it.

Wintergreen (*Gaultheria procumbens*)

Seasonal importance: The wintergreen, or checkerberry, is a food consistently used throughout the year but which assumes significant volume only from fall to spring. It is not generally taken in very large quantities, but the regularity of use enhances its importance. In spite of its relative unavailability under the winter snows, it is most important as a winter and early spring food.

Parts used: Leaves, fruit.

Geographical importance: An important fall to winter food throughout the Northeast, possibly used somewhat more in the South due to greater availability through the winter.

The wintergreen is a low, evergreen plant of the woodland floor, with creeping stems that are somewhat woody. It fruits only when sunlight is available through openings in the crown. The fruit is eaten by the ring-necked pheasant, bobwhite, and chipmunks, and the browse by white-tailed deer.

Chemical composition: (dried leaves) water—6.9 per cent; protein—6.0 per cent; fat—6.1 per cent; nitrogen-free extract—60.1 per cent; fiber—16.5 per cent; ash—4.4 per cent (Hosley, 1938).

Laurel (*Kalmia* spp.)

Species utilized: Mountain laurel (*K. latifolia*), and narrow-leaved or sheep laurel (*K. angustifolia*); the former is more important by far from southern New York and south, the latter is more important, if only a secondary food, in New England.

Seasonal importance: Eaten during fall, winter and early spring, by far most important during the winter when green leaves of most plants are lacking.

Parts used: Leaves primarily, buds and flower capsules to some extent.

Geographical importance: Mountain laurel is an important winter food from the Catskills of southeastern New York southward, increasing in importance to the south. In Virginia it was found in nearly half the late fall and early winter stomachs and amounted to almost eight per cent of the volume of food. It probably increases in importance later in the winter. The narrow-leaved, or sheep laurel, is used from New York through New England but apparently is not ordinarily taken in significant amounts.

The laurels are low-to-medium evergreen shrubs found in acid soils in the woodland understory and along woods margins. The leathery leaves are poisonous to domestic livestock but apparently have no ill effects on grouse or on deer if not taken to the exclusion of other foods (Van Dersal, 1938).

Canada Mayflower (*Maianthemum canadense*)

Seasonal importance: Fall, winter and spring, with somewhat greater volume taken in winter even though less available at that time.

Parts used: Fruits.

Geographical importance: From the stomach records it appears that *Maianthemum* is used only in New York and New England, although the plant ranges much farther south. The fact that Pennsylvania and Virginia records taken during the season when the plant is readily eaten farther north fail to show any trace of it substantiates this conclusion.

Canada mayflower (also called two-leaved false Solomon's seal,

and false lily of the valley) is a low herb of the woodland floor, frequently associated with conifers (see Plate 20D).

Wild Apple (*Malus pumila*)

Species utilized: The records identify apple only to genus, but the common wild apple (*M. pumila*) unquestionably supplies most of the apple food taken. Cultivated apple is also eaten, as is evidenced by the damage done to apple orchards in New England, and the native crabs are probably utilized too although there are no specific records to prove this.

Seasonal importance: Primarily a fall, winter, and early spring food, although taken somewhat throughout the year. Fruit is of some importance from late summer to winter; the buds are taken all winter and the blossoms and leaves when available.

Parts used: Leaf buds and twigs, fruit pulp, seeds, leaves, and blossoms, in order of importance (see Plate 20C).

Geographic importance: An important food from fall to spring from Maine to Pennsylvania, with greatest use in New England. The New York records show some inconsistencies. Darrow found it among the first ten important foods in only two seasons (one of them summer), and only in the Adirondack region of the state. The 1937 New York report failed to list it at all among the first ten for any season, and Kelso's records show a sharp break in January that is not logical, perhaps due to deficiencies in the material examined. In Pennsylvania and Southern New England apple appears to be somewhat less important while the species is little represented in the Virginia records.

An interesting sidelight on the use of apple by grouse is the occasional damage to cultivated orchards from budding by grouse. This reached such serious proportions in parts of New England that bounties were declared and damage claims paid. In the middle of the nineteenth century certain Massachusetts townships paid a price of twenty-five cents a head for "partridge." With the declining importance of the apple industry, the bounties were abandoned but damage has not entirely ceased. In 1924 New Hampshire paid out nearly a quarter of the income from sportsmen's licenses (about $25,000) on valid grouse damage claims (Bartlett, 1924), and as recently as the mid-thirties, Massachusetts has paid orchard dam-

age claims on account of grouse. New Hampshire continues this practice today, paying thirteen claims totaling $338.44 in 1940. Highest annual payment was in 1926—$26,000. In the 1930–40 period, the highest was $3488.07 on seventy-five claims in 1935; the lowest was $12.57 in 1938.

The wild apples are small-to-medium-sized trees, rather short-lived and very light demanding. They grow best on fertile soils but often seed in on abandoned fields with acid and worn out soils. They are subject to damage by numerous insect and fungus pests.

The browse and fruit of the apple are among the most important wild-life foods in the Northeast. Hosley (1938) says "If all the animals using the apple were known it would probably rank as the most universal wild-life food of the northeast." In addition to the grouse, it is a staple food of the white-tailed deer, raccoon, red fox, and skunk; is also eaten by the bobwhite, ring-necked pheasant, many song birds, opossum, woodchuck, gray fox, red squirrel, snowshoe hare, and cottontail. In spite of this competition for the fruit and foliage of the apple, the buds that are most important to the grouse are relatively secure.

Chemical composition: (fruit) water—63.3 per cent; protein—.3 per cent; fat—.3 per cent; nitrogen-free extracts—10.8 per cent; fiber—25.0 per cent; ash—.3 per cent; calories per pound—220 (Hosley, 1938).

Partridgeberry (*Mitchella repens*)

Seasonal importance: Eaten rather consistently in a small way throughout the year, the fruit from fall until spring, the leaves at all times.

Parts eaten: Fruit and leaves.

Geographical importance: *Mitchella* is used about evenly throughout the northeastern range.

A small, evergreen, trailing, herblike shrub, partridgeberry (see Plate 21C) is found in the ground cover of dry woodlands, often associated with conifers. The fruits are eaten by several other species of birds besides the grouse including the bobwhite and by the red fox. Their competition is of no significance to the grouse.

Chemical composition (dry leaves and stems): water—4.8 per cent; protein—7.3 per cent; fat—2.2 per cent; nitrogen-free extract

–64.4 per cent; fiber–14.5 per cent; ash–6.9 per cent (Hosley, 1938).

Hophornbeam (*Ostrya virginiana*)

Seasonal importance: Winter and early spring; eaten to a lesser extent in the fall, most important as a winter food (see Plate 20C).

Parts used: Leaf buds, and, to a small degree, seeds (nutlets) in the fall.

Geographic importance: Hophornbeam is primarily important in New York and Pennsylvania. It is apparently of slight importance in New England and negligible south of Pennsylvania.

A small slow-growing tree of the northern-hardwoods and beech-maple associations, it is found in the woodland understory on most upland soils. The nutlets are eaten by ring-necked pheasant and bobwhite quail as well as by grouse, and the browse is taken by the white-tailed deer and cottontail rabbit. The competition is of no significance to the ruffed grouse.

Ferns (*Polypodiaciae*)

Species utilized: For convenience, and because the food records often show identity only to family, all genera of the fern family are lumped together. Most important is that of the shieldferns (*Thelypteris*), which would rank in the first twenty-five food-producing genera by itself. Spiny-toothed shield fern (*T. spinulosum*, including var. *intermedium*) is probably used most, but marginal shield fern (*T. marginalis*) too is regularly eaten. Probably other species also are used. Christmas fern (*Polystichum acrostichoides*) and polypody fern (*Polypodium vulgare*) rank next in importance. Several other species are known to be utilized, including sensitive fern (*Onoclea sensibilis*) and royal fern (*Osmunda regalis*), some being locally important. The grape ferns (*Botrychium obliquum*, *B. dissectum*, and possibly others), while not in the family *Polypodiaciae*, are closely related plants that are eaten to some extent.

Seasonal importance: Ferns are eaten throughout the year and are a staple food in all seasons except summer. While the spring records are inadequate for complete analysis over the whole region, it

is probable that ferns are of greatest use at this season. In the New York state-wide average (*N.Y.S. Cons. Dept. Ann. Rep. 1937*) ferns appear in the first ten only in the spring. Their importance in winter is substantiated by abundant data. The relative inaccessibility of the plants at this season in the northern states adds even greater weight to the evidence of their importance. In autumn ferns are taken in significant amount but in lesser quantity than from December to May.

Parts used: Fronds.

Geographical importance: The ferns are an important food throughout the Northeast. There is evidence that shield ferns (*Thelypteris*) (see Plate 20A) are of greatest value in the northern range, and that Christmas fern (*Polystichum*) is more important in Virginia, and rattlesnake fern (*Botrychium*) in Ohio. This differentiation is probably the result of local variation in abundance.

Christmas fern is found in the ground cover of dry woodlands while the shield ferns are adapted to the floor of damp woods. Both are most prevalent on the banks of ravines.

Popples, or Poplar (*Populus* spp.)

Species utilized: Quaking aspen (*P. tremuloides*), large-toothed aspen (*P. grandidentata*), and balsam poplar (*P. balsamifera*) are eaten, the first two as staple foods, the third usually incidentally.

Seasonal importance: An important food all year round, used most intensively in the spring (buds and catkins). The buds are also one of the most important foods all through the winter. During the spring and summer the catkins and leaves are eaten by adult grouse, while in the fall the birds gradually take to the buds again.

Parts used: Leaf buds, flower buds, catkins, and leaves, the buds being by far the most important (see Plate 20C).

Geographical importance: From Pennsylvania and Ohio northward for *P. tremuloides* and *P. grandidentata*. The range of *P. balsamifera* restricts its use to New England, northern New York, and northward.

The popples are short-lived, small-to-medium-sized trees that establish themselves quickly on old fields and burns when seeding conditions are right. In climax or subclimax stands they are restricted largely to the forest edges.

Popples are cut by beavers as one of their most important foods. Locally this competition may well affect the grouse. These trees are also browsed by the white-tailed deer and snowshoe hare but without significant competition for the grouse.

Chemical analysis—*P. grandidentata,* fresh buds: water—49.8 per cent; protein—6.4 per cent; fat—5.1 per cent; nitrogen-free extract—24.1 per cent; fiber—13.3 per cent; ash—1.4 per cent (Hosley, 1938).

Cherries (*Prunus* spp.)

Species utilized: Black cherry (*P. serotina*), pin cherry (*P. pennsylvanicum*), chokecherry (*P. virginiana*), all these three provide staple foods in approximately that order of importance and furnish most of the subsistence derived from plants of the genus. However, wild plums (*P. americana*), sweet cherry (*P. avium*), plum (*P. domestica* var.), and peach (*P. persica* var.) also contribute more or less to the diet of the grouse.

Seasonal importance: The cherries furnish an important part of the food supply throughout the year. Both adults and young consume the fruit during summer, fall, and into the winter, as long as available. Buds are taken in fall, winter and spring. The cherry genus probably assumes greatest importance as a food resource in winter, increasing steadily from December to March, but ranks high also in early spring, summer, and fall. Use is less in late spring than at other times.

Parts used: Fruit, buds (see Plate 20C) and twigs, and leaves.

Geographical importance: The cherries are among the most important grouse food producers from Pennsylvania northward. From Nelson's report they seem to be of little value in Virginia; however, this finding from a limited area and period may not hold in general.

Black cherry (see Plate 26A) is a large tree of the Appalachian highlands, reaching its best growth in the hemlock-hardwoods type. To the north and south of its optimum range it is usually found considerably dwarfed. The fruit ripens in August and September and is taken from tree or ground throughout the fall and into the winter.

Pin cherry (see Plate 26B) is a small, short-lived tree, most commonly associated with recent burns. It is often found in nearly pure stands in burns or old fields, but is ultimately entirely displaced by

subclimax and climax species. The fruit ripens from July to September and is eaten until early winter from tree and ground.

Chokecherry (see Plate 22C) is a large shrub or small tree found abundantly in hedge-rows and along woodland borders. As with the other two species above, it is widely adaptable to a variety of soils. The fruit ripens in late summer and is eaten through the fall and into the winter.

All of these cherries provide food also for the bobwhite, ring-necked pheasant, numerous song birds, and the cottontail. Black cherry is also a food plant of the white-tailed deer, red fox, raccoon, squirrels, and black bear; pin cherry for the white-tailed deer, chipmunk, and beaver; and chokecherry for the black bear. As far as the fruit is concerned, this competition may sometimes affect grouse food habits locally, but not seriously. Competition for leaves and buds is of no importance, except in spots where beavers may destroy small stands of pin cherry.

Oaks (*Quercus* spp.)

Species utilized: White oak (*Q. alba*), northern red oak (*Q. borealis*), red oak (*Q. rubra*), bear oak (*Q. ilicifolia*), pin oak (*Q. palustris*), chestnut oak (*Q. montana*), and chinquapin oak (*Q. prinoides*), in the approximate order of their importance. As most of the records show identity only to the genus, it is impossible to appraise accurately the relative importance of the several species with the information now available (see Plate 22A).

Seasonal importance: The oak group is one of the most important, and at times and places the most important source of fall food. Where snow conditions permit, it is also a valuable winter food. Acorns appear more prominently in the written records than is warranted because of the predominance of fall records, that is, from grouse killed in the hunting season. That is really the only period when oak mast is of great importance. Even though not available throughout the year, acorns still are a very important grouse food.

Parts used: nuts (acorns).

Geographical importance: The area of greatest use for acorns is middle and southern New England, and from Ohio and Pennsylvania southward. The acorns are of moderate importance in northern New England and in New York outside the Adirondacks. The value

of the oaks varies immensely in different years according to which species, if any, have a good crop of acorns. This results in somewhat inconsistent records from a single area, depending on years of collection. Smyth in 1919–23, with a considerable proportion of New York records, found relatively little utilization of acorns from October to March, and none in November when it should have been at its peak. Kelso's winter records taken prior to 1935 show very little consumption of acorns, and the *New York State Conservation Department's Annual Report* in 1937 pointed out the notable scarcity of foods of this group in the specimens taken by the study from 1930 to 1937. But Darrow two years later in summarizing the same records, together with new accessions, reported oak foods in excess of three per cent in the whole year food averages in New York outside the Adirondacks.

White oak is a large tree of the climax association of the Appalachian and Transition zones. It tolerates most soils except wet ones, but prefers fertile sites. It is among the least dependable of the oaks in acorn production, having a good crop only once in every three years or longer. However, white oak acorns seem to be most palatable of all and are small enough for the grouse to swallow whole.

Northern red oak is a large tree of the hemlock-hardwood association. It is more shade tolerant than white oak and, therefore, reproduces better under old-field white pine. The acorns are large and this probably hinders their utilization by grouse to some extent. Crops are usually produced in alternate years. South, and at lower altitudes, northern red oak is replaced by the common red oak which is a very similar tree.

Bear oak and chinquapin oak are shrub species found on dry, sandy barrens and rocky hillsides. Their habitat keeps them out of the better grouse coverts in most regions, but their patronage is considerable where available to the birds.

Chestnut and pin oak acorns are known to have been taken by grouse, but probably are not very important. It is probable that those of other oaks too are taken by grouse in varying quantities.

The oaks are an important food-producing group for many species of wild life. Acorns are a staple for the bobwhite, wild turkey, squirrels, white-tailed deer, wood duck, and mallard. They are also eaten by the ring-necked pheasant, mourning dove, numerous song birds, and by the opossum, muskrat, raccoon, black bear, gray fox, red

fox, and no doubt other species of mammals. The supply of acorns often being exhausted by this heavy drain, these competing species no doubt affect grouse food habits by forcing the birds to shift locally to less palatable foods. Over most of the northeast range, this does not materially affect grouse numbers or general distribution, but in the oak-hickory type range from Pennsylvania southward, it probably is a factor in determining the carrying capacity for grouse.

Chemical analysis of acorns (Hosley, 1938): water—2.4 per cent; protein—7.1 per cent; fat—4.9 per cent; nitrogen-free extract—81.0 per cent; fiber—2.2 per cent; ash—2.5 per cent. *Q. rubra* (Wright, 1940): water—1.8 per cent; protein—7.6 per cent; fat—22.6 per cent; nitrogen-free extract—61.0 per cent; fiber—4.8 per cent; ash—2.2 per cent.

Sumacs (*Rhus* spp.)

Species utilized: Dwarf sumac (*R. copallina*), smooth sumac (*R. glabra*), poison ivy (*R. toxicodendron*), staghorn sumac (*R. typhina*) (see Plate 24), and poison sumac (*R. vernix*). All five are staple food producers in parts of the northeast range, and the group as a whole is consistently important over the whole Northeast. Other species also patronized are fragrant sumac (*R. aromatica*) and lemonade sumac (*R. trilobata*).

Seasonal importance: All of the sumacs, including both the poisonous and nonpoisonous types, are of value to the grouse in late fall, through the winter, and in early spring. They are utilized to a minor extent in October and May, at the extremes of the season of greatest consumption.

Parts used: The fruits, heads of which are called "bobs."

Geographical importance: The sumacs as a group are important throughout the Northeast, and generally to the same degree. The total of *Rhus* products taken seems to average quite consistently, during the seasons used, from one to six per cent of the food. Geographical variation in importance of the five key species is probably determined in the main by availability. From the records it appears that *R. copallina* is most used in New York, Pennsylvania, and Virginia, *R. glabra* in Connecticut, Ohio and Virginia, *R. toxocodendron* in New Hampshire, Massachusetts, and Rhode Island, *R. typhina* in Maine, New Hampshire, New York, Pennsylvania, Ohio

and Virginia, and *R. vernix* in Maine and Massachusetts. Summarized by states, the species most patronized are: Maine, *R. typhina,* and *R. vernix*; New Hampshire, *R. toxicodendron,* and *R. typhina*; Vermont, none; Massachusetts, *R. toxicodendron,* and *R. vernix*; Rhode Island, *R. toxicidendron*; Connecticut, *R. glabra*; New York, *R. copallina,* and *R. typhina;* Pennsylvania, *R. copallina,* and *R. typhina*; Virginia, *R. copallina, R. glabra,* and *R. typhina*; Ohio, *R. aromatica, R. typhina,* and *R. glabra.*

Dwarf sumac, contrary to its name, is not always a small shrub, but sometimes grows to be a large shrub or even a tree. It is a sparsely-branched, thicket-forming plant, usually found on acid soils on dry or well-drained sites, either in full sun or partial shade.

Smooth sumac is a small-to-large shrub, sparsely branched, sometimes thicket-forming. It is found only in full sunlight, but is adapted to either dry or wet soils.

Poison ivy is a vine, or sometimes a shrub, very bushy, and at home in both sun and shade. It is adapted to dry or well-drained soils. The fruit is a smooth wax-covered drupe, quite unlike the hairy drupes of the non-poisonous species.

Staghorn sumac is a large shrub or small tree that often grows in loose thickets. It is found mainly in full sun, but grows occasionally in partial shade. Dry or well-drained soils on old fields and woods borders are its usual habitat. Poison sumac is a large shrub or small tree, rather sparsely branched, found on most soils from open sun to rather overgrown bogs or swamps.

Fruits of all the sumacs are eaten by a great variety of birds and mammals. Those of poison ivy alone are known to be consumed by more than sixty species of birds. Poison sumac berries are an important food of the bobwhite and ring-necked pheasant. Drupes of most of the species are eaten by these two game birds, mourning dove, wild turkey and by cottontail rabbit and white-tailed deer. Staghorn sumac is important as a deer browse food and smooth sumac as a rabbit food. Competition for products of the abundant sumacs is of no particular significance to the grouse.

Chemical analysis (Hosley, 1938, species not named): of fresh bobs: water—9.6 per cent; protein—6.9 per cent; fat—17.2 per cent; nitrogen-free extract—38.1 per cent; fiber—22.9 per cent; ash—5.3 per cent. *Rhus toxicodendron* (Wright, 1940): water—3.4 per cent; protein—6.8 per cent; fat—26.1 per cent; nitrogen-free extract—32.2

per cent; fiber—30.1 per cent; ash—1.5 per cent. *R. copallina* (Wright, 1940): water—4.1 per cent; protein—4.9 per cent; fat—11.2 per cent; nitrogen-free extract—46.6 per cent; fiber—31.0 per cent; ash—2.3 per cent. The amount of fat is surprising, being exceeded in only a few other species such as *Fagus* and *Juglans*. This may explain why this seemingly rather unpalatable food is so well liked by wild life.

Wild Roses (*Rosa* spp.)

Species utilized: Because of the difficulty of identifying the species of rose represented by the remains found in grouse crops or gizzards, and because the classification of these plants is rather confused, the records give only the genus. It is probable that fruits of any of the roses found in grouse habitat are eaten; at least we do not know that any species are not used (see Plate 25C).

Seasonal importance: Fall, winter, and early spring.

Parts used: Fruit (hips) and, to a minor extent, the leaves.

Geographical importance: The records indicate that this genus is more important as a food producer for grouse in Virginia than farther north. In Pennsylvania it appears to be definitely secondary, while in New York and New England it is fairly consistently used, and composes around one to two per cent of the fall to early spring food.

The wild roses are shrubs, often climbing to some degree, or low-growing. The flora includes both natives and acclimated exotics, often difficult to identify. The fruits vary immensely in size from the pea-size of those of *R. multiflora* to the small tomato-sized hips of *R. rugosa*; most of the species produce intermediate-sized fruits about half an inch in diameter. They are usually retained on the plant the year round. The roses generally require full sunlight and fairly fertile, well-drained soil, although some thrive on poor or wet soils.

The fruits, or hips, are eaten by many birds, including the bobwhite, ring-necked pheasant, and wild turkey, and by the opossum, white-tailed deer, red squirrel, porcupine, snowshoe hare, and cottontail rabbit. Their competition for this plentiful food is of no importance to the grouse.

Chemical composition (Hosley, 1938, for *R. multiflora,* fresh fruit): water—29.5 per cent; protein—7.9 per cent; fat—3.5 per cent;

nitrogen-free extract—41.2 per cent; fiber—14.9 per cent; ash—3.0 per cent.

Brambles, or Blackberries and Dewberries (*Rubus* spp.)

Species utilized: The majority of records identify bramble foods only to genus but a number are specifically known to be eaten by grouse. These are blackberry (*R. allegheniensis*) (see Plate 21A), trailing blackberry (*R. hispidus*), wild red raspberry (*R. idaeus aculeatissimus*), thimbleberry (*R. occidentalis*), salmonberry (*R. parviflorus*), and dewberry (*R. villosus*). No doubt other species also are used. We can surmise that the most important species are those most prevalent in grouse habitat. These are mainly *R. allegheniensis, R. idaeus aculeatissimus,* and *R. hispidus.*

Seasonal importance: A very important summer food for both chicks and adults, and also of value during the fall and early winter months. Use of the fruit begins in July and continues through August. The leaves are eaten in the summer, fall, and early winter, and the buds in fall and winter.

Parts used: Fruit, leaves, and buds.

Geographical importance: One of the highest ranking summer foods of adults and chicks throughout the Northeast, in New York the most important. During the fall and winter their consumption is much reduced, but still remains significant. The records indicate that they may be less important in the extreme North (Maine) and the extreme South (Virginia) of the grouse's northeastern range in the fall and winter, but this may not be a finally dependable conclusion.

The brambles are low-growing, sometimes trailing, shrubby plants found in old fields, slashings, and burns (see Plate 21A). They often form dense thickets. Their adaptability to poor soils enables them to pioneer on abandoned, worn-out soils. When other woody plants seed in, it is not long before the brambles are killed off by shade of which they are very intolerant.

Rubus products are one of the most important of wild-life foods. They are staple for the bobwhite, ring-necked pheasant, cottontail, skunk, and white-tailed deer as well as for the ruffed grouse. Altogether, more than 140 species of nongame birds in addition to the opossum, chipmunk, red fox, gray fox, red squirrel, black bear,

beaver, and snowshoe hare are known to eat them. There is no indication, however, that this heavy competition adversely affects the grouse.

Chemical composition (Hosley, 1938, average figures for blackberry fruit): water—86.3 per cent; protein—1.3 per cent; fat—1.0 per cent; nitrogen-free extract—10.9 per cent; fiber—2.5 per cent; ash—0.5 per cent. (Hosley, 1938, dry leaves of *R. hispidus*): water—7.8 per cent; protein—9.8 per cent; fat—4.1 per cent; nitrogen-free extract—60.8 per cent; fiber—13.7 per cent; ash—3.9 per cent.

The high water content of the fruit of *Rubus* may explain its great importance as a summer food. During the hot summer months grouse obtain much of their water requirement through foods of this type.

Sheep Sorrel (*Rumex acetosella*)

Seasonal importance: From late summer or early fall until midspring, with greatest use probably in late fall and early winter.

Parts used: Leaves.

Geographical importance: Sheep sorrel is eaten by grouse throughout the Northeast but assumes its greatest importance in the southern portion, from Pennsylvania to Virginia. Here it ranks as one of the most important fall and winter foods whereas farther north it is used somewhat less, particularly in winter when snow limits its availability. It is taken to some extent by grouse chicks in late summer. Darrow found it to rate tenth among chick food plants in the Catskill portion of New York.

Sheep sorrel (or field sorrel) is a common weed (see Plate 20D) that has been naturalized from Europe. It is a perennial herb which spreads by rootstocks. The leaves have a sour taste. It is a low plant, from five to fifteen inches high, found along field borders in sparse cover, in old fields, on roadsides, and in poor soils.

Greenbriars (*Smilax* spp.)

Species utilized: Most of the records give the identification of foods derived from this group only to genus. Products of three species have been positively identified in grouse stomach records but it is highly probable that those of other *Smilax* also are used. Cat

greenbriar (Nelson, 1938) (*S. glauca*) and common greenbriar (*S. rotundifolia*) are among the most important species patronized. The fruits of the carrion flower (*S. herbacea*), an herbaceous species, also are known to have been taken.

Seasonal importance: A fall and winter food, probably most valuable in deep winter although used in greatest volume in late fall and early winter.

Parts used: Fruit, mainly, and leaves.

Geographical importance: The greenbriars assume their greatest importance as food producers in the southern part of the grouse's northeastern range, notably Virginia and Ohio, where they rank first as a fall and winter food. They are also valuable in Pennsylvania and Rhode Island. Elsewhere they are of secondary ranking, especially in the higher altitudes and more northern areas.

The important greenbriars are spiny, shrubby, thicket-forming vines. The nonwoody *S. herbacea*, although patronized by grouse, is not of great importance. Of the two leading species, *S. glauca* is found on dry or well-drained soils, while *S. rotundifolia* occurs in moist to well-drained sites. Both prefer fertile bottom lands. They are primarily plants of the woods, being most prolific along woodland edges. The young plants produce good crops of fruit, while old growth is usually barren.

Greenbriar berries are known to be eaten by the bobwhite, ring-necked pheasant, wild turkey, and about forty other kinds of birds; also by the opossum, gray fox, white-tailed deer, and cottontail rabbit. This competition is normally not serious to grouse but might affect their local distribution, and possibly even abundance, in the southern part of their range.

Chemical analysis (Wright, 1940): *S. rotundifolia* (dried fruit): water—2.8 per cent; protein—9.3 per cent; fat—5.3 per cent; nitrogen-free extract—60.8 per cent; fiber—18.8 per cent; ash—3.1 per cent. *S. glauca* (dried fruit): water—3.7 per cent; protein—10.9 per cent; fat—7.7 per cent; nitrogen-free extract—57.1 per cent; fiber—18.4 per cent; ash—2.9 per cent.

Blueberries (*Vaccinium* spp.)

Species utilized: Lowbush blueberry (*V. angustifolium*), Canada blueberry (*V. canadense*), highbush blueberry (*V. corymbosum*),

cranberry (*V. macrocarpon*), deerberry (*V. stamineum*), dryland blueberry (*V. vacillans*), cowberry (*V. vitis-idaea*), and rock cranberry (*V. vitis-idaea minus*) are all known to be eaten by grouse. It is entirely probable that numerous other species of blueberries also are taken. The relative importance of the several species is probably determined largely by their distribution and abundance. The lowbush blueberry is most important in southern New York, followed in order by highbush blueberry, deerberry, and dryland blueberry.

Seasonal importance: There are two distinct seasons of use for *Vaccinium*: July to August for the fruit by both adult and young grouse; and fall, winter, and early spring for the buds and twigs, with the most intensive use from November through January. The leaves also are eaten to a considerable extent in summer and fall.

Parts used: Fruit, in summer, by both adults and young; buds and twigs in fall, winter and early spring; and leaves in summer and fall. The fruit and buds are the parts most used.

Geographical importance: As a summer food, the fruit is important to both adults and young throughout the Northeast. In New York it ranked higher in the Adirondacks than elsewhere. During fall and winter the buds are used in all parts of the Northeast, but with apparently less intensity in New York than elsewhere. Possibly western New England is also included with New York in this area of restricted importance.

The blueberries are low-to-medium-height shrubs (see Plate 21B) found mainly on acid soils in open fields and along roadsides and woodland edges. The more important species for grouse are those growing in dry sites, but several species are confined to bogs. They are pioneers in plant succession and often become established following a burn. Some are quite intolerant of shade and competition. The native, wild blueberries are highly prized for human food and are an important crop in some areas. Blueberry products, mainly the fruit, are eaten by many species of songbirds, by the ring-necked pheasant, bobwhite, Hungarian partridge, skunk, white-tailed deer, opossum, cottontail, black bear, raccoon, and moose. Most of this competition comes in the summer when food is plentiful. There is normally little possibility of its having a serious effect on either distribution or abundance of ruffed grouse. Harvest of blueberries by man probably affects grouse distribution locally.

Chemical analysis (Hosley, 1938) for fresh fruit: water—83.4 per cent; protein—0.6 per cent; fat—0.6 per cent; nitrogen-free extract —13.9 per cent; fiber—1.2 per cent; ash—0.3 per cent; calories per pound—310.

Viburnums (*Viburnum* spp.)

Species utilized: mapleleaf viburnum (*V. acerifolium*) (see Plate 23A); witherod (*V. cassinoides*); nannyberry (*V. lentago*) (see Plate 27A); blackhaw (*V. prunifolium*) (see Plate 27C); and highbush cranberry (*V. trilobum*) (see Plate 25B) are the species used most generally and in greatest quantity. Among these, nannyberry, highbush cranberry, and witherod appear to be most important in New England, mapleleaf viburnum, nannyberry, and witherod in New York, and blackhaw and mapleleaf viburnum to the south. Other viburnums used to a lesser degree are: hobblebush (*V. alnifolium*) (see Plate 27B); arrowwood (*V. dentatum*) (see Plate 27D); wayfaring tree (*V. lantana*) (usually cultivated); squashberry (*V. pauciflorum*); and hairy nannyberry (*V. pubescens*).

Seasonal importance: Fall and winter, diminishing in volume of use as winter passes.

Parts used: Fruit.

Geographical importance: Some species of viburnums are of significance in the fall diet of the grouse throughout the Northeast, with the possible exceptions of Vermont and Rhode Island. However, if more records from these states were available, it is reasonably sure that they would show that at least a small part of the grouse food is derived from plants of this genus. The highest use intensities are recorded from New Hampshire, Massachusetts, Connecticut, New York, and Virginia.

It is interesting to note a discrepancy in the geographical use of a food species in connection with highbush cranberry. This species is readily patronized by grouse in New England and Pennsylvania, and yet we have observed that it is almost completely avoided in New York. No explanation for this variation in selection is apparent.

The viburnums are medium-to-tall shrubs found in the woodland understory, along woods edges, and in fence rows. They usually grow in well-drained, fairly fertile soils, although nannyberry and

some others can endure rather wet soils too. They are eaten by the bobwhite, ring-necked pheasant, and some twenty-odd species of songbirds, as well as by the chipmunk, cottontail, porcupine, raccoon, skunk, gray squirrel, moose, gray fox, and white-tailed deer. This competition is apparently of no importance to the grouse.

Chemical analysis (Hosley, 1938): fresh fruit, *V. cassinoides:* water—72.6 per cent; protein—1.7 per cent; fat—2.9 per cent; nitrogen-free extract—19.8 per cent; fiber—2.3 per cent; ash—0.8 per cent. *V. opulus* (almost identical with *V. trilobum*), fresh fruit: water—47.3 per cent; protein—2.7 per cent; fat—4.9 per cent; nitrogen-free extract—37.1 per cent; fiber—6.3 per cent; ash—1.7 per cent.

Wild Grapes (*Vitis*)

Species utilized: Summer grape (*V. aestivalis*), blueleaf grape (*V. argentifolia*), frost grape (*V. cordifolia*), fox grape (*V. labrusca*) (see Plate 28), riverbank grape (*V. vulpina*), and probably others not specifically identified as yet in grouse food habit records. All of the five species known to be eaten are taken in quantity where available; hence, their importance depends mainly on distribution and abundance.

Seasonal importance: Fall and early winter is the season of greatest use, quickly falling off from January on as the fruit is consumed by wild life or drops off the vines. Some species hold part of their fruit well into the winter when it is used as long as available, and some fruit is picked from the ground.

Parts used: Fruit.

Geographical importance: Grapes are an important fall and early winter food throughout the northeastern states, with the exception of Maine. The areas of greatest use are southern New England, southeastern New York, and from Ohio and Pennsylvania to Virginia. In the north, New York and New England, *V. argentifolia, V. labrusca,* and *V. vulpina* are most important; to the south, notably in Virginia, *V. aestivalis* and *V. cordifolia* are most used. As a group the wild grapes are among the top-ranking foods from October to January, often exceeding all others in volume consumed.

The grapes are high-climbing, vigorous vines found mainly along woodland borders and fence rows. They generally prefer a fairly

fertile soil but occur on a variety of sites from dry to wet. They require lots of light to fruit well and climb to the top of the tallest trees to gain full exposure to the sun.

Grapes are a favorite food of many kinds of wild life besides grouse. The fable of the fox and the grapes indicates the taste for grapes that characterizes both the red and gray foxes. These fruits are also a staple food of the ring-necked pheasant, bobwhite, and skunk; and are eaten also by the wild turkey, mourning dove (seeds) and Hungarian partridge. Nearly a hundred kinds of songbirds are known to eat grapes. Among mammals, other than foxes and skunks, that eat grapes are the raccoon, opossum, white-tailed deer, red squirrel, and cottontail. This competition very likely alters the local distribution of grouse, and may sometimes affect abundance locally.

Chemical analysis (Hosley, 1938, frost grape—fresh fruit): water —11.6 per cent; protein—9.5 per cent; fat—4.8 per cent; nitrogen-free extract—43.7 per cent; crude fiber—26.4 per cent; ash—4.0 per cent. *Vitis* sp. (dried fruit) (Wright, 1940): water—8.4 per cent; protein—7.4 per cent; fat—2.1 per cent; nitrogen-free extract—56.1 per cent; fiber—22.8 per cent; ash—4.0 per cent.

SECONDARY GROUSE FOODS

The twenty-five genera supplying the greatest volume of food throughout the year have been discussed in some detail as the primary foods of the species. There are numerous other foods that either furnish a significant amount of food generally or are of special value in restricted areas. These secondary foods are here arbitrarily restricted to those that have constituted one per cent or more of the seasonal food of grouse in the records of a study covering one or more states. Added to the volume of the twenty-five primary foods, from ninety-four to ninety-nine per cent of the birds' normal food in the Northeast is covered by the two groups. The forty-one genera of plants and the insects and miscellaneous animal foods that are included in the category of secondary foods are here annotated.

Maples (*Acer*): Buds and seeds of at least four species are taken. Seeds composed two and three-tenths per cent of the summer food of grouse chicks in the Adirondacks of New York, one and one-tenth per cent in the rest of the State outside the Catskills, and from two and four-tenths to three and nine-tenths per cent of summer

food at different times in New Hampshire (MacGregor). Maple buds are listed eighth among winter foods and tenth among spring foods in the Adirondacks (Darrow), ninth among winter foods in New York (*N. Y. S. Cons. Dept. Ann. Rep. 1937*) and as over one per cent of winter food in the Northeast (Bi-1297) and recorded in small amounts throughout the region from Maine to Virginia. The most palatable food producer appears to be mountain maple.

Alders (*Alnus*): Buds and seeds of two species have been recorded as grouse foods, but probably others are sampled too. Alder products were recorded by Smyth as composing four and eight-tenths per cent of grouse food in October, three and three-tenths per cent in November and two and two-tenths per cent in winter in the Northeast; they are taken in small amounts during the winter in all parts of the Northeast. Speckled alder is probably the most important species.

Serviceberries (*Amelanchier*): Buds have been listed as a fall and winter food. The fruit is used during the summer and fall by both young and old birds. Only *A. canadensis* has been specifically identified but other species no doubt also are patronized. Darrow recorded *Amelanchier* products as comprising five and two-tenths per cent of the summer food of grouse chicks in the Catskill region of New York and one and one-tenth per cent in the remainder of the state outside the Adirondacks. Kuhn (1941) records them as forming two and three-tenths per cent of the November food in Pennsylvania. In Virginia the buds amounted to one and one-tenth per cent of the early-winter food (Nelson). Remains of these plants have also been reported as a fall and winter food in small quantities in Pennsylvania, New York, and New Hampshire (see Plate 30E).

Everlasting (*Antennaria*): The leaves are taken during fall and winter but have not been definitely identified as to species. Nelson found the early winter food in Virginia to have been derived to the extent of two and three-tenths per cent from plants of this genus. It has been listed as a moderate food producer in other records from Pennsylvania to New England.

Chokeberry (*Aronia*): Both fruit and buds of the two common species are taken in fall and winter from New York to Maine. In Massachusetts they composed one and eight-tenths per cent of the fall and winter food, in Rhode Island one and two-tenths per cent, and in Connecticut one and seven-tenths per cent (Hosley). Red

chokeberry appears to be used most in New England and black chokeberry (see Plate 29A) in New York.

Aster (*Aster*): The leaves of asters, species not identified, are used as a fall and early winter food from New York to Virginia. They composed three and three-tenths per cent of the November-December food in Virginia (Nelson) and appear to be more important in the South than in the North.

Barberries (*Berberis*): The fruit of both the European and Thunberg barberries is eaten to some extent during the winter in New York and New England. It composed three and six-tenths per cent of the total fall-and-winter food in Massachusetts and one and two-tenths per cent in Rhode Island, with lesser amounts from New Hampshire to New York (Hosley). MacGregor found it to compose one and five-tenths per cent of the October food in New Hampshire.

Blue beech (*Carpinus caroliniana*): Both buds (see Plate 20C). and seeds are taken in late fall and winter, the buds being the more important. Parts of this plant composed four and one-tenth per cent of the winter food in New York (December eight and seven-tenths per cent, January three and one-tenth per cent, February four and five-tenths per cent (Kelso); three per cent of fall-and-winter food in New York (Hosley), two and five-tenths per cent of year-round food in New York outside the mountains (Darrow). In other states blue beech products appear to be little used, although they have been recorded in grouse food from Virginia to New Hampshire.

Chestnut (*Castanea dentata*): An important food prior to the sweep of the chestnut blight (Judd, Smyth), now no longer significant. As late as 1923, Smyth found that it composed one and four-tenths per cent of the October food in the Northeast. It is noted here as a matter of history, and a hope for the future.

Climbing bittersweet (*Celastrus scandens*): (see Plate 29B). The fruit is eaten during fall and winter from New York to New Hampshire. It composed one per cent of the fall and winter diet in New Hampshire (Hosley) and over one per cent of the winter food in the Northeast (Bi-1297).

Beech-drops (*Epifagus virginiana*): Seeds composed one and one-tenth per cent of October food in the Northeast (Smyth).

Trailing arbutus (*Epigaea repens*): Leaves and buds are eaten in fall and winter; they composed one and two-tenths per cent of the

November-December food in Virginia (Nelson) and are also taken throughout the region in small quantities.

Buckwheat (*Fagopyrum esculentum*): The seed is a fall food, mainly in Pennsylvania and New York. It composed one and two-tenths per cent of the November food in northeastern records, slightly less in October (Smyth).

Huckleberries (*Gaylussacia*): Fruit and buds are taken in summer and winter, respectively. Of the two species definitely identified, black huckleberry is the more important, but other species probably are used too. Huckleberries were recorded by Hosley as contributing one per cent of the fall and winter food in Massachusetts. They were lumped with blueberries (*Vaccinium*) in the significant use records of Kuhn in Pennsylvania and Nelson in Virginia. They have been recorded as utilized in other New England states as far northeast as New Hampshire.

Avens (*Geum*): Seeds and leaves are taken in fall and winter. Only one species has been definitely identified (*G. strictum*) but others also are probably patronized. Composed one and two-tenths per cent of October food in the Northeast (Smyth); smaller but significant quantities have been recorded as taken by grouse from Virginia to New England.

Witch hazel (*Hamamelis virginiana*): The seeds, flowers, and buds are taken in rather small but consistent quantities during fall and winter from Maine to Virginia. They composed one per cent of the fall-and-winter food in New Hampshire (Hosley); one per cent of the November diet in the Northeast (Smyth); and two and six-tenths per cent of November subsistence in Pennsylvania (Kuhn, 1941).

Holly (*Ilex*): The fruit, and to a small extent the leaves, of at least three species of Ilex are fall and winter foods from Virginia to Maine. The most important species by far is winterberry (see Plate 29C). Plants of this genus produced over one per cent of the winter food in the Northeast (Bi-1297); one and one-tenth per cent in Maine, and one and three-tenths per cent in New Hampshire (Hosley). Smaller quantities are recorded in all parts of the region south to Virginia.

Jewelweed (*Impatiens*): The seeds and leaves are an important summer and early fall food of both chicks and adults. Spotted jewelweed is the more important and the only one specifically identified,

but pale jewelweed also probably is used. It is listed as tenth in importance as a summer food producer for both adults and young (*N. Y. S. Cons. Dept. Ann. Rep. 1937*). Darrow found that jewelweed products composed one per cent of the food of the chicks in the Adirondacks, two-tenths of one per cent in the Catskills, and one and nine-tenths per cent in the remainder of the state. In New Hampshire, MacGregor found this food to rank second from mid-June to mid-July (five and six-tenths per cent), second also during August and September (five and eight-tenths per cent), then dropping to a mere trace in fall.

Minnie-bush (*Menziesa pilosa*): The buds furnished one and three-tenths per cent of the November-December food in Virginia (Nelson).

Bishop's cap (*Mitella diphylla*): The leaves are taken in the fall, and to a small extent in the winter from New England to Pennsylvania. Smyth found them to comprise six and two-tenths per cent of the October food and seven and three-tenths per cent of the November food in the Northeast.

Bayberry (*Myrica*): The fruits of two species, *M. carolinensis* (see Plate 30B) and *M. cerifera*, and the buds of sweet fern (*M. asplenifolia*) are used during the fall and winter. *M. carolinensis* is the only one of much importance to grouse. It contributed one and two-tenths per cent of the fall food in New England (Gross). Hosley recorded bayberries as comprising one and two-tenths per cent of the fall and winter food in Massachusetts, four and three-tenths per cent in Rhode Island, and four and five-tenths per cent in Connecticut. In grouse range near the seacoast they become a primary food from Maine southward to Connecticut, and are used to a lesser extent in New York and Pennsylvania.

Black gum (*Nyssa sylvatica*): The fruit, leaves, and buds are taken during fall and winter from Maine to Virginia, but not usually in very significant amounts. In Pennsylvania, Hosley records one and one-tenth per cent of black gum seeds; all other records show less than one per cent.

Sorrel (*Oxalis*): Leaves of at least three species of sorrel are taken during fall, winter, and spring. This foliage ranked eighth in the spring food records in the Adirondacks of New York (Darrow). Smyth recorded it as totaling one per cent of October food in the Northeast, and somewhat less in November. It is also recorded from

New England to Pennsylvania, including for the latter state Kuhn's (1941) record of one and three-tenths per cent for November.

Virginia creeper (*Parthenocissus quinquefolia*) (see Plate 30A): The fruit is eaten during fall and winter from New Hampshire to Virginia. In Connecticut it constituted one per cent of the fall and winter food (Hosley).

Milkworts (*Polygala*): The leaves are a summer, fall, and winter food from New York to Virginia. Darrow records these greens as tenth among summer foods of adults in the Adirondacks of New York and eighth (five-tenths of one per cent) in the summer diet of chicks in the Catskills.

Smartweeds (*Polygonum*): Seeds of this group are taken during summer, fall, and early winter from New England to Pennsylvania. Darrow lists them as tenth (nine-tenths of one per cent) in the summer foods of young birds in New York outside the mountainous areas. MacGregor ranks them as seventh (two and one-tenth per cent) among late-summer foods in New Hampshire.

Cinquefoils (*Potentilla*): Taken from New England to Virginia, the leaves are recorded by Smyth as making up two and two-tenths per cent of the November food in the Northeast; MacGregor lists them as seventh (two and eight-tenths per cent) among November foods in New Hampshire; their use is recorded in smaller but consistent amounts elsewhere by other authors.

Heal-all (*Prunella vulgaris*): The leaves are taken during the fall from New England to Virginia. They composed one and one-tenth per cent of the November food in Pennsylvania (Kuhn), almost as much in Virginia, and smaller amounts in New England.

Shin leaf (*Pyrola*): The leaves are a fall-and-winter food, sometimes in quantities that place them for a time among the most important foods. They amounted to six per cent of the February food in New York and one per cent of January food (Kelso). Gross records shin leaf foliage as comprising one and two-tenths per cent of the fall food in New England; a smaller but significant amount was taken in Pennsylvania, and a trace in Virginia.

Buttercups (*Ranunculus*): The leaves are used as a summer, fall, and winter food throughout the region. Two species have been identified, but no doubt others are used. Smyth records buttercup foliage as being four and eight-tenths per cent of the October food in the Northeast, while Darrow found it amounting to one and eight-

tenths per cent of the summer food of the young in the Adirondacks of New York, three per cent in the Catskills, and two and six-tenths per cent in the rest of the state. He also lists it as fifth in importance among the summer foods of the adult birds in the Adirondacks.

Rhododendrons (*Rhododendron*): The leaves and buds of both the evergreen and deciduous types of this genus are taken in fall and winter. Such material composed one and five-tenths per cent of the fall-and-winter food in Rhode Island (Hosley), and smaller quantities from New Hampshire to Virginia, mainly near the coast except in the south.

Willows (*Salix*): The buds and leaves are eaten in fall and winter throughout the region. In Maine they composed one and four-tenths per cent of the fall and winter food (Hosley, 1938), while the Bi-1297 summary for the Northeast records willow as contributing more than one per cent of the winter food. Elsewhere it has supplied food in smaller amounts.

Elders (*Sambucus*) (see Plate 30C): The fruits of both northeastern species are utilized as summer-and-fall food. Darrow found them to compose two and one-tenth per cent of the summer food of young grouse in the Adirondacks of New York. Other records in New England and in general northeast summaries are of very small quantities, mainly because information on summer foods and on the diet of young birds is so scant.

False Solomon's seal (*Smilacina*): The fruit is taken as a fall-and-early-winter food, mainly in the northern part of the region. Smyth recorded that it amounted to two and two-tenths per cent of the winter food in his northeastern records and MacGregor as sixth (two and two-tenths per cent) among October foods in New Hampshire.

Bitter nightshade (*Solanum dulcamara*): Both fruits and leaves are used in fall and winter. Smyth found them to compose one and four-tenths per cent of October food in the Northeast, probably mostly in the north, as other records are from New York and New England.

Mountain ash (*Sorbus*) (see Plate 30D): Fruit and buds are taken of both the native and introduced species during fall and winter. They compose one and one-tenth per cent of fall and winter food in New Hampshire (Hosley) and are recorded in smaller quantities from New York and other parts of New England.

Skunk cabbage (*Symplocarpus foetidus*): The seeds are eaten in fall and winter from New England to Pennsylvania. In spring the flowers and leaves also are taken. Darrow lists products of this plant as ninth in importance among winter foods in the Adirondacks region of New York, while Kelso found them to make up over one per cent of the winter food of New York grouse. Hosley (1941) lists skunk cabbage as first among herbaceous foods in Connecticut and second in Rhode Island. It has also been recorded in smaller but still significant amounts in the fall food in New England and Pennsylvania.

False miterwort (*Tiarella*): Leaves have been recorded as a fall and early winter food. They are probably taken to some extent throughout the Northeast but seem definitely most important from Pennsylvania to Virginia. Smyth found them to compose three and two-tenths per cent of October food in the Northeast, one and four-tenths per cent in November and one and one-tenth per cent in the winter. They ranked seventh in the list of November foods in Pennsylvania (Kuhn, 1940), amounting to four and seven-tenths per cent of total food, and sixteenth in 1941 with one and seven-tenths per cent (Kuhn); and were taken in small amounts in Virginia.

Clovers (*Trifolium*): The leaves of both wild white and red clovers are taken during fall and winter, the former being the more important. Clover is used throughout the Northeast region but is primarily important in the North, New York and New England. Nowhere in this region does it approach the use it receives in the midwest states, however. Smyth found that it composed two and four-tenths per cent of October food in the Northeast, one and four-tenths per cent in November, and less in the winter. Gross lists it ninth among fall foods in New England, where it amounted to three per cent of total food. Hosley (1941) records it as first among herbaceous foods in Vermont and second in New Hampshire and Massachusetts. MacGregor ranks it second among October foods in New Hampshire comprising six and eight-tenths per cent of all food, and ninth among November foods (two and three-tenths per cent).

Violets (*Viola*): Both the leaves and seeds are used throughout the Northeast. They are most important as a summer food for chicks and adults but are used to some extent in the fall. From the existing records, the area of greatest importance of violets in grouse diet is clearly New York, but if summer records were available from other states, it is likely that they would prove to rank highly elsewhere.

They are listed sixth among summer foods of chicks and seventh for adults in New York (*N. Y. S. Cons. Dept. Ann. Rep., 1937*). As summer food for young birds, violets were ranked as ninth in the Adirondacks with one and four-tenths per cent, sixth in the Catskills with one and three-tenths per cent, and sixth in the remainder of New York with two and one-tenth per cent; in the Adirondacks they ranked eighth among fall foods (Darrow). MacGregor placed them fourth among late-July foods in New Hampshire, amounting to four and three-tenths per cent of the total subsistence.

Barren strawberry (*Waldsteinia fragarioides*): The leaves are taken during late fall and winter, from New York to Virginia. Kelso listed them eleventh among winter foods in New York, averaging one and four-tenths per cent of total food; in January they amounted to two per cent, and in February three per cent of the food taken. In Pennsylvania this foliage ranked tenth among November foods one year and constituted three and eight-tenths per cent of all food (Kuhn, 1940), then twenty-second the next year with one and two-tenths per cent (Kuhn, 1941).

Insects: The most important groups of insects patronized for food by the grouse are Hymenoptera (ants, wasps, bees) and Coleoptera (beetles). These two orders are primary contributors to the food of the young birds from hatching time to mid-July, and are of secondary importance to the adults. Some of the larger divisions (families) of these two orders, and occasionally so small a group as a genus, may in certain areas provide enough prey to be classed as secondary foods. Other kinds of insects and insect allies may compose over one per cent of the food of the young birds in some areas, most commonly *Lepidoptera* (moths and butterflies), *Opiliones* (harvestmen), *Hemiptera* (bugs) and *Diptera* (flies).

Animal foods constituted from forty-six and eight-tenths per cent of the food of the young birds in June in the Adirondacks region of New York to sixty-eight and three-tenths per cent in the Catskills, with the records from the rest of the state totaling about sixty per cent. In July these percentages dropped to from ten to fifteen per cent of total food for the chicks. In August the utilization of animal life by the young birds approached the proportions used by adults, being highest again in the Adirondacks (six and nine-tenths per cent), practically the same in the Catskills, and only one and three-tenths per cent over the remainder of New York (Darrow).

For the adults, the animal food amounts to less than one per cent (in New York six-tenths of one per cent) of the total food. In the summer it exceeds the annual average, ranging from one per cent to three per cent in New York, and highest in the Adirondacks (Darrow). Occasionally insects will exceed one per cent of the food in spring or fall too.

Smyth examined four May–June chick stomachs and found sixty-six and nine-tenths per cent of the food to be insects and their relatives; in three July stomachs the proportion was only eleven per cent. One August stomach contained ten per cent animal food. Judd (1905) reported on four chicks less than one-quarter grown, the stomach contents of which were found to be ninety-five per cent insects, while seven adults taken at the same season contained only thirty per cent of insects.

Judd's adult records are very notable in that he found insects and related animal life to constitute ten and nine-tenths per cent of total food (including Coleoptera—four and six-tenths per cent; Lepidoptera larvae one and two-tenths per cent; Orthoptera eight-tenths of one per cent). This is the more unusual because a great majority of the birds were taken during the cold months. Possibly the grouse were more insectivorous formerly, but this does not seem likely. Other fall and winter records are in marked contrast, insects ranging from one and eight-tenths per cent of the October food (Smyth) and one and four-tenths per cent of fall food in New England (Gross) to a mere trace of the winter food in New York (Kelso). Kuhn (1940) lists animal food as amounting to thirteen-hundredths per cent of the November food in Pennsylvania. Nelson found only seven-hundredths per cent in November–December stomachs in Virginia. Smyth gave the November insect diet as totaling eight-tenths per cent of food taken, but he found none at all in stomachs collected from December through March.

Occasional Foods. The kinds of plant and animal foods acceptable to the ruffed grouse are without doubt more numerous than presently recorded. The New York investigation is continuing its study of the grouse food habits and finds new food items with each new season's collections. The list of foods now known to be taken will be considerably enlarged with more study, but the importance of the newly discovered items is likely to be slight (see Tables 5 and 6).

Table 5

Plant Foods Eaten by Ruffed Grouse in the Northeast

Herbaceous Plants

Common Name	*Scientific Name*	*Parts Eaten*	*References*
Yarrow	*Achillea*	Leaves	Kuhn (1940)
White baneberry	*Actaea alba*	Fruit	MacGregor
Cohosh	?	Leaves	Kuhn
Mushrooms	*Agaricini*	All	Smyth
Agrimony	*Agrimonia*	Seeds	Allen, Nelson
Broomsedge	*Andropogon virginicus*	Seeds	Davison & VanDersal (1941)
Angelica	*Angelica*	Leaves	Nelson
Everlasting	[2] *Antennaria neglecta*	Leaves	MacGregor
Everlasting	*A. plantaginifolia*	Leaves	MacGregor
Everlasting	(sp.)	Leaves	
Columbine	*Aquilegia canadensis*	Leaves	MacGregor
Wild ginger	*Asarum*	Leaves	Nelson
Milkweed	*Asclepias*	Seeds	Kuhn (1941)
Aster	[2] *Aster*	Leaves	
False goats beard	*Astilbe biternata*	Leaves	Judd
Blackberry lily	*Belmacanda chinensis*	Seeds	Smyth
Beggar-ticks	*Bidens frondosa*	Seeds	Smyth
Grape fern	*Botrychium obliquum*	Fronds	Judd
Grape fern	*B. obliquum dissectum*	Fronds	Gross
Rattlesnake fern	*B. virginianum*	Fronds	MacGregor
Grape fern	(sp.)	Fronds	Gross
White mustard	*Brassica alba*	Seeds	Allen
Brome grass	*Bromus*	Leaves	Gilfillan & Bezdek
Sedge	[1] *Carex crinita*	Seeds	Gross

Sedge	*Carex flexuosa*	Seeds	Gross
Sedge	*C. gracillima*	Seeds	Gross
Sedge	*C. intumescens*	Seeds	Gross
Sedge	*C. lupulina*	Seeds	Smyth
Sedge	*C. oederi pumila*	Seeds	N. Y. Cons. Dept. Ann. Rep., 1937
Sedge	*C. plantaginea*	Seeds	Smyth
Sedge	*C. tenella*	Seeds	Gross
Sedge	*C. tuckermani*	Seeds	MacGregor
Sedge	(sp.)	Seeds	
Mouse-ear chickweed	*Cerastium*	Leaves	Kuhn (1940)
Oxeye daisy	*Chrysanthemum leucanthemum*	Leaves	MacGregor
Goldenstar	*Chrysogonum virginianum*	Leaves	MacGregor
Golden saxifrage	*Chrysosplenium*	Leaves	Kuhn (1940)
Chicory	*Cichorium intybus*	Leaves	Nelson
Thistle	*Cirsium*	Leaves	Nelson
Three-leaved goldthread	*Coptis trifolia*	Fruit	Gross
Bunchberry	[1] *Cornus canadensis*	Fruit	
Fungus	*Crucibulum*	Fruiting body	MacGregor
Moss	*Cryptogamia*	Leaves	Smyth
Sedges	*Cyperaceae*	Leaves, seed	Kuhn (1940)
Galingale	*Cyperus*	Leaves, seed	Smyth
Wild carrot	*Daucus carota*	Leaves	Nelson
Tick trefoil	*Desmodium*	Seeds	Smyth
Duck millet	*Echinochloa crus-galli*	Seeds	Merritts
Beech-drops	[2] *Epifagus virginiana*	Seeds	Smyth
Trailing arbutus	[2] *Epigaea repens*	Leaves, buds	
Willow herb	*Epilobium*	Leaves	MacGregor

[1] Genera among the twenty-five most used plant foods.
[2] Genera among the forty-one secondary plant foods.
Names of authorities are listed only in cases where the species has not been commonly reported as eaten by ruffed grouse.

Common Name	*Scientific Name*	*Parts Eaten*	*References*
Horsetail	*Equisetum*	Leaves	Judd
Fleabane	*Erigeron*	Leaves	Nelson
Thoroughwort	*Eupatorium*	Leaves, seeds	Nelson
Buckwheat	[2] *Fagopyrum esculentum*	Seed	
Strawberry	[1] *Fragaria virginiana*	Fruit, leaves, blossoms	
Strawberry	(sp.)	Fruit, leaves, blossoms	
Fungus		All	Gross
Bedstraw	*Galium*	Leaves, seeds	Gross
Cranesbill	*Geranium*	Leaves	Gross
White avens	[2] *Geum canadense*	Seeds	Merritts
Yellow avens	*G. strictum*	Seeds, leaves	Smyth
Yellow avens	(sp.)	Seeds, leaves	
Purplish cudweed	*Gnaphalium purpureum*	Leaves	Judd
Everlasting	(sp.)	Leaves	Nelson
Grasses	*Gramineae*	Leaves	
Mock pennyroyal	*Hedeoma*	Seeds	Nelson
Frostweed	*Helianthemum canadense*	Seeds	Smyth
Sunflower	*Helianthus*	Seeds	Smyth
Liverleaf	*Hepatica*	Leaves	Kelso
Alumroot	*Heuchera americana*	Leaves	Judd
Alumroot	(sp.)	Leaves	Nelson
Hawkweed	*Hieracium*	Leaves	Kelso
Sorghum	*Holcus sorghum*	Seeds	Merritts
Sudan grass	*S. sudanensis*	Seeds	Merritts
Bluet	*Houstonia*	Leaves	Nelson
Common St. John's-wort	*Hypericum perforatum*	Leaves	MacGregor
St. Johnswort	(sp.)	Leaves, seeds	Nelson
Spotted jewelweed	[2] *Impatiens biflora*	Seeds, leaves	Smyth
Jewelweed	(sp.)	Seeds	

Rush	*Juncus*	Seeds	Smyth
Wild lettuce	*Lactuca*	?	Gilfillan & Bezdek
Deadnettle	*Lamium*	Leaves	Nelson
Wild peppergrass	*Lepidium virginicum*	Leaves	Nelson
Wand lespedeza	*Lespedeza frutescens*	Seed	Merritts
Bush clover	(sp.)	Leaves, seed	Nelson
Deervetch	*Lotus* (sp.)	Seed	Graham
Club moss	*Lycopodium lucidulum*	Buds	MacGregor
Canada mayflower	[1] *Maianthemum canadense*	Seeds, leaves	
Medick	*Medicago*	Leaves	Gilfillan & Bezdek
Cow wheat	*Melampyrum lineare*	Seeds	Gross
Cow wheat	(sp.)	Seeds	Nelson
Sweet clover	*Melilotus altissima*	Seeds	Allen
Peppermint	*Mentha piperita*	Leaves	Smyth
Mint	(sp.)	Seeds	Nelson
Bishop's cap	[2] *Mitella diphylla*	Leaves	
Horsemint	*Monarda*	Leaves	Nelson
One-flowered pyrola	*Moneses uniflora*	Leaves	MacGregor
Moss	*Musci*	Leaves	Kuhn (1940)
Catnip	*Nepeta cataria*	Leaves	Judd
Catmint	(sp.)	Leaves	Kuhn (1940)
Evening primrose	*Oenothera*	Leaves	Nelson
Sensitive fern	*Onoclea sensibilis*	Leaves	MacGregor
Royal fern	*Osmunda regalis*	Leaves	MacGregor
Common wood sorrel	[2] *Oxalis acetosella*	Leaves	Kelso
Lady's sorrel	*O. corniculata*	Leaves	Gross
Yellow wood sorrel	*O. stricta*	Leaves	Judd
Wood sorrel	(sp.)	Leaves	
Switch grass	*Panicum virgatum*	Seeds	Graham, E. H. (letter)

Common Name	Scientific Name	Parts Eaten	References
Panic grass	*Panicum* (sp.)	Seeds	Gross
Wild bean	*Phaseolus*	Seeds	Gilfillan & Bezdek
English plantain	*Plantago lanceolata*	Leaves	Smyth
Plantain	(sp.)	Leaves	Nelson
Fringed polygala	[2] *Polygala paucifolia*	Leaves	Kelso
Milkwort	(sp.)	Leaves	
Small Solomon's seal	*Polygonatum biflorum*	Fruit	Judd
Great Solomon's seal	*P. commutatum*	Fruit	Judd
Solomon's seal	(sp.)	Fruit	Gross
Tearthumb	[2] *Polygonum arifolium*	Seeds	MacGregor
Knotweed	*P. aviculare*	Seeds	Allen
Persicaria	*P. pennsylvanicum*	Seeds	Smyth
Lady's thumb	*P. persicaria*	Seeds	MacGregor
Arrow-leaved tearthumb	*P. sagittatum*	Seeds	MacGregor
Knotweed	(sp.)	Seeds	
Ferns	[1] *Polypodiaceae*	Fronds	
Polypody fern	*Polypodium vulgare*	Fronds	Judd
Christmas fern	*Polystichum acrostichoides*	Fronds	Kelso
Silvery cinquefoil	[2] *Potentilla argentea*	Leaves	Judd
Cinquefoil	*P. canadensis*	Leaves	MacGregor
Cinquefoil	(sp.)	Leaves	
Heal-all	[2] *Prunella vulgaris*	Leaves	
Shin leaf	[2] *Pyrola americana*	Leaves	Gross
Shin leaf	(sp.)	Leaves	
Water cress	*Radicula*	Leaves	Pa. Game News, April, 1936
Buttercup	[2] *Ranunculus abortivus*	Leaves	MacGregor
Tall buttercup	*R. acris*	Leaves	Judd
Bulbous buttercup	*R. bulbosus*	Leaves	Judd

Buttercup	*Ranunculus* (sp.)	Leaves	
Rhynchosia	*Rhynchosia*	Seeds	Nelson
Sheep sorrel	[1] *Rumex acetosella*	Leaves, seeds	
Bloodroot	*Sanguinaria canadensis*	Leaves, flowers	Judd
Sanicle	*Sanicula canadensis*	Seeds	Kuhn (1940)
Sanicle	(sp.)	Seeds	Nelson
Calamint	*Satureja*	Leaves	Kuhn (1940)
Early saxifrage	*Saxifraga virginiensis*	Leaves	Nelson
Saxifrage	(sp.)	Leaves	
Stonecrop	*Sedum*	Leaves	Judd
Groundsel	*Senecio*	Leaves	Nelson
False Solomon's seal	[2] *Smilacina racemosa*	Fruit	
False Solomon's seal	*S. stellata*	Fruit	Smyth
False Solomon's seal	(sp.)	Fruit	
Carrion-flower	[1] *Smilax herbacea*	Fruit	
Horse nettle	*Solanum carolinense*	Fruit	Nelson
Goldenrod	*Solidago*	Leaves	
Sow thistle	*Sonchus*	Leaves	Smyth
Common chickweed	*Stellaria media*	Leaves, seeds	Smyth
Great chickweed	*S. pubera*	Leaves, seeds	Judd
Chickweed	(sp.)	Leaves, seeds	Kelso
Twisted stalk	*Streptopus roseus*	Fruit	Kuhn (1941)
Skunk cabbage	[2] *Symplocarpus foetidus*	Seeds	
Common dandelion	*Taraxacum officinale*	Leaves	Gross
Dandelion	(sp.)	Leaves	
Early meadow rue	*Thalictrum dioicum*	Leaves	Smyth
Tall meadow rue	*T. polygamum*	Fruit	MacGregor
Meadow rue	(sp.)	Leaves	Judd
Meadow parsnip	*Thaspium barbinode*	Leaves	Nelson
Marginal shield fern	[1] *Thelypteris marginalis*	Fronds	

Common Name	Scientific Name	Parts Eaten	References
Spiny-toothed shield fern	*T. spinulosum*	Fronds	
Spiny-toothed shield fern	*T. spinulosum intermedium*	Fronds	
Wood fern	(sp.)	Fronds	
Field penny cress	*Thlaspi arvense*	Leaves	Smyth
False miterwort	[2] *Tiarella cordifolia*	Leaves	
False miterwort	(sp.)	Leaves	
Starflower	*Trientalis americana*	?	Gross
Red clover	[2] *Trifolium pratense*	Leaves	
Low hop clover	*T. procumbens*	Leaves	Graham
White clover	*T. repens*	Leaves	
Clover	(sp.)	Leaves, seeds	Allen
Feverwort	*Triosteum perfoliatum*	Fruit	Judd
Wheat	*Triticum vulgare*	Seed	Smyth
Common speedwell	*Veronica officinalis*	Leaves	Judd
Ironweed	(sp.)	Leaves	
Vetch	*Vicia caroliniana*	Leaves, seeds	Smyth
Vetch	(sp.)	Leaves, seeds	Nelson
Violet	[2] *Viola*	Leaves, seeds	
Barren strawberry	[2] *Waldsteinia fragarioides*	Leaves	
Corn	*Zea mays*	Seed	
Zizia	*Zizia cordata*	Leaves	Nelson
	SHRUBS AND VINES		
European black alder	[2] *Alnus glutinosa*	Buds	VanDersal
Speckled alder	*A. incana*	Buds, catkins, seeds	Smyth
Alder	(sp.)	Buds, catkins, seeds	
American hogpeanut	*Amphicarpa bracteata*	Seeds	Graham
Bristly sarsaparilla	*Aralia hispida*	Fruit	
Sarsaparilla	(sp.)	Fruit	

Bearberry	*Arctostaphylos uva-ursi*	Fruit	
Red chokeberry	[2] *Aronia arbutifolia*	Fruit, buds	
Black chokeberry	*A. melanocarpa*	Fruit, buds	
Chokeberry	(sp.)	Fruit, buds	
Spicebush	*Benzoin aestivale*	Buds	
Thunberg barberry	[2] *Berberis thunbergii*	Fruit	Hosley
European barberry	*B. vulgaris*	Fruit	
Jersey-tea	*Ceanothus americanus*	Leaves	Nelson
Climbing bittersweet	[2] *Celastrus scandens*	Fruit	
Creeping snowberry	*Chiogenes hispidula*	Fruit	Gross
Heartleaf ampelopsis	*Cissus ampelopsis*	Fruit	Nelson
Blue cornel	[1] *Cornus alternifolia*	Fruit	
Silky cornel	*C. amomum*	Fruit	
Roughleaf cornel	*C. asperifolia*	Fruit	Hosley
Roundleaf cornel	*C. circinata*	Fruit	
Flowering dogwood	*C. florida*	Fruit	
Gray dogwood	*C. paniculata*	Fruit	
Red osier	*C. stolonifera*	Fruit, buds	Allen
Dogwood	(sp.)	Fruit	
American hazelnut	[1] *Corylus americana*	Buds, leaves, nuts	
Beaked hazelnut	*C. rostrata*	Buds	
Hazelnut	(sp.)	Buds	
Hawthorn	[1] *Crataegus coccinea*	Fruit, leaves	Judd
Hawthorn	*C. crus-galli*	Fruit, leaves	Judd
Hawthorn	(sp.)	Fruit, leaves	
Bush-honeysuckle	*Diervilla lonicera*	Buds	Kuhn (1940)
Crowberry	*Empetrum nigrum*	Fruit	Gross
Strawberry bush	*Evonymus americanus*	Fruit	Hosley
Burning bush	*E. atropurpureus*	Fruit	Hosley
Teaberry	[1] *Gaultheria procumbens*	Fruit, leaves	

Common Name	Scientific Name	Parts Eaten	References
Black huckleberry	[2] *Gaylussacia baccata*	Fruit, buds	
Dangleberry	*G. frondosa*	Fruit, buds	
Huckleberry	(sp.)	Fruit, buds	
Witch hazel	[2] *Hamamelis virginiana*	Seeds	
Shrubby St. Johnswort	*Hypericum*	Seeds	
Holly	[2] *Ilex collina*	Fruit	Brooks (1943)
Gallberry	*I. glabra*	Fruit	Hosley
Mountain holly	*I. montana*	Fruit	Edminster
Winterberry	*I. verticillata*	Fruit	
Holly	(sp.)	Fruit, leaves	
Dwarf juniper	*Juniperus communis*	Seeds	
Narrow-leaved laurel	[1] *Kalmia angustifolia*	Leaves, buds	
Mountain laurel	*K. latifolia*	Leaves, buds	
Laurel	(sp.)	Leaves, buds	
Privet	*Ligustrum vulgare*	Fruit	Hosley
Privet	(sp.)	Fruit	Hosley
Twinflower	*Linnaea borealis*	Seed	VanDersal
Japanese honeysuckle	*Lonicera japonica*	Fruit	Nelson
Minnie-bush	[2] *Menziesa pilosa*	Buds	Nelson
Partridgeberry	[1] *Mitchella repens*	Fruit, leaves	
Sweetfern	[2] *Myrica asplenifolia*	Buds	Hosley
Bayberry	*M. carolinensis*	Fruit	
Waxmyrtle	*M. cerifera*	Fruit	
Mountain holly	*Nemopanthus mucronata*	Fruit	VanDersal
Virginia creeper	[2] *Parthenocissus quinquefolia*	Fruit	
Shrubby cinquefoil	*Potentilla fruticosa*	Seeds, leaves	Hosley
Chokecherry	[1] *Prunus virginiana*	Fruit, buds	
Bear oak	[1] *Quercus ilicifolia*	Nuts	Hosley
Dwarf chinquapin oak	*Q. prinoides*	Nuts	Hosley

Rhododendron	[2] *Rhododendron maximum*	Leaves, buds	Hosley
Azalea	*R. nudiflorum*	Buds	N. Y. S. Cons. Dept. Ann. Rep., 1937
Azalea	(sp.)	Leaves, buds	
Fragrant sumac	[1] *Rhus aromatica*	Fruit	Allen
Dwarf sumac	*R. copallina*	Fruit	
Smooth sumac	*R. glabra*	Fruit	
Poison ivy	*R. toxicodendron*	Fruit	
Lemonade sumac	*R. trilobata*	Fruit	VanDersal
Staghorn sumac	*R. typhina*	Fruit	
Poison sumac	*R. vernix*	Fruit	
Sumac	(sp.)	Fruit	
Pasture gooseberry	*Ribes cynosbati*	Fruit	Smyth
Wild rose	[1] *Rosa* (sp.)	Fruit, leaves	
Blackberry	[1] *Rubus alleghaniensis*	Fruit, leaves, buds	Judd
Trailing blackberry	*R. hispidus*	Fruit, leaves, buds	
Wild red raspberry	*R. ideaus aculeatissimus*	Fruit, leaves, buds	Judd
Thimbleberry	*R. occidentalis*	Fruit, leaves, buds	Judd
Salmonberry	*R. parviflorus*	Fruit, leaves, buds	Smyth
Dewberry	*R. villosus*	Fruit, leaves, buds	Smyth
Brambles	(sp.)	Fruit, leaves, buds	Smyth
American elder	[2] *Sambucus canadensis*	Fruit	
Red elder	*S. pubens*	Fruit	
Elder	(sp.)	Fruit	
Buffalo berry	*Shepherdia*	Fruit	VanDersal
Sawbrier	[1] *Smilax glauca*	Fruit, leaves	
Catbrier	*S. rotundifolia*	Fruit, leaves	
Greenbriers	(sp.)	Fruit, leaves	
Bitter nightshade	[2] *Solanum dulcamara*	Fruit, leaves	
Meadowsweet	*Spiraea latifolia*	Leaves	Hosley

Common Name	*Scientific Name*	*Parts Eaten*	*References*
Spiraea	*Spiraea* (sp.)	Leaves	Hosley
Snowberry	*Symphoricarpos albus*	Fruit	VanDersal
Coralberry	*S. orbiculatus*	Fruit	Hosley
Snowberry	(sp.)	Fruit	
Canada yew	*Taxus canadensis*	Leaves	Hosley
Lowbush blueberry	[1] *Vaccinium angustifolium*	Fruit, leaves, buds	
Canada blueberry	*V. canadense*	Fruit, leaves, buds	Hosley
Highbush blueberry	*V. corymbosum*	Fruit, leaves, buds	VanDersal
Cranberry	*V. macrocarpon*	Fruit	Hosley
Deerberry	*V. stamineum*	Fruit	VanDersal
Dryland blueberry	*V. vacillans*	Fruit	VanDersal
Cowberry	*V. vitis-idaea*	Fruit	Smyth
Rock cranberry	*V. vitis-idaea minus*	Fruit	Judd
Blueberry	(sp.)	Fruit, leaves, buds	
Mapleleaf viburnum	[1] *Viburnum acerifolium*	Fruit	
Hobblebush	*V. alnifolium*	Fruit	Hosley
Witherod	*V. cassinoides*	Fruit	
Arrowwood	*V. dentatum*	Fruit	Hosley
Wayfaring tree	*V. lantana*	Fruit	Hosley
Nannyberry	*V. lentago*	Fruit	
Squashberry	*V. pauciflorum*	Fruit	VanDersal
Blackhaw	*V. prunifolium*	Fruit	
Hairy nannyberry	*V. pubescens*	Fruit	Hosley
Highbush cranberry	*V. trilobum*	Fruit	
Viburnum	(sp.)	Fruit	
Summer grape	[1] *Vitis aestivalis*	Fruit	
Blueleaf grape	*V. argentifolia*	Fruit	
Frost grape	*V. cordifolia*	Fruit	
Fox grape	*V. labrusca*	Fruit	

Riverbank grape	*V. vulpina*	Fruit	
Grape	(sp.)	Fruit	

TREES

Balsam fir	*Abies balsamea*	Buds, leaves	Allen
Striped maple	[2] *Acer pennsylvanicum*	Buds, seeds	
Red maple	*A. rubrum*	Buds, seeds	Smyth
Sugar maple	*A. saccharum*	Buds, seeds	Hosley
Mountain maple	*A. spicatum*	Buds, seeds	Hosley
Maple	(sp.)	Buds, seeds	
Serviceberry	[2] *Amelanchier canadensis*	Buds	
Serviceberry	(sp.)	Buds	
Sweet birch	[1] *Betula lenta*	Buds	
Yellow birch	*B. lutea*	Buds	
Paper birch	*B. papyrifera*	Buds	
Gray birch	*B. populifolia*	Buds	
Birch	(sp.)	Buds	
Blue beech	[2] *Carpinus carolineana*	Buds, seeds	
Hickory	*Carya*	Nuts, buds	
American chestnut	[2] *Castanea dentata*	Nuts	Smyth
Hackberry	*Celtis occidentalis*	Leaves	Hosley
Southern white cedar	*Chamaecyparis thyoides*	Buds	Hosley
Beech	[1] *Fagus grandifolia*	Nuts, leaves, buds	
Eastern red cedar	*Juniperus virginiana*	Buds	Hosley
Tamarack	*Larix laracina*	Leaves	
American crabapple	[1] *Malus coronaria*	Leaves, fruit	Merritts
Wild apple	*M. pumila*	Buds, leaves, fruit	
Apple	(sp.)	Buds, leaves, fruit	
Red mulberry	*Morus rubra*	Buds	Judd
Mulberry	(sp.)	Buds	

Common Name	*Scientific Name*	*Parts Eaten*	*References*
Black gum	[2] *Nyssa sylvatica*	Fruit, buds	
Hophornbeam	[1] *Ostrya virginiana*	Buds, seed	
Spruce	*Picea*	Leaves	
Pitch pine	*Pinus rigida*	Leaves, seeds	
Northern white pine	*P. strobus*	Leaves, seeds	Smyth
Pine	(sp.)	Leaves, seeds	Kelso
Sycamore	*Platanus occidentalis*	Leaves (?)	Smyth
Balsam poplar	[1] *Populus balsamifera*	Buds, catkins	
Largetooth aspen	*P. grandidentata*	Buds, catkins	
Quaking aspen	*P. tremuloides*	Buds, catkins	
Poplar	(sp.)	Buds, catkins	
Wild plum	[1] *Prunus americana*	Leaves, fruit	Smyth
Sweet cherry	*P. avium*	Leaves, fruit	Judd
Plum	*P. domestica* var.	Leaves, fruit	Judd
Pin cherry	*P. pennsylvanicum*	Leaves, fruit	
Peach	*P. persica* var.	Leaves, fruit	Judd
Black cherry	*P. serotina*	Leaves, fruit	
Cherry	(sp.)	Leaves, fruit	
Pear	*Pyrus communis* var.	Leaves, fruit	Judd
White oak	[1] *Quercus alba*	Nuts	VanDersal, Allen
Northern red oak	*Q. borealis*	Nuts	VanDersal
Chestnut oak	*Q. montana*	Nuts	
Pin oak	*Q. palustris*	Nuts	
Red oak	*Q. rubra*	Nuts	
Oak	(sp.)	Nuts	
Black locust	*Robinia pseudoacacia*	Seed	
Willow	[2] *Salix*	Buds, leaves	
Sassafras	*Sassafras varifolium*	Fruit	Kuhn (1941)
American mountain ash	[2] *Sorbus americana*	Buds, fruit	

European mountain ash	*S. aucuparia*	Buds, fruit	Hosley
Mountain ash	(sp.)	Buds, fruit	
Northern white cedar	*Thuja occidentalis*	Buds	
Basswood	*Tilia glabra*	Buds	
Eastern hemlock	*Tsuga canadensis*	Buds, seeds	
American elm	*Ulmus americana*	Buds	VanDersal
Elm	(sp.)	Buds	

Table 6

Animal Foods Eaten by the Ruffed Grouse in the Northeast

Scientific and Common Names	*Eaten by*	*References*
Phylum Arthropoda		
Class Hexapoda		
Order Orthoptera		
Gryllidae (Crickets)		
Gryllus assimilis	Adult	Gross
(sp.)	Adult	Judd
Acrididae (Shorthorned grasshoppers)		
Melanoplus femur-rubrum	Adult	Judd
Unidentified	Adult and young	Smyth
Locustidae (Longhorned grasshoppers)		
Xiphidium (sp.)	Adult	Judd
Unidentified	Adult and young	Judd
Phasmidae (Walking sticks)		
Diapheromera femorata	Adult	Smyth
Order Neuroptera		
Chrysopidae (Lacewing flies)		
Chrysopa (sp.)	Young	N. Y. S. Cons. Dept. Ann. Rep.
Order Corrodentia		
Psocidae (Psocids)		
Unidentified	Adult	Smyth
Order Homoptera		
Membracidae (Tree hoppers)		
Unidentified	Adult and young	Judd
Cicadellidae (Leaf hoppers)	Adult and young	Smyth, Kuhn
Aphididae (Aphids)		
Unidentified	Adult and young	Smyth
Order Hemiptera		
Miridae (Leaf-bugs)		
Unidentified	Adult and young	
Reduviidae (Assassin-bugs)		
Zelus (sp.)	Adult	Kelso
Unidentified	Adult and young	Judd
Unidentified (Nymph)	Adult	Smyth
Phymatidae (Ambush-bugs)		
Phymata (sp.)	Adult	Judd
Lygaeidae (Chinch-bugs)		
Drymus crassus	Adult	Kelso
Blissus leucopterus	Adult	Judd
Eremocoris ferus	Adult	Gross
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.

Table 6 (*Continued*)

Animal Foods Eaten by the Ruffed Grouse in the Northeast

Scientific and Common Names	*Eaten by*	*References*
Aradidae (Flat-bugs)		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Pentatomidae (Stink-bugs)		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Order Coleoptera		
Cicindelidae (Tiger-beetles)		
Cicindela punctulata	Adult	Smyth
Carabidae (Ground-beetles)		
Sphaeroderus (sp.)	Adult	Gross
Harpalus (sp.)	Adult	Judd
Bothriopterus (sp.)	Adult	Gross
Anisodactylus (sp.)	Adult	Judd
Pterostichus (sp.)	Adult	Judd
Chlaenius (sp.)	Young	
Unidentified	Adult and young	Judd
Staphylinidae (Rove-beetles)		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Lampyridae (Fireflies)		
Lucidota corrusca	Adult	Kelso
L. nigricans	Adult and young	Smyth
(sp.)	Adult	Gross
Unidentified	Adult and young	Judd
Cantharidae (Soldier-beetles)		
Cantharis (sp.)	Adult	Gross
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Elateridae (Click-beetles)		
Unidentified	Adult and young	Judd
Helodidae		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Buprestidae (Metallic wood-borers)		
Unidentified	Adult	Judd
Ostomatidae		
Calitys scabra	Adult	Smyth
Coccinellidae (Lady-bugs)		
Chilocorus bivulucrus	Adult	Gross
Unidentified	Adult	Kuhn

Table 6 (*Continued*)

Animal Foods Eaten by the Ruffed Grouse in the Northeast

Scientific and Common Names	*Eaten by*	*References*
Lagriidae		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Anobiidae		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Scarabaeidae (Lamellicorn beetles)		
Aphodius (sp.)	Adult	Kelso
Dichelonycha (sp.)	Adult	Judd
Lachnosterna hirsuta	Adult	Judd
(sp.) (larva)	Young	Judd
Unidentified	Young	F. C. Edminster
Cerambycidae (Longhorned beetles)		
. . *Hapalosalia vibex*	Adult and young	Smyth
Chrysomelidae (Leaf-beetles)		
Diabrotica vittata	Adult	Smyth
Leptinotarsa decemlineata	Adult	Judd
Phaedon armoraciae	Adult and young	Smyth
Lina tremulae	Adult	Kuhn
Haltica chalybea	Adult	MacVicar '18
Donacia (sp.)	Adult	Smyth
Galerucella sexvittata	Adult and young	Smyth
G. cavicollis	Adult	Gross
G. sagittariae	Adult	Judd
Microrhopala (sp.)	Young	
Calligrapha (sp.)	Adult	Gross
Adoxus vitis	Adult	Judd
Chaetocnema (sp.)	Adult	Judd
Systena hudsonias	Adult	Judd
S. blanda	Adult	Judd
Disonycha caroliniana	Adult	Judd
Unidentified	Adult and young	Judd
Curculionidae (Snout-beetles)		
Sitones hispidulus	Adult	Judd
Unidentified	Adult and young	Smyth, N. Y. S. Cons. Dept. Ann. Rep.
Order Mecoptera		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Order Trichoptera		
Phryganeidae		
Unidentified	Adult and young	Gross, N. Y. S. Cons. Dept. Ann. Rep.

Table 6 (*Continued*)

Animal Foods Eaten by the Ruffed Grouse in the Northeast

Scientific and Common Names	*Eaten by*	*References*
Order Lepidoptera		
Olithreutidae		
Carpocapsa pomonella (codlin moth)		
Carpocapsa larva	Adult	Smyth
Geometridae		
Unidentified larva	Adult	Smyth
Notodontidae		
Symmerista albifrons	Adult	Judd
Schizura concinna	Adult	Judd
Noctuidae (owlet-moths)		
Alabama argillacea	Adult	Judd
Cirphis unipuncta	Adult	Judd
Noctua (sp.)	Adult and young	Judd
Unidentified larva	Adult and young	Smyth, N. Y. S. Cons. Dept. Ann. Rep.
Unidentified larva	Adult and young	Smyth
Unidentified eggs	Adult and young	Smyth
Order Diptera		
Tipulidae (Crane-flies)		
Unidentified	Adult and young	Judd, Smyth
Culicidae (Mosquitoes)		
Unidentified	Adult	Smyth
Mycetophilidae (Fungus-gnats)		
Mycetophila (sp.)	Adult and young	Smyth
Bibionidae (Marsh-flies)		
Bibio (sp.)	Adult	Gross
Dilophus (sp.)	Adult	Gross
Leptidae (Snipe-flies)		
Rhagio mystacea	Adult and young	Smyth
Unidentified	Adult	Smyth
Asilidae (Robber-flies)		
Unidentified	Adult and young	Kelso, N. Y. S. Cons. Dept. Ann. Rep.
Empididae (Dance-flies)		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Syrphidae (Syrphus-flies)		
Unidentified	Adult and young	Kuhn, F. C. Edminster
Muscidae		
Unidentified pupa	Adult and young	Smyth
Unidentified larva	Adult	Smyth
Unidentified pupae	Young	Smyth, N. Y. S. Cons. Dept. Ann. Rep.

Table 6 (*Continued*)

Animal Foods Eaten by the Ruffed Grouse in the Northeast

Scientific and Common Names	*Eaten by*	*References*
Order Hymenoptera		
Tenthredinidae (Sawflies)		
Neodiprion (sp.) larva	Adult	Judd
Nematus (sp.)	Adult	Judd
Unidentified	Young	Smyth
Braconidae (Braconids)		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Ichneumonidae (Ichneumon-flies)		
Amblyteles (sp.)	Adult	Kelso
Unidentified	Adult and young	Smyth
Serphidae		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Pelecinidae		
Pelecinus polyturator	Adult	Judd, Gross
P. polyturator larva	Adult	Judd
Cynipidae (Gall-wasp)		
Amphibolips (sp.)	Adult	Judd
Unidentified	Adult	Judd
Chalcididae (Chalcid-flies)		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Formicidae (Ants)		
Formicina (sp.)	Adult	Gross
Formica (sp.)	Adult and young	Gross, F. C. Edminster
Camponotus pennsylvanicus	Adult and young	Judd
C. herculeanus	Adult	Gross
(sp.)	Adult	Gross
Tetramorium caespitum	Adult and young	Judd
Unidentified	Adult and young	Smyth
Vespidae (Wasps)		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Sphecidae		
Unidentified	Adult and young	N. Y. S. Cons. Dept. Ann. Rep.
Andrenidae		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.

Table 6 (*Continued*)

Animal Foods Eaten by the Ruffed Grouse in the Northeast

Scientific and Common Names	*Eaten by*	*References*
Tiphiidae		
Unidentified	Young	N. Y. S. Cons. Dept. Ann. Rep.
Unidentified cocoon	Young	F. C. Edminster
Class Arachnida		
Order Araneae (Spiders)		
Lycosidae (Wolf spiders)		
Unidentified	Adult	Judd
Attidae (Jumping spiders)		
Unidentified	Adult and young	Judd
Unidentified	Adult	Gross
Order Phalangida (Harvestmen)		
Phalangiidae		
Unidentified larva	Adult and young	Judd
Class Myriopoda		
Order Diplopoda (Millipedes)		
Julus (sp.)	Adult and young	Smyth
Unidentified	Adult	Judd
Phylum Mollusca		
Class Gastropoda		
Order Pulmonata (Snails, slugs)		
Helix (sp.)	Adult and young	Judd, N. Y. S. Cons. Dept. Ann. Rep.
Limax (sp.)	Adult	Judd
Tebennophorus carolinensis	Adult	
Phylum Chordata		
Class Reptilia		
Suborder Serpentes (Snakes)		
Colubridae		
Unidentified	Adult	Smyth

TABLE 7

SUMMARY OF NORTHEAST GROUSE FOOD RECORDS OF A. A. ALLEN

State			*New York*			*Pennsylvania*	*New Jersey*	*New England*
Years Involved			*1925–27; few 1928–30*			*1925–27; few 1928–30*	*1925–29*	*1925–28*
Period of Records			*Oct.*	*Nov.*	*Dec.–Apr.*	*Oct.–Feb.*	*Nov.–Dec.*	*Fall*
No. of Specimens			126	112	10	51	13	9
Food Taken		*Parts Eaten* [1]	*% Incidence*	*% Incidence*	*% Incidence*	*% Incidence*	*% Incidence*	*% Incidence*
	VEGETABLE							
Hawthorn	*Crataegus*	f	49.3	34.0	10.0	29.4	30.8	33.3
	Leaves and green matter	l	36.5	47.4	20.0	54.9	53.8	11.1
	Buds and twigs	b	19.9	25.0	50.0	19.6	15.4	...
Cherry	*Prunus*	f,b	15.9	7.2	...	2.0	7.7	...
Grape	*Vitis*	f	14.3	16.2	20.0	21.6	15.4	11.1
Dogwood	*Cornus*	f	12.7	20.6	...	43.2	38.5	22.2
Oak	*Quercus*	f,b	6.4	5.4	...	13.7	15.4	...
Viburnum	*Viburnum*	f,l	5.6	3.6	...	...	7.7	...
Teaberry	*Gaultheria procumbens*	f,l	4.8	7.2	10.0	7.8	7.7	...
Apple	*Malus*	f,l	4.8	.9	...	...	...	11.1
Partridgeberry	*Mitchella repens*	f,l	4.8	2.7	...	3.9	...	...
Elder	*Sambucus*	f	4.8	...	...	...	...	...

Clover	*Trifolium*	f,l	4.8	.9	...	3.9	...	...
	Fruits or seeds	..	4.0	8.0	...	5.9	...	...
Birch	*Betula*	b	2.4	1.8	...	...	...	...
Tick trefoil	*Desmodium*	f	2.4	...	...	...	...	...
Solomon's seal	*Polygonatum*	f	2.4	1.8	...	...	...	...
Sumac	*Rhus*	f	2.4	9.8	20.0	29.4	...	...
Buckwheat	*Fagopyrum esculentum*	f	1.6	1.8	...	...	...	...
Beech	*Fagus grandifolia*	f	1.6	4.5	...	...	...	...
Strawberry	*Fragaria*	l	1.6	3.6	30.0	2.0	7.7	...
Geum	*Geum*	f	1.6	3.6	...	...	...	...
Knotweed	*Polygonum*	f	1.6	...	...	...	...	...
Wild rose	*Rosa*	f	1.6	.9	...	3.9	15.4	...
Corn	*Zea mays*	f	1.6	...	...	...	..	...
Alder	*Alnus*	b	.8	1.8	...	2.0	...	...
Chestnut	*Castanea*	f	.8	...	...	..	...	...
Bishop's cap	*Mitella*	f,l	.8	3.6	...	...	...	...
Buttercup	*Ranunculus*	l	.8	...	10.0	...	...	...
Ferns	*Polypodiaceae*	l	...	5.4	...	2.0	...	...
Wood sorrel	*Oxalis*	l	...	3.6	...	...	...	...
Brambles	*Rubus*	l	...	2.7	...	...	...	...
	Galls	..	...	1.8	...	...	...	...
Greenbrier	*Smilax*	f	...	1.8	...	...	...	...
Virginia creeper	*Parthenocissus quinquefolia*	f	...	.9	...	...	...	...
Poplar	*Populus*	b	...	.9	...	3.9	7.7	11.1
Skunk cabbage	*Symplocarpus foetidus*	f	...	.9	...	...	7.7	...
Dandelion	*Taraxacum*	l	...	.9	...	...	...	...
Aster	*Aster*	l	...	...	10.0	...	...	...

[1] Parts eaten: f=fruit, seeds or nuts; b=buds, twigs; l=leaves, catkins.

State Years Involved Period of Records No. of Specimens			New York 1925–27; few 1928–30 Oct. 126	 Nov. 112	 Dec.–Apr. 10	Pennsylvania 1925–27; few 1928–30 Oct.–Feb. 51	New Jersey 1925–29 Nov.–Dec. 13	New England 1925– 28 Fall 9
			% Incidence	% Incidence	% Incidence	% Incidence	% Incidence	% Incidence
Grasses	*Gramineae*	l	...	...	10.0	...	...	...
Witch hazel	*Hamamelis virginiana*	b	...	...	10.0	15.7	...	...
Laurel	*Kalmia*	l	...	...	...	3.9	...	...
Black chokeberry	*Aronia melanocarpa*	f	...	...	...	2.0	...	...
White mustard	*Brassica alba*	f	...	...	...	2.0	...	...
Sweet clover	*Melilotus altissima*	f	...	...	...	2.0	...	...
Bitter nightshade	*Solanum dulcamara*	f	...	...	...	2.0	...	...
Agrimony	*Agrimonia*	l	...	...	...	...	7.7	...
Barren strawberry	*Waldsteinia*	l	...	...	...	...	7.7	...
False Solomon's seal	*Smilacina*	f	...	...	...	...	...	11.1
ANIMAL								
Insects		..	4.8	.9	...	...	...	...
Spiders		..	.8	...	...	...	...	...

References listed for animal food records are cited fully in the list at the end of this chapter. "N. Y. S. Cons. Dept. Ann. Rep." refers to *Annual Reports of the New York State Conservation Department.* "F. C. Edminster" indicates records obtained by the author: the identifications for these are by John C. Jones.

I am indebted to Earl C. Murdoch, formerly of the U. S. Soil Conservation Service for assistance in checking insect names and in arranging them in order, and to Dr. J. C. Bradley of Cornell University for checking names found in references.

It will be noted that in genera having records of definite species eaten, there is often also a listing of the genus "sp." This may in some cases result in duplication since the material identified only to genus by one author may be the same as one fully identified by another. Since such duplication is not definite, it was determined best to list them both when this situation arose.

The above summary of ruffed grouse food-habit records (Table 7) covers 321 specimens received by Dr. A. A. Allen in connection with his disease studies between 1925 and 1930. The analyses were largely made by his students. Only incidence of occurrence of each type of food is available since volumetric measurements were not made. This material has not heretofore been published.

QUALITY OF DIFFERENT GROUSE FOODS

Wild-life foods have been variously classified according to their availability, palatability, and physiological effects (Leopold, 1933). Terms such as "preferred," "staple," "incidental," "emergency," "stuffing," and "salad" have been used to distinguish and describe them. The first three of these adjectives apply to many grouse foods according to their quality.

A preferred food is one that is selected by the bird when other usable items are available. It stands among the highest ranks of palatable foods.

A staple food is one that furnishes a large proportion of the bird's food in a given season, and probably is highly palatable. However, it may be lower in the scale of palatability than the preferred foods.

Incidental foods are those taken normally in small quantities and quite variably in different localities. They either rank below staple foods in the palatability scale or are less available.

Since the grouse is a browser, it is doubtful that it ever has to make a choice of an emergency food. If any foods are accessible, some of its regular articles of diet will be among them. No evidence of the consumption of "stuffing" or "salad" foods was obtained. As a matter of fact, it is difficult in many cases to distinguish between preferred and staple foods of the grouse.

Some grouse foods, however, are clearly preferred. Beechnuts, red haws, apple fruit or foliage, acorns, strawberry fruits and leaves, bramble fruits, greenbrier berries, and grapes are so utilized, and birch, apple, fern, popple, cherry, and blueberry are choice among the leaf and bud foods. Certainly in a sense, birch buds are preferred, as they are regularly taken in preference to many other equally available foods of this type, as those from beech, maple, elm, ash, and hickory, for example. Yet, it is likely that if beechnuts, hawthorn fruits and certain other foods were available in winter much less of birch buds would be taken.

Preference must be interpreted with due regard to availability. It is likely that chestnuts would be a preferred food if available, since they probably once were of primary rank. Being absent now over most of the range, they rank merely as an incidental food.

Most of the foods listed above as primary and secondary may also be considered staple, while those not so classed are ordinarily incidental.

VARIATION IN SUMMER FOOD HABITS OF YOUNG AND ADULTS

The groups of plants and animals providing the bulk of the summer food are essentially the same for both adults and young. The quantities taken by birds of these age classes, however, may vary widely. Young birds in early summer consume a very high proportion of animal food whereas the adults use only a moderate quantity. The two topmost food-producing groups of plants, brambles (*Rubus*) and sedges (*Carex*) are the same throughout New York for the chicks. *Rubus* ranks first for adults, but one or the other of *Carex*, cherries (*Prunus*) and popples (*Populus*) takes second place in different localities. The volume of raspberries used by chicks (twenty-nine per cent–thirty-eight per cent summer average) greatly exceeds that taken by adults. There are numerous other variations in summer food habits between the adults and young, mostly, however, of minor importance.

RELATION OF FOOD SUPPLY TO COVER TYPES

There is great variation in the composition of the major cover types including the species that furnish food for the grouse. Some types are more satisfactory than others from the standpoint of food, even that supplied by the same species. For example, plants as a rule produce more fruit when in full sunlight than when partly shaded. Thus grapevines are more productive when in slashings or other brushy areas than in a woodland. Further, the fruit that is produced inside a woodland is mostly at the top of the vines up in the crown where it is rather inaccessible for grouse.

Some vegetational types are more valuable for the food they produce at one season, than at another, as an example, the pure popple subtype which has its greatest value in winter, for the buds, and again for a time in summer, for the catkins. The value of the several cover types as food or shelter producers is of prime importance when considering the need for interspersion of types. The perfect mingling would result in the best feeding and roosting coverts being adjacent for each of the seasons.

The major relations of food supply to cover types may be summed up as follows:

Cover type	*Season*	*Relative food-producing value*
Open land	Summer and fall	High
	Winter and spring	Low
Overgrown land	Fall and summer	Very high
	Spring and winter	Medium to high
Slashings	Summer	Very high
	Fall, spring and winter	Medium
Hardwood woodland	Winter and spring	High to very high
	Summer and fall	Low to medium
Mixed woods	Winter and spring	Medium to high
	Summer and fall	Low to medium
Coniferous	All year	Low to medium

As to cover types in which various foods are produced, we may make the following generalizations, the cover types being listed about in the order of their productiveness:

Fruits—overgrown land, slashings
Nuts—hardwood woodland, mixed woods
Seeds—overgrown land, open land, slashings
Buds—hardwood woodland, mixed woods, overgrown land
Leaves—hardwood woodland, mixed woods, overgrown land, slashings
Insects—slashings, overgrown land, open land

DISTRIBUTION OF BIRDS AS AFFECTED BY FOOD SUPPLY

The distribution of grouse is affected by the food supply both daily and seasonally. Each morning, weather permitting, the birds leave their roost, selected for its shelter value, and seek the food-producing covert most readily available. This may be right where they roosted, but more likely it is a little distance away. Again at evening the feeding coverts are sought, after which the birds retire to the roosting place. Thus the proper location of feeding coverts with respect to shelter is of immense importance in determining the carrying capacity of an area, since both must occur within the daily cruising radius of the birds and must be suitable for all seasons of the year.

In a more extensive manner the location of certain types of food-producing coverts affects the seasonal distribution. Overgrown land, particularly that with preferred foods such as the fruits of hawthorn or dogwood, markedly affect the range of grouse in the fall. Slashings and some types of overgrown land draw many grouse during the summer, while in the spring the hardwood woodlands probably have their greatest effect on distribution as affected by food habits. Food supply has least effect in winter, when widely available buds are the dominant food and shelter the prime need for existence.

EFFECTS OF CULTURAL OPERATIONS ON THE FOOD SUPPLY

It is well recognized that the workings of man may have profound effects on grouse range. What are the effects on the food supply of the birds? Let us consider this question for each of the important cultural practices.

Lumbering: Woodland cutting practices change the food conditions of a woodland in proportion to their severity. In some respects food supplies for grouse may be increased, in others, decreased. The cutting of a growth of mast-producing trees, as oak and beech, removes it from production for decades. This is probably the most serious destructive effect of lumbering on the food of the grouse and is most injurious in the southern part of the range. In the same way, lumbering takes some of the important bud-supplying species as cherry, poplar, and birch, out of production for several years. A

by-product of lumbering is the common destruction of the so-called weed species, which often include important food-producing trees, including hornbeam, beech, and hophornbeam. In a table classifying thirty-seven New York tree species of upland woodlots according to usefulness (Cope, 1933), three important grouse food-producing trees are among the fourteen valuable species (red and white oak and black cherry), eight are among the thirteen intermediate species, and eight of ten inferior species are important grouse food plants. A similar list classifying forty-six trees of West Virginia ". . . according to their cash value" includes but three important grouse food-producers (the same three as above) among eighteen valuable species. The sixteen inferior species included six important grouse food plants while the twelve weed species had nine (Smith & Byers, 1941).

Fortunately, woodland cutting often results in more improvement than injury. Shrubs are released so that they produce larger crops of fruit. Brambles, pin cherry, quaking aspen, and other desirable woody plants germinate in the new openings; the herbaceous food plants are usually greatly increased. Insect food also is much more plentiful in slashings and woodland openings than in the woodland proper.

It is clear then that taking out wood products may readjust the grouse food situation in many respects. Since the changes depend upon the type of cutting operation and upon the conditions existing before cutting, it is apparent that regulation of woodland cuttings may be made an important method of improving food conditions for grouse.

Burning: Woods fires initially destroy grouse food. However, the plant succession resulting from a fire often brings in a more desirable food supply than formerly existed, or at least adds variety. A light ground fire temporarily removes most of the herbaceous ground cover and some of the shrubby understory. The plants that then spring up are likely to be somewhat but not strikingly different from those destroyed. A crown fire, or a very hot understory fire, however, will create an entirely different cover type which at first is practically useless for grouse. In a few years, however, it may become an important food-producing area serving the purpose of a slashing. The vegetation on these burns is often dominated by pin cherry, poplar, brambles, and blueberry.

Fencing and Livestock: Woodlands adjacent to pastures present a management problem to a farmer. The desirability of fencing the woodlands so that the livestock may not have access to them is gaining increasing recognition. It is generally true in the Northeast that one cannot have a good pasture and a good woodland on the same ground. Likewise the pasturing of woodland has a detrimental effect on the area as grouse cover.

The most obvious effect of pasturing a woodland is the reduction of the understory and ground cover. That materially affects the supply of grouse food and often entirely eliminates important food-producing herbs and shrubs. The changes that grazing brings about in soil conditions may affect the plant succession on the area for a long time following abandonment of grazing; the effect is to set back the ecological stage toward the field weed complex. If grazing is continued intensively it eventually results in the transformation of the woodland into a park-like area, and ultimately into an open field.

Ploughing and Cultivating: Since the use of the plough and other crop field tools are normally confined to the better-quality open fields, these practices do not materially affect grouse in a direct sense. It is true that a cultivated field is less desirable to grouse than a weedy meadow, but their use as cover is too small to be important. As openings to provide edges, one field type is as good as another.

From the long-time point of view, the maintenance of land in field crops prevents it from becoming grouse cover and is a restriction on the increase of available grouse foods as well as of shelter.

FOOD AS A LIMITING FACTOR

There are few species of game birds that have as little trouble finding food year in and year out as the ruffed grouse. If a covert is of a nature to permit grouse existence from the standpoint of size and shelter, it is likely to provide enough food for the maintenance of at least some grouse. This does not in any way imply that food is not an important factor. It is. But the grouse can get along on such a wide variety of foods. It uses parts of plants that are almost always available, regardless of weather conditions or competition of other animals, that almost any type of woody area will provide some food.

This may not be true everywhere in the range of the ruffed grouse but is generally true in the Northeast.

That the supply of food is a possible limiting factor in areas that are well stocked with grouse is conceivable although not likely. Let us consider this prospect under some of the most likely conditions.

Food Shortages: A shortage of food for adults at any time of the year except winter and early spring, or for chicks except during the first six weeks of life is altogether unlikely. So far as fruits, seeds, and succulent leaves are concerned, a drastic food shortage in late winter and early spring is conceivable. A lack of buds of hardwood trees and shrubs, however, is out of the question. As grouse are well able to thrive for considerable periods on a diet of buds, we can rule out shortage of foods for the adult as a limiting factor on the usual grouse range.

A shortage of insects in June or early July, at which time they are a vitally necessary food for the young bird, would be disastrous. Normally, grouse coverts contain from one hundred to five hundred thousand insects and other arthropods per acre at this time of year in the zone from the loose ground litter to a height of one foot above ground, the area of availability to young grouse (estimates from measurements taken on Connecticut Hill). Variation in normal years depends upon the cover type and the weather. While we have not measured the insect populations in severely abnormal seasons, we do know enough about the effect upon them of exceedingly cold and wet weather to surmise the possible consequences to young grouse. Shortage of animal food during seasons of cold, or cold and wet from mid-May to the end of June is one of the likely contributing causes of excessive juvenile mortality that often precede years of greatly decreased grouse numbers (see effects of weather on grouse, Chapter VI). The question as to whether these losses in young birds occur primarily as a result of food shortage or directly from the cold is not clear. Surely the two factors sometimes combine to take a heavy toll.

Availability during Emergencies: We have already pointed out that foods provided by low-growing vegetation, mainly leaves, fruits, and seeds, may be completely covered with snow for considerable periods in the winter. These, then, are relatively inaccessible although the birds are surprisingly able in seeking them out. But tree

buds are always available above the snow, and the grouse turn largely to them for food when snow is deep.

What then, if sleet or freezing rain puts a coating of ice upon all vegetation? This condition probably renders completely unavailable foods under the snow. It may make budding difficult but probably does not entirely prevent it. Even if the ice coating is complete enough and thick enough to prevent feeding by grouse, it seldom lasts long enough to cause starvation of the birds. It is normal for grouse to refrain from eating for a day or two during bad storms anyway. The fact that not a single normally healthy[1] grouse has been known to die of starvation is proof enough of the ability of the species to forage satisfactorily under any winter conditions that have been observed.

If cold or wet early summer weather may be considered an emergency, then we probably have one type of food emergency that young grouse are sometimes unable to meet. This condition has just been discussed.

Competition of Other Species for Food: In considering the major grouse food plants, notes were made concerning competition for these foods with other forms of wild life. Most of the preferred foods are also taken by other species in considerable amounts, but in only a few cases does this noticeably affect the grouse. Even in these few cases,[2] only the local distribution of the birds is modified. Rarely, if ever, is the number of grouse over a large area materially affected by food competition.

Maintenance of Grouse Health: Does the availability of certain foods affect the health of grouse? More particularly, does the relative lack of fruits and green leaves in late winter in the northern range and the resulting dependence on a bud diet so affect the bodily health of the birds that their breeding-season vigor is impaired? If that were true, would it result in weakened young birds the following spring or summer? Does the quality of certain types of important foods used in winter and early spring, such as buds, vary in different years in a manner that affects the health of the birds in the spring, resulting in weakened offspring? Conceivably the chemical content of tree leaf buds, possibly in regard to the representa-

[1] We have observed cases of starvation in birds with injuries to their digestive system.

[2] Swanson (1942) notes that grouse are never abundant in an overbrowsed deer yard due to the destruction by deer of important grouse food plants.

tion of some important vitamin, might be affected by changes in the character of sunlight reaching the earth in different years. And that change might be brought about by the cycles in sunspots.

These questions and others of similar import have been seriously asked in recent years. Sunspot cycles have been clearly recognized, and some correlations with fluctuations in life on the earth seem to be satisfactorily established. It followed, therefore, that the records of grouse cycles would be compared with the sun phenomenon. The correspondence is not conclusive, although there appears to be enough relationship to maintain one's further interest.

The evidence at hand refutes the probability of any serious relationship between quality of food and high mortality among grouse. However, the matter is far from settled, and the opportunity for direct testing of the possible relationships is practically virgin. It seems probable that if a deficiency in winter food quality resulted in weakling chicks, it would show a definite effect in one or more of the leading factors in reproduction: size of clutch, degree of fertility, proportion of females nesting, or percentage of loss of embryos during incubation. None of these, however, show any connection with excessive infant mortality that we can discern. We must conclude tentatively, therefore, that the hypothesis of a major connection between food quality and grouse health is unlikely to be valid.

ECONOMIC ASPECTS OF GROUSE FOOD HABITS

Early investigators rated the ruffed grouse an important economic asset to the farmer from the standpoint of its insect consumption. According to Judd (1905) "Bugs . . . are much more often destroyed by bobwhite and the ruffed grouse than by other birds. The ruffed grouse has been known to prey on the chinch bug, which at times is the most injurious insect in our country, and seldom destroyed by any gallinaceous birds. Farmers who permit market hunters to rob them of their game should remember this point." This inclination to point up the insect-consuming habits of grouse as a benefit to agriculture was natural but the conclusion reached has not withstood the test of further study. In the first place, the grouse are dominantly insectivorous only as chicks, and then only for a few weeks. Secondly, the insects are taken primarily from

woodland coverts, not from crop fields where agricultural benefits might be involved. Thirdly, while many of the insects taken are of injurious types, many others are beneficial, or neutral in economic importance. Lastly, grouse are never abundant enough near farm fields to be a real factor in controlling insects under any conditions. And so we must conclude that the direct economic aspects of grouse insect eating are practically negligible. The grouse may be considered, however, as part of the combined force of all insect-eating birds that tends to lower the number of all insects—doubtless a desirable accomplishment.

Another phase of grouse food habits has proved to be significantly destructive to agriculture in some localities. The habit of budding apple trees sometimes results in sufficient damage to the trees to impair their productivity. In Massachusetts and New Hampshire this habit has resulted in bounty payments and state-paid damage claims in years past. In recent years the damage claims paid by New Hampshire due to grouse budding apple trees has varied from about $26,000 in 1926 to a low of $12.57 in 1938. The highest amount for the past decade was $3,488.07 in 1935 on seventy claims.[1] It is interesting to note that these claims are based on a twofold damage: to the succeeding apple crop, and to the tree itself. Grouse have been known to take as high as ninety per cent of the buds from individual trees in a single season. Fortunately this damage does not occur commonly in commercial orchards.

In other respects the food habits of the grouse are of little or no significance to man's interests. We may, therefore, summarize their economic importance as generally neutral.

USE OF GRIT

The grouse is one of the type of birds that have a strong, muscular gizzard that crushes the food after receiving it from the crop. In order that the gizzard walls may perform this function satisfactorily, hard particles must be present in the gizzard to act as a grinding agent. Ordinarily, small stones are swallowed deliberately by the birds for this purpose. Occasionally hard seeds assist in the crushing of other foods. Red haw (*Crataegus*) seeds are notable in this con-

[1] Records kindly made available by the New Hampshire Fish and Game Department.

nection and they are often retained in the gizzard for considerable lengths of time, as evidenced by their worn condition.

In Smyth's records for October, the gizzards averaged thirty-four particles of grit each which composed nine and three-tenths per cent of the gizzard contents. The extremes ranged from several having no grit at all to one having three hundred and ten bits of gravel (thirty-two per cent of contents). Other highs were two hundred and ninety-seven (thirty-six per cent) and one hundred and seventy-seven (forty-five per cent) stones. Two having no stones contained worn *Crataegus* seeds.

In Smyth's November records, the gizzards averaged thirty-seven bits of grit, which were nine and nine-tenths per cent of the contents. Eleven had quartz stones and four had worn *Crataegus* seeds but no gravel. His winter records showed an average of twenty-seven stones each (seven and three-tenths per cent of gizzard contents). In six spring records, the gizzards averaged fifty-eight stones each, fourteen per cent of the total contents.

Kuhn (1940) found gravel in only nine crops out of two hundred and thirty examined, but he did not report on the gizzard contents. This indicates the slow rate of ingestion of gravel needed to maintain the required quantity in the gizzard. Similarly, Nelson et al. (1938) found only eight crops out of one hundred and eighty-four to contain gravel, while of one hundred and seven gizzards from the same specimens, seventy-six contained gravel averaging eight-tenths cubic centimeters or one-third teaspoonful each. Of those not containing gravel, all had hard seeds showing wear, including those of rose, greenbrier, sumac, dogwood, witch hazel, and black gum.

Kelso's (1935) report gives the winter average of grit in the gizzards as seven and nine-tenths per cent in New York, ranging from four and eight-tenths per cent in March to nine and eight-tenths per cent in January. There is clearly a considerable variation in need for grit at different times of the year, depending upon the nature of the foods being eaten. Probably buds and twigs demand the most grit while soft insects require the least. Hard seeds, if digested, also would require a lot of grinding, while soft fruits would need little. We can, therefore, generalize that grit is most needed in winter, when hardest to get, and least required during the summer.

WATER REQUIREMENTS OF GROUSE

The ruffed grouse, like all warm-blooded animals, has an ingestion requirement of moisture. Unlike many birds, the ruffed grouse meets this need easily through a variety of sources. Open water, snow, dew, soft fruits, succulent vegetation, and juicy insects all contribute to satisfy the need for water.

It has been suggested that serious summer drought may impair the survival of the young grouse due to lack of available water. However, the evidence indicates that the chicks are as adaptable in getting their water requirement as are the adults. In fact both chicks and adults are so independent of open water, that their summer distribution is not affected materially by the location of water courses, swamps, or springs. The occasions when the birds are found near surface water ordinarily result from food or shelter availability rather than from the seeking of water for drinking. Many grouse broods and adults have been observed to spend the entire period of an abnormally dry summer in coverts completely lacking surface water. In some cases there was even a complete absence of dew for days at a time.

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6

Weather Conditions in Relation to Grouse

From the instant a potential grouse comes into existence as a fertilized egg to the time it meets its usually violent end, it faces the continuous vicissitudes of the weather. In its incubation period the primary hazard is that of excessive chilling; when a chick, hazards from the heat or cold, the wind, and rain all play a part; while in adult life the bleak cold, snow, ice, and storminess of winter must be faced as they come. Humans, who also face essentially the same handicaps, fare well or poorly in proportion to the adequacy of our shelter and our food supply. To a considerable extent this is true also with the grouse. The better their food and shelter, the better may they cope with the dangers that adverse weather brings. In actuality, since food and shelter are seldom perfect, the weather plays an important part in limiting or reducing grouse numbers, or in preparing the way for destruction by predators.

EFFECTS OF WEATHER ON THE HABITS AND NUMBERS OF GROUSE

Sunshine Gauges the Time of Nesting. The laying of eggs by a hen grouse comes about only after a considerable period of internal physiological change. The dormant ovaries are stimulated to growth in early spring by the lengthening hours of daylight. Once started the development of these organs and the laying of fertile eggs (following mating) comes about systematically. However, the date of the beginning of egg-laying varies considerably in different years. To illustrate: On Connecticut Hill the average first egg in 1931 was laid on April 18; in the succeeding year it did not appear until April 27.

Correlating the variations in nesting dates with the weather factors brings out clearly that sunshine is the guiding element. When we

compare Weather Bureau records of sunshine with grouse egg-laying dates, we conclude that the greater the number of hours of sunshine in March and early April the earlier egg-laying will begin. There seems to be no correlation with precipitation and only a slight one with temperature. The latter is probably a by-product of the effect of day length and the involved sunniness on temperatures.

The part played by sunlight (or light) in determining the time of egg-laying is corroborated by laboratory experiments which show that grouse, as well as other game birds, poultry, trout, etc., can be stimulated to egg production months ahead of the normal time by the use of artificial light.

Egg Losses Little Affected by Cold or Rain. A bird's egg has remarkable ability to resist the hazards of changeable spring weather. With eggs in the nest and before incubation has begun, temperatures as low as twenty-one degrees Fahrenheit have been observed and in no case has any adverse effect been noted. After incubation the temperature is kept constant most of the time by the mother's body, but even then the eggs can withstand surprisingly adverse conditions. Temperatures well below freezing far into May, storms that leave snow on the ground for as long as four days, and many gully-washer rains, occur many times with no discernible effect on the eggs. Eggs taken from a nest two days after the mother had been killed, when temperatures had been below forty degrees, hatched in an incubator a few days later.

Evidently the eggs can stand considerable hardship without themselves being destroyed. How much weakening of the young is caused by such adversity, with resulting delayed mortality, is unknown. It is reasonable to assume that chicks from eggs that have been seriously exposed will be somewhat weaker than normal and may, therefore, have a higher subsequent mortality. However, we have not been able to correlate egg losses with variations in weather conditions.

Leopold (1933) referred to the drowning of nests or young in heavy rain or floods as due to accident. We have observed only one nest destroyed by water and believe that such losses are ordinarily of no particular significance.

Brood Mortality Affected by Weather. One of the most baffling problems in the life history of the grouse is the high mortality of

the young birds during the first three weeks after hatching (see page 303). Long an enigma to those interested in the welfare of this bird, this loss has been conjectured by many authorities to be the result of adverse weather. The evidence does indicate that unfavorable conditions of precipitation and temperature are often connected with abnormally high brood losses, but it does not answer the question of what causes the normally high losses at that period.

One of the first to suggest that excessive rain might be at the bottom of the infant mortality was Sandys (1902). He points out that young grouse cannot stand a wetting. Conversely, he suggests that five consecutive favorable seasons, i.e., dry from hatching time till the chicks are past the critical stage, would mean a grand lot of birds. He then concludes that the reversed conditions would mean scarcity. Eaton (1910) says that in cold, wet seasons the eggs hatch poorly and the young die from exposure. Forbush (1912) linked the unseasonable weather from April to June of 1907 throughout the Northeast with the great grouse decline of that year. He says that eggs got chilled when females left the nest for food; setting hens died from exhaustion, starvation, cold or disease; and chicks that hatched disappeared. Stoddart (1918) listed bad weather in May and June as second in importance among the many factors contributing to the grouse scarcity in New York in 1916 and 1917. Bump (1932) summarized some of the early experiences of the New York study on this subject and pointed out instances in which some grouse broods hatched in a protracted rainy period suffered severe losses while others fared normally. Such an inequality of effect of a given period of supposedly adverse weather on different groups of grouse chicks has been noted repeatedly. On the occasion of one severe and quite cold rainstorm in early June (temperature down to 50° F., no sunshine for two succeeding days) we deliberately flushed and thoroughly dispersed four different grouse broods only a few days old. Each group was well soaked. Each of the four bands was observed again during the next two weeks and in no case was the loss greater than average.

Contrasting with these instances are many others wherein serious losses immediately followed severe cold and rain in June. Grouse allowed to hatch their eggs in natural enclosures in captivity are almost always poor mothers, and the young may often become chilled and wet. In all such cases observed, most of the

chicks died within ten days after exposure. Some of the broods cited by Bump (*op. cit.*) lost from half to three quarters of their numbers within a few days after the bad weather. Prompt and adequate brooding by the mother grouse no doubt aids in preventing such losses.

If we assume that adverse weather in June will cause excessive chick mortality, we might expect that the reverse conditions—warm, dry weather in June—would be particularly beneficial, other things being equal. However, 1933, a good season from this standpoint in New York, had a very high brood loss. Other instances also provide a full range of inconsistencies in respect to this factor.

The best opportunity that we had to evaluate the possibilities of excessive rainfall affecting grouse brood survival occurred in 1935. On July 7 and 8, at a time when grouse broods were past the usual period of high mortality, came the most severe cloudburst in the recorded history of southern New York. During this two-day period, approximately ten inches of rain fell (a summer's normal supply), about eight inches of it the first day. This storm caused unprecedented floods and destruction over an area of about ten counties. It was immediately apparent that disaster had overtaken the young grouse. Observations both in and out of the flood area clearly showed that the abnormal brood losses were in the area of high rainfall. As a result of this one storm, an additional twenty per cent of the grouse chicks were lost over what would have been expected to perish. This meant that the survival of chicks was only fifty per cent of the normal, as an increase in mortality from the normal sixty per cent to 1935's eighty per cent left only twenty per cent of maturing birds instead of forty per cent (*N. Y. S. Cons. Dept. Ann. Rep., 1936*). This extra loss resulted in a marked decrease in grouse on the area that fall and illustrated how a moderate addition to the normal mortality will cause a big loss in the proportion of birds maturing.

Hence, while severe cold and rain can prove disastrous to very young grouse, the average annual early-season losses are only partly explained. A normal, healthy grouse chick, with proper maternal care, can get along pretty well in spite of the chilly nights, rainstorms, and periods of protracted cloudiness.

Effects of Winter Weather on Adult Losses. Throughout the year the condition of the weather causes marked changes in the selec-

tion of cover by grouse (see page 94). In a direct sense, adult grouse practically never succumb to the weather, that is, die of exposure or freezing. The "practically" is included to admit the remote possibility that death from exposure may conceivably occur. It has not been observed, however, in all our observations under extremes of weather of all sorts. In an indirect sense, weather often makes grouse susceptible to accelerated predation, hence is an important element in their mortality story.

The literature is full of references to hardships brought on grouse by winter. Most often these are associated with supposed starvation induced by imprisonment under a heavily crusted snow following snow-roosting. Samuels (1870) evidently considered this to be commonplace, for he wrote: "It is a common occurrence to find them in the spring dead, where they have been imprisoned under the crust . . ." Allen (1927) considers this problem from the bird's point of view, "quoting" a hen grouse in such a predicament thus: "Rain or snow would freeze, making it impossible for me to get out and I spent several days in hunger, imprisoned beneath the snow." Forbush (1913) recognized that such an event was not usual and concluded: ". . . usually they are vigorous enough to find a way out somewhere." It is credible that death beneath the snow may happen but it seems likely that most authors have overplayed a theory or misinterpreted their observations. We do not know of a single authenticated case of this phenomenon.

In enduring stormy winter weather, grouse regularly seek shelter in coniferous trees or beneath the snow, often remaining there for several days at a time, as attested by the accumulation of their droppings. Apparently they take little or no food during these "holing up" periods, yet ordinarily are not adversely affected.

The more snow there is on the ground and the more blustering the weather, the more will the birds resort to snow-roosting. The winter of 1935–36 in southern New York was a season of unusual snow-roosting; deep snows lay on the ground all winter with no important thaws. No instances of death from imprisonment were observed, but the conditions did induce a higher than normal loss from predation. We have already noted the increased vulnerability of grouse in snow roosts (see page 46). During the 1935–36 winter, it was common to find the story written in the snow of a grouse pounced upon while at rest beneath its cool, white blanket. The mor-

tality rate was very high, from twenty-five to one hundred per cent more than in normal years. The increased losses occurred in February and March, coinciding with the period of unusual snow-roosting. Whereas the normal curve of mortality reaches a peak in April, or is at about the same height for March and April, the years of increased winter predation brought on by adverse weather show a peak in February or March. In 1936 it occurred in March.

Weather conditions other than snow and sleet are of little importance in causing or inducing grouse mortality. Low winter temperatures, unless accompanied by a heavy snow, do not seem materially to affect the birds. The winter of 1933–34 gave ample chance to learn of any possible connection between temperature and winter loss. Over half the days of February gave below zero (Fahrenheit) readings, with an extreme of thirty degrees below. The monthly mean was thirteen degrees, which is twelve degrees below average. Yet there was no indication of accelerated predation, and the mortality records indicated only the normal winter losses.

Extremes of summer heat send the birds to coniferous shelter, as does cold weather. Mousley (1919) attributed a noticeable increase in grouse in Stanstead County, Quebec, in the summer of 1919 to a prolonged hot spell. If rain could cause any increase in deaths of adults, this should have been reflected in the 1935 summer cloudburst that so affected the youngsters. No losses of grown-ups attributable to this storm could be recognized.

Snow and Sleet in Relation to the Food Supply. The deep snows of the northern winter conceal and largely render unavailable the fruits and leaves on the ground and on low-growing plants. Under these circumstances the birds resort to budding but it is remarkable the quantities of food as ferns, wintergreen, Canada mayflower, and the like that they manage to obtain under even the worst of conditions. A man may be wholly unable to see any of these plants, but the grouse get at them somehow. The ability of the bird to subsist on buds alone, for how long or how well we do not know, reduces the chance of its being starved when so much of its preferred foods is covered by snow.

Occasionally a freezing rain will encrust a snow, making the food supply on the ground even less available, and at the same time may sheath the tree buds with ice. Under such a condition grouse may be

hard pressed to get food, but it rarely lasts long enough to affect them seriously, as they can go several days without food and suffer no apparent ill effects.

POPULATION FLUCTUATIONS AFFECTED BY WEATHER CONDITIONS

We have already noted instances in grouse trends where extreme weather conditions resulted either directly or indirectly in abnormal grouse losses. How great a part such meteorological extremes have played in causing or precipitating the large grouse declines of former years cannot be gauged by these observations, but they do indicate the possibilities inherent in climatic factors. As we have already noted, Woodruff (1907) gave "the extremely cold, wet, and late spring of 1907" as second in his list of three factors that caused the decline of that year. Forbush (1912) likewise correlated the 1907 grouse collapse with bad weather.

Knowing rather accurately when some of the most extraordinary grouse reductions have taken place in New York and other parts of the Northeast, we have examined the Weather Bureau records for New York State in an attempt to ferret out any broad correlations that might exist and the results seem too significant to be accidental. The temperature and precipitation records are adequate as far back as 1890, and sunshine data are available since 1909. The period from 1890 to date covers four major and three minor grouse declines in this state.

If a certain weather condition, or a combination of conditions, could explain important decreases in the grouse population, presumably severe instances of those circumstances would occur during all years of these decreases and in no others. However, no single weather factor does this, nor does any combination completely agree. But the coincidence between periods of grouse decline and certain severe weather conditions seems too close to be wholly accidental.

Since 1890 there have been four primary periods of sharply decreasing grouse abundance, approximating the years 1896–97, 1907, 1916–17, and 1927. Minor declines occurred in 1904, 1924 and 1935–37. The evidence indicates that serious trouble from adverse weather occurs from February to July and we may therefore confine our analysis to these months.

The temperature and precipitation records for 1896–97 show a very severe late winter in 1896 and a very cold June in 1897. February and March snows in 1896 exceeded twenty-five inches each month, more than fifty per cent above normal. Temperatures in February were normal, but in March the mean was seven degrees below the thirty-two degree norm. This low March temperature condition was rivaled in only one year, 1916, another year of grouse decrease. The 1897 June temperature mean was some three degrees below the sixty-five degree norm, a condition that has occurred outside of grouse decline years only in 1902 and 1903, and in the latter possibly contributing to the minor decline in 1904. Other conditions were close to average in these two years.

The next big decline period of 1907 was notable for its cold spring. April was four and seven-tenths degrees below normal in its mean,[1] May five and five-tenths and June two and one-tenth, the latter being even worse during the first half of the month. This coolness was accompanied by a marked deficiency in sunshine in April and May. Precipitation was average though Woodruff (1907) and Forbush (1912) called it a cold and wet spring. The late winter of 1907 was normal except for a six degree deficiency in the February mean.

As there is some indication that the 1907 grouse drop-off may have begun in some areas in 1906, let us examine the records for that year before proceeding further. A severely cold March (six degrees below norm) with snowfall well above average succeeded an ordinary February. The spring was normal throughout.

The decline of 1916–17 concurred with some of the most severe weather in the history of the state. The February temperatures in 1916 averaged three and five-tenths degrees low, and there was seven and nine-tenths inches of snowfall in excess of the typical. During March, an eight and one-tenth degrees deficiency in the temperature mean, accompanied twenty-one and six-tenths inches of snowfall above the usual. In the spring, sunshine was low throughout, especially in April and June. Temperatures were normal in April and May but very cool in June, being four and two-tenths degrees below the average. Precipitation was normal in April, but excessive in May and June. Turning to the winter of 1917, we find that it included severe February temperatures and March precipitation, but

[1] "Mean" weather records are deemed "average" or "normal," and are the standards used by the Weather Bureau.

was otherwise normal. April was abnormal only in being short in sunshine, while May was deficient in both sunshine and temperature. Precipitation in June was five and eight-tenths inches, which is very high; temperatures were low throughout, especially in the first half of the month.

The most recent major die-off in New York took place in 1927, but apparently began in 1926. This two-year period shows essentially the same weather characteristics from late winter to early summer as those just discussed. Snowfall in February 1926 exceeded twenty-five inches, far above average, and was followed by March temperatures that were some five degrees below normal. The other manifestations of the winter weather were about typical. The April temperature mean was thirty-nine and five-tenths degrees, the same as in 1907, both the lowest on record. This cold weather continued through May, but to a less abnormal degree, then in June maintained an unfavorable spring record with a mean of sixty and eight-tenths degrees, the same as in 1916, and next to lowest on record. Other conditions were not adverse.

The winter and early spring periods in 1927 were average, except for a small excess of snow in February. In May, however, temperatures were low, rainfall high, and sunshine very much below normal. Following this came another cold June, though not as bad as the year before. The precipitation and sunshine factors in this June were good.

Before examining the weather situation accompanying the minor periods of decline, we may take note of the elements common to the four occasions just discussed. In all, there was a condition of late winter weather severity, with heavy snow and unusually extreme cold. Likewise there was a cold June; only in 1906–07 were June temperatures not extreme; in 1907 both April and May, as well as June, had low thermal records.

The minor decline of 1904 was attended by extremely low February and April temperatures, and March too was colder than usual. Conditions through other parts of the winter and spring were not severely adverse. It may well be that the very low June temperature and high rainfall in 1903, together with lack of sunshine, contributed to this drop in grouse numbers.

Another intermediate decrease occurred in 1924. Then the weather record was mostly orthodox but with some extremes. There was

somewhat more snow in February than usual, but not a serious amount; April had very high rainfall and was somewhat colder than usual; May was very cold, its rainfall high, and sunshine lacking; June was somewhat colder than the normal. Its first half was very cold. The previous year, 1923, was not notable for any extremes, although June was very cloudy and the late winter was quite cold.

The most recent minor decline in New York began in 1935. During the critical months from February through June all weather factors were normal or favorable. The cloudburst and flood of early July (see page 187) offers the only apparent correlation of weather with this decline. Since this catastrophe was effective over ten counties in the best grouse range of the state, it probably offers the explanation for the rather small decrease that was revealed in the state hunting kill, as well as for the severe drop on Connecticut Hill within the flood area.

The 1935 decline indicates how an individual short-lived storm may affect great numbers of grouse. If such a phenomenon was connected with any of the previous drop-offs we were unable to single it out. It must be recognized though that if such a storm did occur it might well explain some of the failures to correlate more general weather conditions with drops in the grouse population.

If there is any certain connection between adverse weather and grouse decimations, it apparently is tied in with excessive snow in February and March, usually linked with extremely low temperatures, or with low temperatures in June, especially during the early part, often supplemented by heavy rains and lack of sunshine, or both. All of the notable grouse declines in New York since 1890, when the weather records began, can be explained by these conditions. If the correlations indicated are only accidental, then there were probably other years having these same weather characteristics but which failed to show widespread grouse declines.

An examination of the corresponding records for all the years since 1890 reveals very low June temperatures (mean below 61.6°) in 1897, 1902, 1903, 1916, 1926, and 1927. Of these 1902 is the only one definitely not of a poor grouse year. It was not preceded by a bad winter. Years of low, but not extremely low, June temperatures (below 63°) were 1907, 1910, 1912, 1918, 1924, and 1928. Of these 1907 and 1924 coincided with grouse decreases and in both, the early June thermal record was very severe. The years 1918 and 1928

were seasons of low abundance, when these conditions could only prolong the existing grouse depression. Both 1910 and 1912 were preceded by mild winters.

Very bad February or March snow conditions occurred in 1893, 1896, 1897, 1900, 1908, 1910, 1916, 1920, 1928, and 1932. Those not happening in a period of declining or low abundance, 1893, 1900, 1910, 1920, and 1932, were all followed by favorable June weather. Several of these periods of excessive snow were of short duration, as for example in 1932.

Every time severe February-March snow conditions and very low temperatures, followed by a very cold June, occurred in two successive years, a grouse decline followed. And every time there was an important grouse decline, these weather conditions had prevailed.

A close scrutiny of the details of this record shows that it was not uniform each time. Each decline was unquestionably the product of several conditions, each of which varied on different occasions. Predation varies widely, even when conditioned by weather factors. We believe that disease played a significant part in the 1927 decline. Was this epidemic set up by weather factors? We don't know. It hardly seems that a half-century record of weather-grouse-trend correlations could have so much in common, as appears to be the case, unless there was actually a real functional connection. It is far from a perfect record of cause and effect; but is so impressive that the importance of climatic factors in relation to grouse population trends can hardly be discounted lightly. Weather conditions play a big part in grouse fluctuations both great and small.

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7

Interrelationships of Ruffed Grouse to Mammals and to Other Birds

SPECIES THAT PREY UPON GROUSE

Discussion of predators is fraught with many dangers. Not the least of these is prejudice in dealing with creatures that compete with us. This attitude we must completely discard. The other major difficulty is the tendency to accept simple action and reaction as a complete story of the relations between predator and prey species. That is far from justifiable. The subject of predation is one of the most intricate, if not the most complex, in the field of animal relationships. But before we consider the drama of predation as it relates to grouse, let us become acquainted with the actors. For present purpose the grouse is the prey species and we know it reasonably well. Let us take a look at its natural enemies, and then some of the other creatures that play subordinate roles to the victim and the "villains."

A bare list of the enemies of the grouse is impressive even though we know little of their specific depredations. Study reveals that some of them exact a greater toll than others. They vary, too, as to the time of their attacks, some during nesting season as egg eaters, others in the summer as destroyers of the young, or at any time as predators on the grown birds. We have listed in three categories in Table 8 those of significance in the Northeast, those of primary, secondary, and occasional importance. It has been necessary to list a few in more than one classification because they require separate ratings for different types of predation.

The species in the first group are listed in probable order of importance for south-central New York. This order varies considerably in different parts of the Northeast, and some of those listed as sec-

PLATE 1. A (Upper). When the white man came, farms were hewn out of the wilderness. B (Lower). Where the land clearance work was confined to small scattered units, the range was improved for grouse. However, extensive agricultural development gradually pushed the grouse out of much of its original range.

Plate 2. A (Upper left). The drumming of the cock grouse is one of the wonders of the bird world. The sound is made by striking the wings against air. B (Upper right). Strutting before the female bird, the male stands stiffly with tail raised and spread, wings drooping at the side, and the head drawn back into its erected ruff. C (Lower). Young grouse in a brood dust bath. In addition to exposed dirt, grouse often use well-decayed wood of old stumps for dusting areas. *Photos by A. A. Allen.*

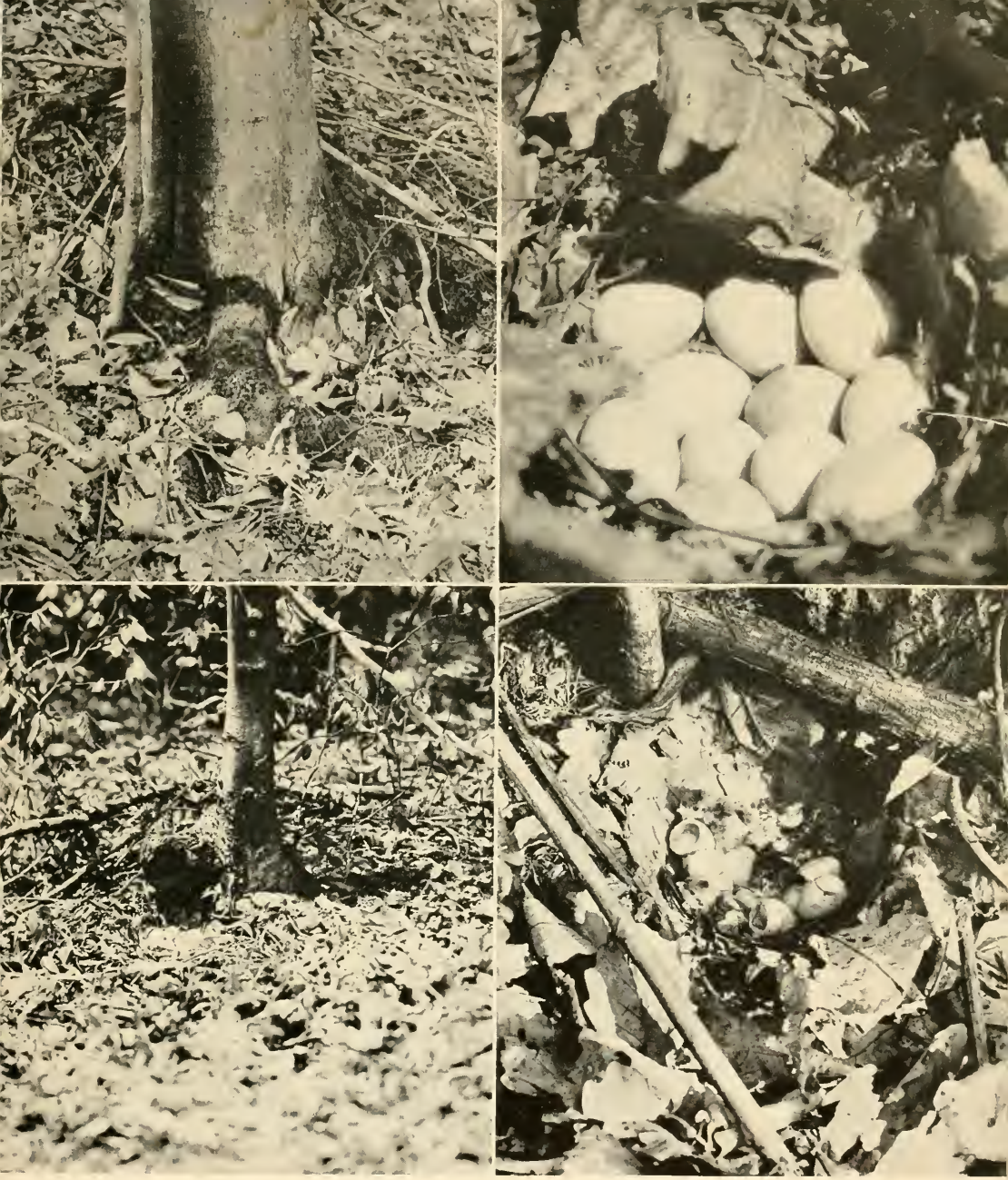


PLATE 3. A (Upper left). The nest was built at the base of a big tree, on the sunny side. B (Upper right). Eleven eggs composed the clutch, an average number. C (Lower left). The hen grouse watches carefully for enemies before stepping onto the nest to continue incubation. Can you pick out clearly the well-camouflaged bird? D (Lower right). The chicks remain in the nest only a few hours after hatching. As soon as they are dried off, and the weather is clear, they leave home, never to return. *C and D photos by A. A. Allen.*

Plate 4. Grouse Chicks at Different Ages. A (Upper left). One day old—a cute, completely downy little fellow. B (Upper right). At five days of age, the chick shows marked improvement in wing feathering. C (Lower left). By the time seventeen days have passed, the wings are well developed, and it can fly short distances. D (Lower right). At five weeks of age the juvenile feathering is quite complete with tail and all. It now resembles a small edition of its parents and can night-roost by itself. *Photos by A. A. Allen.*

PLATE 5. Grouse roosts are likely to be almost anywhere in spring, summer or fall, but in winter they usually sleep in trees, or if the weather is bad, in the snow. A (Upper left). Grouse going to roost in a tree. B (Upper right). Grouse just after landing in the snow. C (Lower left). Pheasant and grouse eggs in one nest. This phenomenon is not common. In all cases observed, the pheasant has been the intruder, the grouse the one imposed upon. *Photo by A. A. Allen.* D (Lower right). A snow roost after being vacated, showing the usual pile of droppings.

PLATE 6. Two Types of Grouse Range. A (Upper). Disconnected cover, woodlands separated by open fields, typical of much of the Northeast. B (Lower). Continuous cover (beyond valley), extensive forests found in the several mountainous areas from the Appalachians to the Adirondacks and Maine. *Photos Courtesy of Pennsylvania Game Commission.*

Plate 7. An aerial view of a portion of the Connecticut Hill submarginal farming area well illustrates the broken nature of this type of grouse range. Woodland is interspersed with open fields, the fencerows and woods margins are generally brushy. Some of the abandoned fields are being reclaimed by woody vegetation. Note the woodland clearings (squares) and lanes in lower part of area. These are grouse management cuttings.

PLATE 8. Overgrown land as a shrubby border to woodlands provides desirable interspersion of cover types. A (Upper left). Open land, overgrown land and hardwood woods in close juxtaposition. B (Upper right). Shrub cover next to coniferous woods. C (Lower left). Woodlands lacking a shrubby edge lose valuable interspersion; the coniferous type above has excellent shelter but is deficient in handy food cover. D (Lower right). Pure alder most often occurs on moist soils, and is much used by broods.

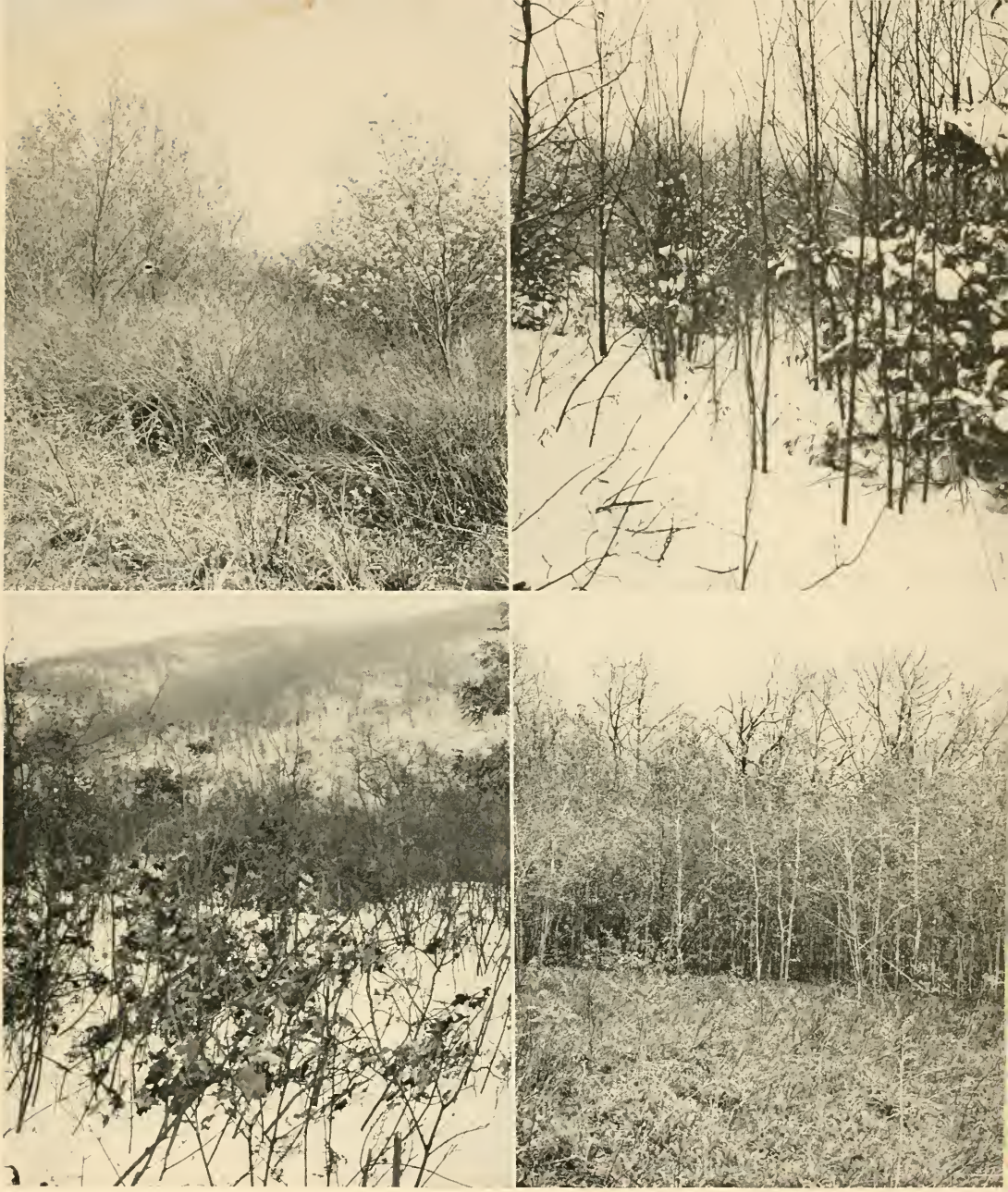


Plate 9. Overgrown land is of particular value as feeding cover, especially in summer and fall. A (Upper left). Subtype of mixed hardwoods composition. B (Upper right). Mixed conifer-hardwood subtype has better shelter. C (Lower left). Mixed oak composition, common from Long Island and Pennsylvania southward. D (Lower right). Pure stand of popple along woods border, one of the most useful types of overgrown land.

PLATE 10. Slashings bring summer food cover to woodland areas. A (Upper). Newly cut subtype is characterized by rank herbaceous growth and briars, lasts from three to ten years usually. B (Lower). Old cuttings have a stand of shrubs and sapling trees, but with fewer herbs and briars. It will soon become a pole-stage woodland, and will then have a very different value as cover for grouse.

PLATE 11. Hardwood Woodlands. Of particular value as nesting cover, this type varies immensely. A (Upper). Pure hardwoods are deficient in shelter. B (Lower left). A scattering of conifers improves this type for grouse. C (Lower right). Broadleaved evergreens, such as mountain laurel, serve the same purpose as conifers, are food plants as well. Mature stands are less valuable to grouse than second growth.

Plate 12. A (Upper). Small openings made by removing a large tree, or two or three, here and there, known as spot lumbering, in hardwood stands is the best of the many subtypes. B (Lower). The mixed oak association, so prevalent in the middle Appalachian range, is quite unproductive of grouse where it occurs in large, unbroken areas.

Plate 13. Mixed Woodland. A (Upper). Hardwood overstory of near-mature trees with much hemlock in lower growth—of less use to grouse than the younger age class. B (Lower). Young stand of hemlock and hardwoods, the best all-purpose type of grouse cover.

PLATE 14. A (Upper). Overstory of mature white pine with completely hardwood understory. The coniferous shelter of this woodland is so high that it is largely useless to grouse. B (Lower). Hard pines (Virginia pine) and oaks compose a mixed woodland cover type common on sandy soils and on burned areas.

PLATE 15. Coniferous Cover. Hemlock, pine, spruce, fir, cedar furnish the basis of the best protective shelter for grouse. Its value depends on species, age, density mainly. A (Upper). Hemlock on left has sheltering branches close to ground, white pine on right has shelter only in crown. B (Lower). Close-up of low-hanging hemlock boughs showing their provision of winter protection.

PLATE 16. A (Upper left). Some of the broad-leaved evergreens, as mountain laurel, may substitute for the conifers in furnishing winter shelter close to the ground. B (Upper right). The hard pines (pitch and Virginia pines shown) are the predominant conifers in much of the Appalachian range from central Pennsylvania south. C (Lower). Spruces furnish most of the winter shelter in the northernmost range, from the Adirondacks and northern New England into Canada. *B and C photos by U. S. Forest Service.*

PLATE 17. Plant succession must be one of the bases of grouse management. A (Upper). An old white pine has established the makings of a stand of solid pine around it while near by (in the foreground) the new woods will be mixed pine and hardwoods in a few years. B (Lower left). A view of the north end of the Connecticut Hill area, showing how natural plant succession of hardwoods with scattered conifers is gradually changing the open fields, first to brush overgrown land, ultimately to forest. No planting has been done on this part of the area. Management must maintain openings and overgrown land with ax and plow. C (Lower right). Among the factors that influence plant succession is the nearness to an existing woodland or hedgerow. Except for light-seeded species, most plants invade an old field slowly from the edges, as the hemlock and maple are here.

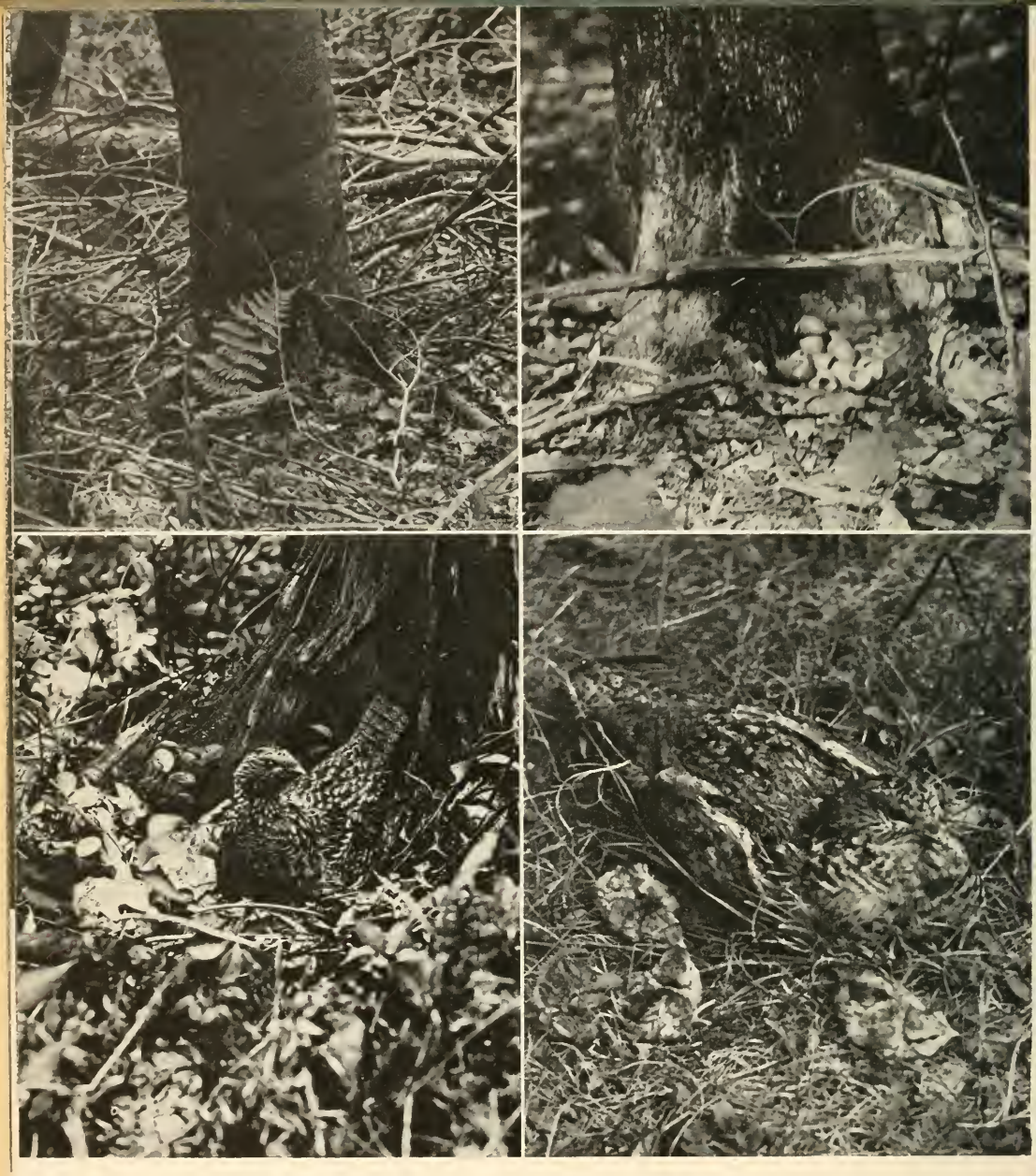


PLATE 18. Grouse nests are usually at the base of some object, most commonly a tree. A (Upper left). Hen grouse on nest at base of a large beech. Note the fern and dead twigs that offer some camouflage. B (Upper right). A successful nest showing the characteristic appearance of hatched eggs. Note the two unhatched eggs. C (Lower left). Grouse incubating on nest at base of stump. *Photo by A. A. Allen.* D. (Lower right). Grouse brooding chicks. *Photo by C. W. Severinghaus.*

Plate 19. A (Upper). A single grouse meal. Crop contents of a female grouse from Sullivan County, Pennsylvania, December 13, 1940. Top: left, leaves of mountain laurel; right, cherry buds. Below: left, birch buds; right, fruit of mountain holly (*Ilex monticola*), the first record of this species being eaten by grouse. B (Lower). A grouse with a full crop, skinned out to show the immense capacity of this organ when fully distended. The food thus stored passes to the gizzard only as fast as it can be ground and digested. *Photo by A. A. Allen.*

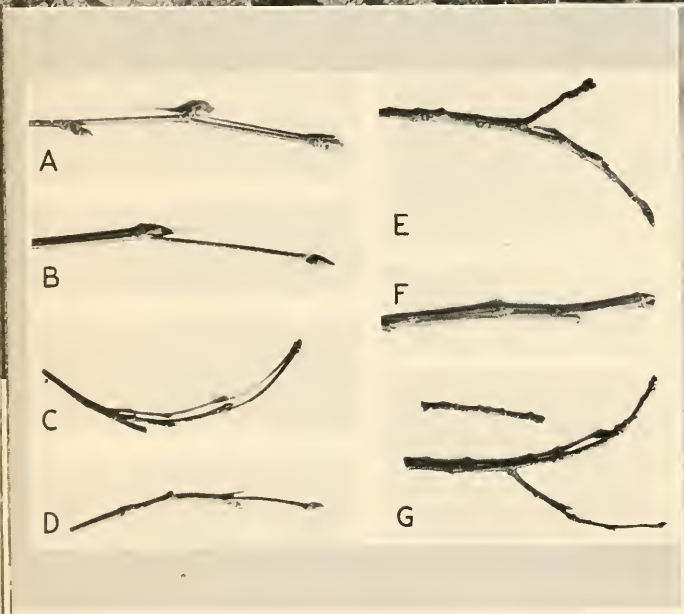


PLATE 20. Herbaceous plants provide the grouse with a considerable part of its food. Among the more important are: A (Upper left). Ferns, especially the woods fern (shown), the fronds of which are eaten mostly from autumn to mid-spring. B (Upper right). Sedges (*Carex*) are used from spring to fall. The leaves are eaten as long as they are green, and the seeds are taken in summer and fall. C (Lower left). Important among winter foods of grouse are tree buds. Some of the most used species are: a. Yellow Birch; b. Black Birch; c. Blue Birch; d. Hophornbeam; e. Trembling Aspen; f. Apple; g. Black Cherry. D (Lower right). Sheep sorrel (upper plant), a small field weed. Its sour-tasting leaves are relished by grouse. The Canada mayflower (lower plant), a plant of the woodland floor, has red berries that are eaten from fall to spring.

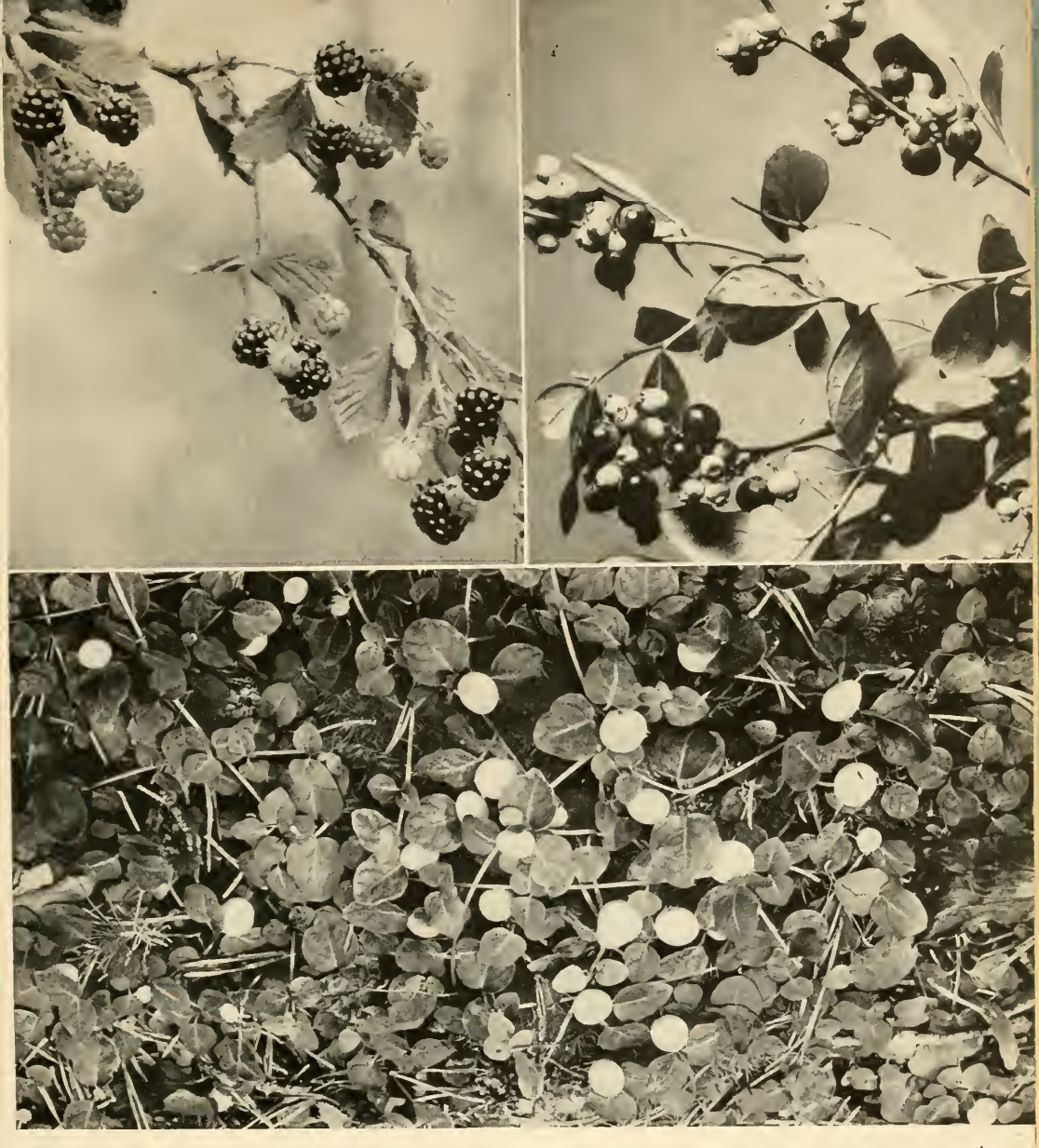


Plate 21. Summer fruits are among the most important foods of grouse for young and old alike. Two of the most important are: A (Upper left). Brambles, of which a blackberry is shown here. B (Upper right). Blueberries. The Dryland blueberry is the one illustrated. *Photos by W. R. Van Dersal.* C (Lower). The partridgeberry provides food all year round, but it is especially useful in the spring when fruit is scarce.

Plate 22. Autumn is the season of plentiful fruits and nuts, and the grouse takes full advantage of them. Among the important fall fruits and nuts that furnish food for grouse are: A & B (upper) the acorns, of which those of the northern red oak (A) and scrub oak (B) are illustrated. C (Lower left). Cherries, the choke-cherry (illustrated) and black cherry being most important. D (Lower right). The dogwoods, among which the gray or panicled is most used.

Plate 23. Other important fall food for grouse. A (Upper left). The viburnums. The mapleleaf viburnum is shown here. B (Upper right). Greenbriers, of which the sawbrier is illustrated. The dogwoods provide fruits for fall and early winter use. Gray dogwood is among the best (see Plate 22D). C (Lower left). Flowering dogwood is most important from southern New England and Pennsylvania south. D (Lower right). Red osier primarily used in northern region.

PLATE 24. A (Upper left). Old apple orchards furnish excellent feeding cover all year, especially if close to a woodland. This orchard with its mixture of briars and other shrubs, is perfectly situated. B (Upper right). Wild apples near pine clumps are a perfect combination in autumn. C (Lower left). The beech furnishes a preferred food when it has a nut crop. It is a component of the woods next to the orchard above. If the old trees are cut out as "weeds" the food value to grouse will be lost. D (Lower right). The sumacs are an important source of winter food. The grouse feeds on the bobs of some species (*R. typhina* shown in center), and on the fruit of the two poisonous ones, of which the poison ivy is shown in D. Note the sumac in the foreground of the orchard above. These shrubs must have full sunlight to survive.

PLATE 25. Winter foods are not a serious problem to the grouse on good range except for variety. These plants help break up the predominance of buds as a winter diet. A (Upper left). Mountain laurel, whose leaves are a staple food. B (Upper right). Highbush cranberry, one of the viburnums. C (Lower left). Wild rose, whose hips are eaten when accessible. D (Lower right). Teaberry, or wintergreen, is a small plant of the woodland floor.

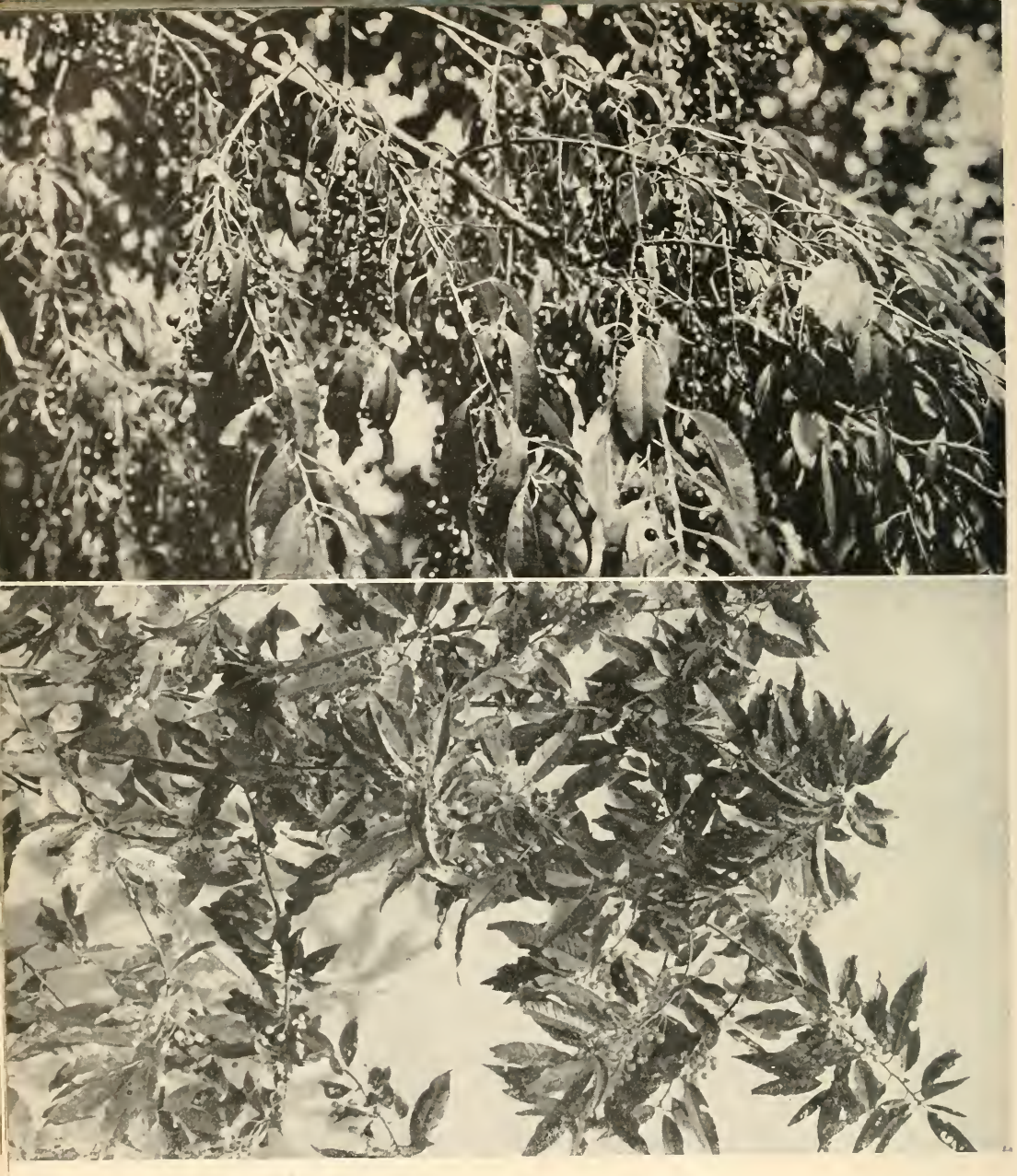


PLATE 26. The cherries are useful for both fruits and buds. Three species are used most: A (Upper). Wild black cherry. B (Lower). Pin cherry; and chokecherry (see Plate 22C).

Plate 27. The viburnums are an important group of shrubs that furnish fruit for fall and winter grouse food. Two of the more important species are the maple-leaf viburnum (see Plate 23A), and the highbush cranberry (see Plate 25B). Among other useful viburnums are: A (Upper left). Nannyberry. B (Upper right). Hobblebush. C (Lower left). Blackhaw. D(Lower right). Arrowwood.

PLATE 28. Wild grape (*Vitis labrusca*), in this instance, is one of the most important fruits in the grouse diet in fall and early winter. A (Upper). Prolific growth along a woodland edge. B (Lower). Close-up of fruit.

PLATE 29. Among the secondary grouse foods are several that furnish fruit that assumes great importance in certain regions and at some periods. Among these are: A (Upper left). Black chokeberry, a small bush. B (Upper right). Bittersweet, a climbing vine. C (Lower). Winterberry, one of the hollies.

PLATE 30. Other secondary grouse foods furnishing fruit are: A (Upper left). Virginia creeper, vine. B (Upper right). Bayberry, most prevalent near the coast. C (Lower left). Elder, a common fencerow shrub. D (Lower right). Mountain ash, a small woodland tree. E (Center). Serviceberry, another woodland tree whose fruits ripen in early summer.

PLATE 31. A (Upper). Farming activities greatly affect the grouse food supply. The type of woodland cutting carried on, care of fencerows (or lack of it), pasture fencing, ploughing and cultivation all show their effects in this picture. The ploughed fields have no cover, but maintain edges against the woods. Some fencerows are clean, others brushy. Pasture is fenced, and some of the former pasture has been abandoned to grow into brushy land, then to woodland. B (Lower). When deep snows blanket the ground, grouse resort to buds for most of their food. When the day is calm, though, they wander through the snow seeking fruits and greens.

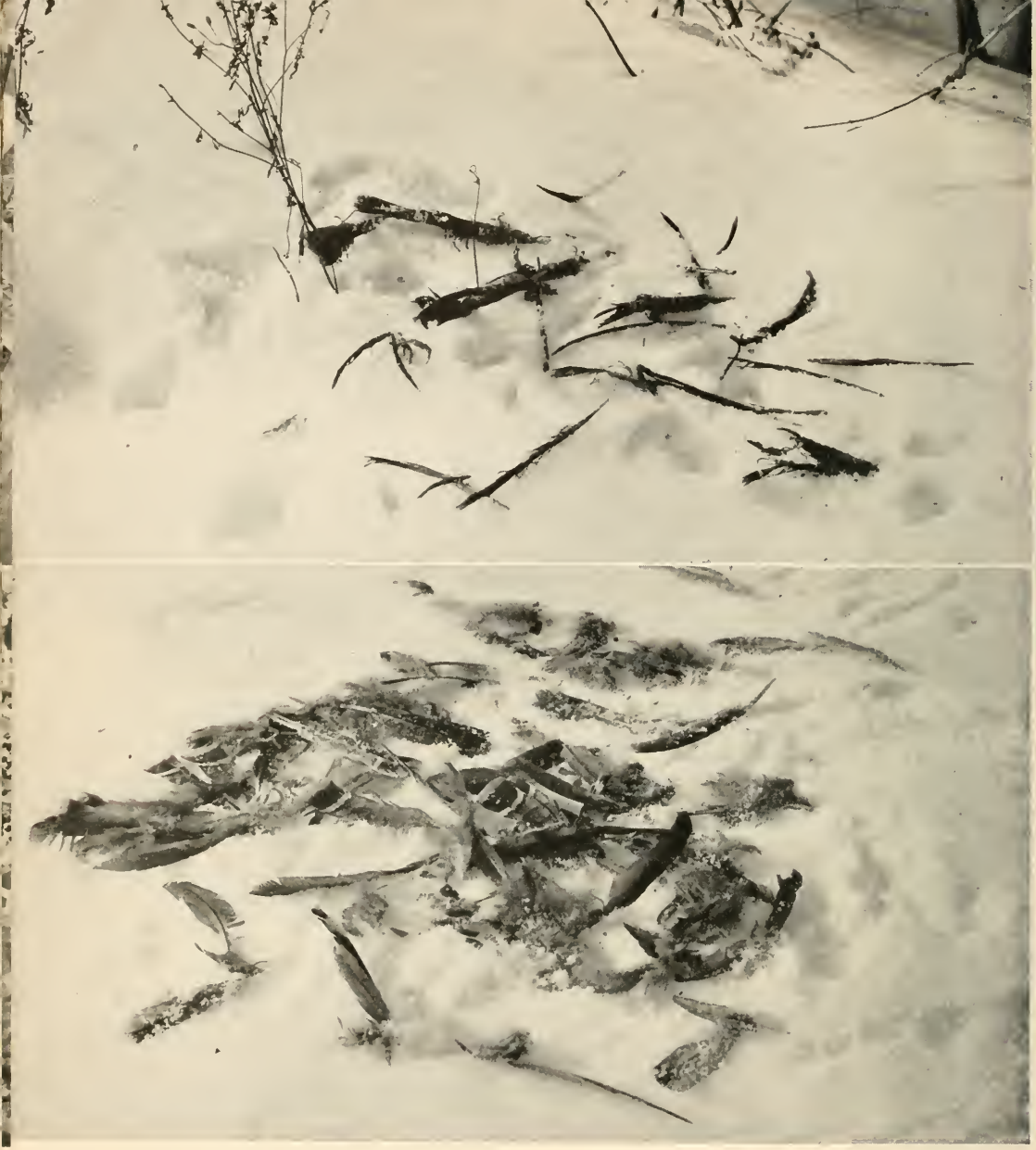
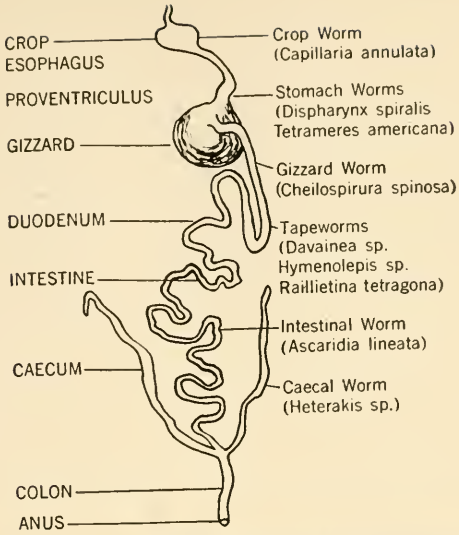


PLATE 32. The telltale marks of feathers and tracks in the snow reveal tragedies for the ruffed grouse. A (Upper). Fox evidence. B (Lower). Horned owl work (whitewash of owl droppings does not show against snow).

PLATE 33. A (Upper). Grouse nest destroyed by a horned owl killing setting hen, after which a fox ate the eggs. Note feathers and broken egg shells. B (Lower left). The common skunk loves eggs, and occasionally stumbles onto a grouse nest. In some areas it may be one of the most destructive of grouse predators. C (Lower right). Great horned owl, one of the most efficient of all predators, a prime enemy of the grouse. *Photo by Pennsylvania Game Commission.*

PLATE 34. The rabbits are among the rodents whose population fluctuations are correlated with those of the grouse. A (Upper left). The cottontail, found mainly in the disconnected cover areas of grouse range. *Photo by A. A. Allen.* B (Upper right). The snowshoe hare, found mainly in the extensive northern forests. C (Insert). The squirrels, of which the gray squirrel is shown, affect the grouse in two ways, as a buffer between the grouse and its enemies, and as a food competitor. D (Lower). The squirrels' love for nuts, and their keen ability to find them, often make the establishment of a direct-seeded oak, walnut or other nut tree plantation impossible. The photograph shows the empty shells of a walnut planting after being dug up and eaten by squirrels.



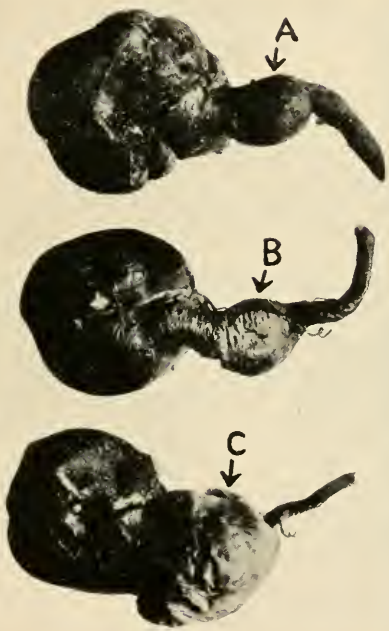


Plate 35. A (Upper). Diagram of alimentary canal of the ruffed grouse showing location of some parasite infestations. B (Lower left). Grouse stomachs: a. normal; b. lightly parasitized with *Dispharynx spiralis;* c. heavily parasitized with *D. spiralis.* C (Lower right). Stomach worms (*Dispharynx spiralis*) (small) and intestinal worm (*Ascaridia lineata*) (large worm), showing comparative size. *Photos by A. A. Allen.*

Plate 36. A (Upper left). The modern hunter pursues grouse as a sport. B (Upper right). To many hunters the grouse is the king of game birds. When a split-second shot brings a clean kill, they feel a sense of real accomplishment. C (Lower). Man's use of well-trained pointing dogs has done much to make hunting a fine sport. In the early part of this century most of the pointing dogs of the northern states were trained on grouse but today the majority have been "spoiled" on pheasants and a top-notch grouse dog is a rarity. *Photo by J. M. Sloan.*

Plate 37. Man's operations as a farmer affect grouse habitat in many ways. His ploughing and cultivation of crop fields prevent woody cover from expanding, and at the same time maintain the valuable woodland edges next to the fields.

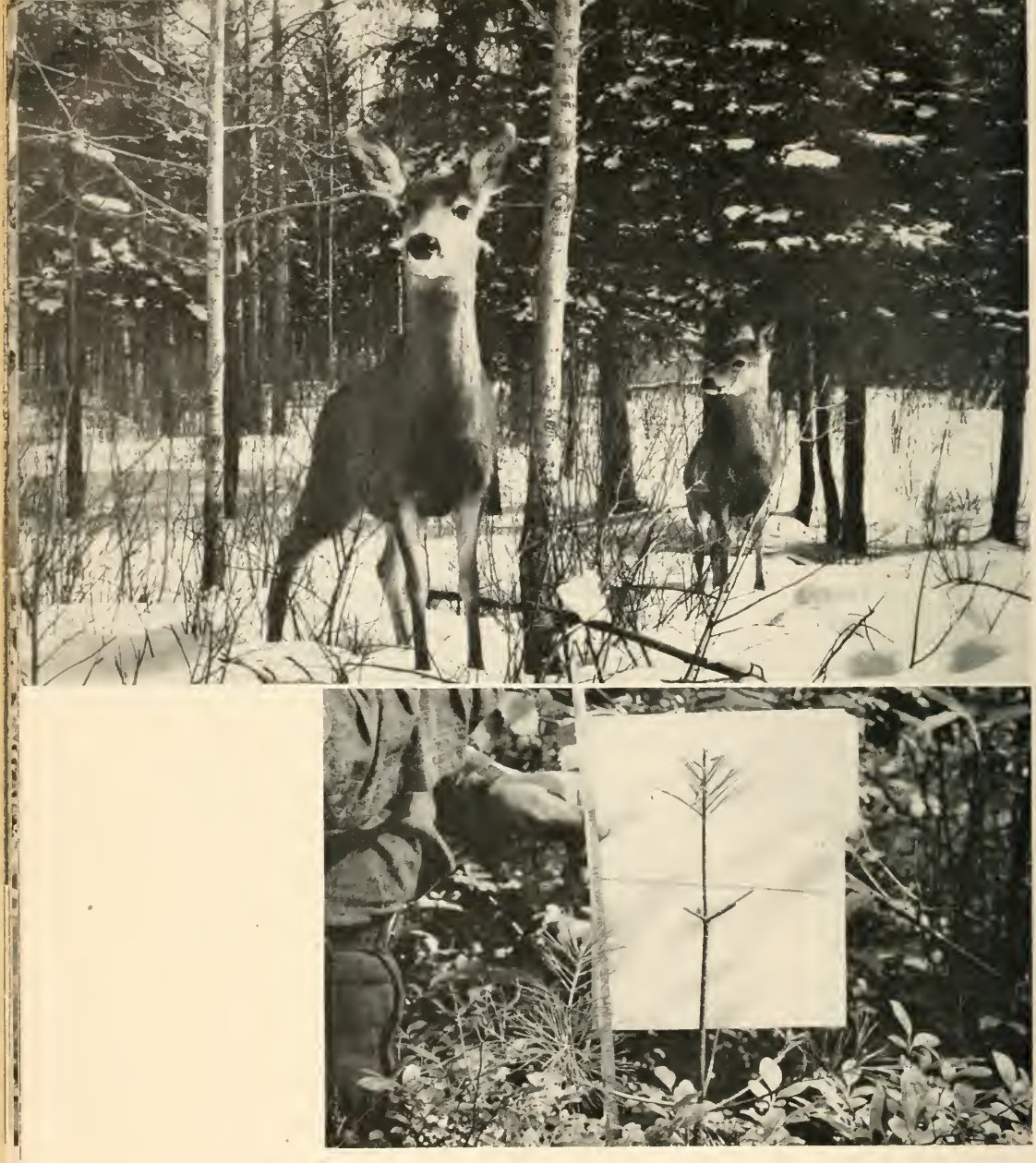


Plate 38. A (Upper). Man's interest in managing the land to produce grouse is often directly affected by what he does or does not do to control other animals, such as deer. In recent years, deer populations in many areas such as parts of Pennsylvania, Wisconsin, the Pisgah National Forest, North Carolina, have been permitted to increase to such an extent that their browsing has partially destroyed the range for deer and grouse alike. B (Lower). When deer populations are too large for the carrying capacity of the range, it is impossible to establish successful tree plantations. Note damage to white pine seedling from deer browsing.

Plate 39. As a lumberman, man sometimes improves and sometimes destroys the cover values. A (Upper). Overcutting destroys shelter, eliminates much of the interspersion of types, and prevents high quality regeneration by eroding the forest floor. B (Lower). Woods roads break up the cover, make valuable edges, feeding lanes, and, in summer, dusting and sunning spots.

PLATE 40. A (Upper). Seed stock refuges as a medium of hunting control are of little value in grouse management except in the most intensely shot areas. Photo shows wire bounding refuge (on right) on New York game lands. B (Lower). The woodcock, shown on its nest, is one of the more important game birds commonly sharing range with the ruffed grouse.

PLATE 41. A (Upper). Protection from grazing is one of the first essentials of woodland management, whether for game or timber. Note the good understory to the right of the fence where protected, and the lack of any saplings or shrubs on the left where grazed. B (Lower left). Overgrazing in a woodland not only prevents plant reproduction, but has a detrimental effect on the soil itself. If carried on for many years, the effects of compaction and erosion may last a long time. C (Lower right). Fire in woodlands may destroy grouse cover almost completely for a period. If an area is repeatedly burned, as is so much of the middle Appalachian range, it cannot support grouse at all.

PLATE 42. Interplantings may sometimes be made to advantage in woodland openings or in partially-seeded old fields. A (Upper). Farm woodlands that have been heavily grazed by cattle can often be interplanted successfully. B (Lower left). Norway spruce interplanted in a woodland glade. C (Lower right). An old field partially taken over by naturally-seeded white pine. The interplanting of other species could well be done here.

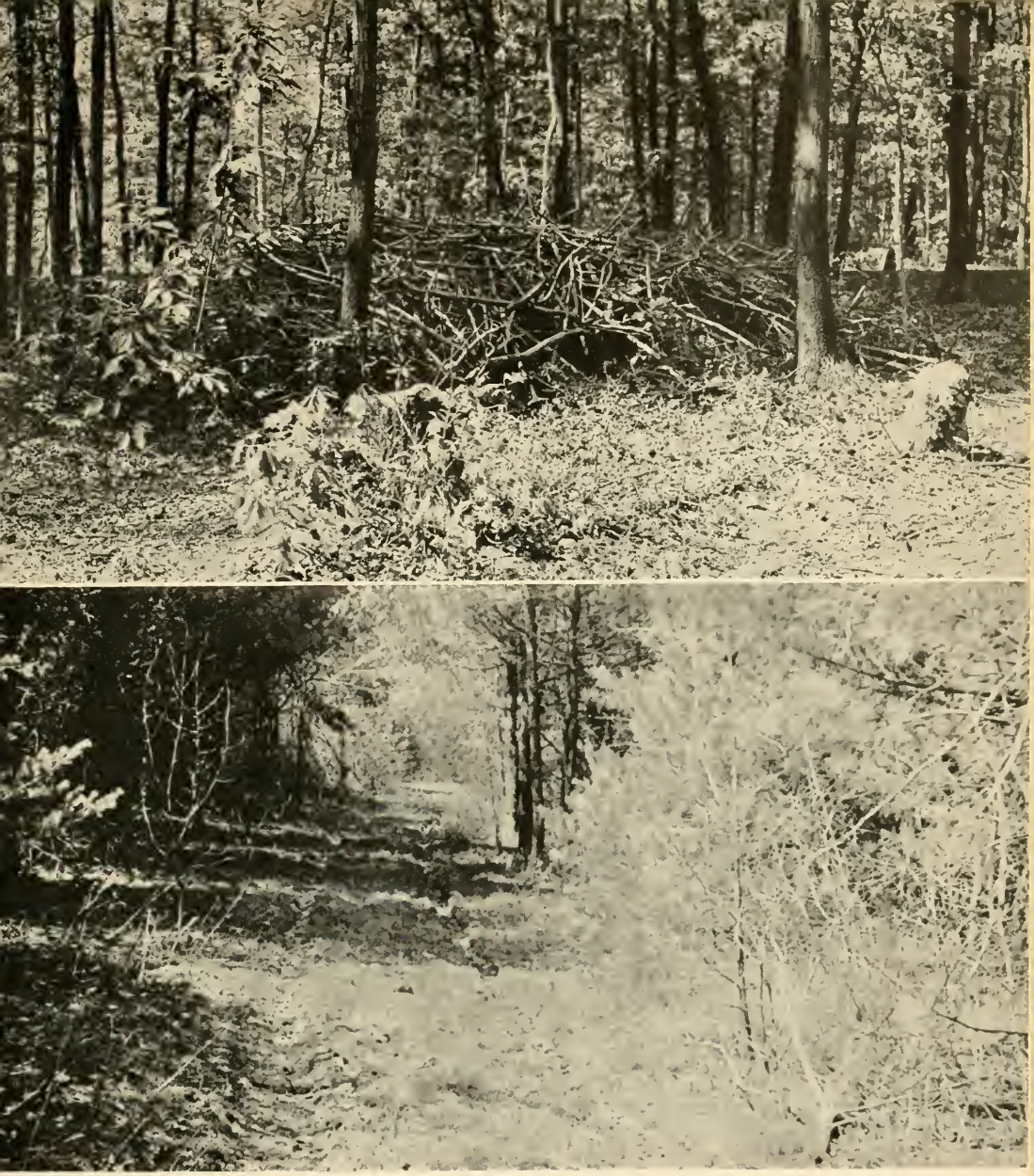


PLATE 43. A (Upper). Brush piles made from the waste tops and branches of cuttings serve well as temporary winter shelter. B (Lower). The margin of the woodland lane is a good place to improve food conditions. By releasing shrubs and herbs where the sun can reach them, fruiting and seeding will improve.

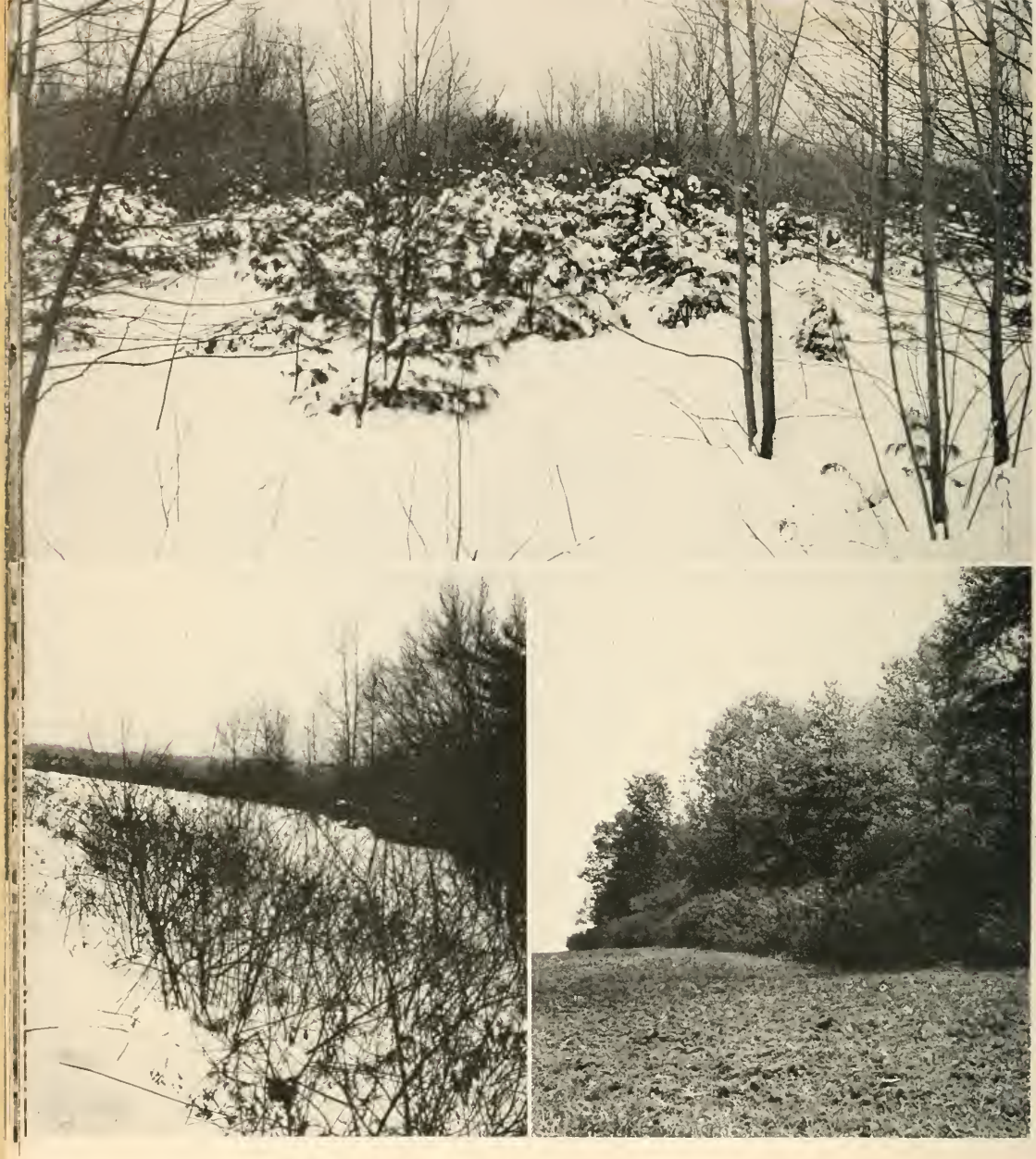


PLATE 44. Plantings may improve existing coverts for grouse. A (Upper). Interplanting of white pine in an area of cut-over hardwoods improves the shelter value. B (Lower left). Shrub border of silky dogwood planted along a woodland edge. C (Lower right). Shrub borders along the woodland edge may be developed by cutting out tree species and favoring the shrubs in the woods margin.

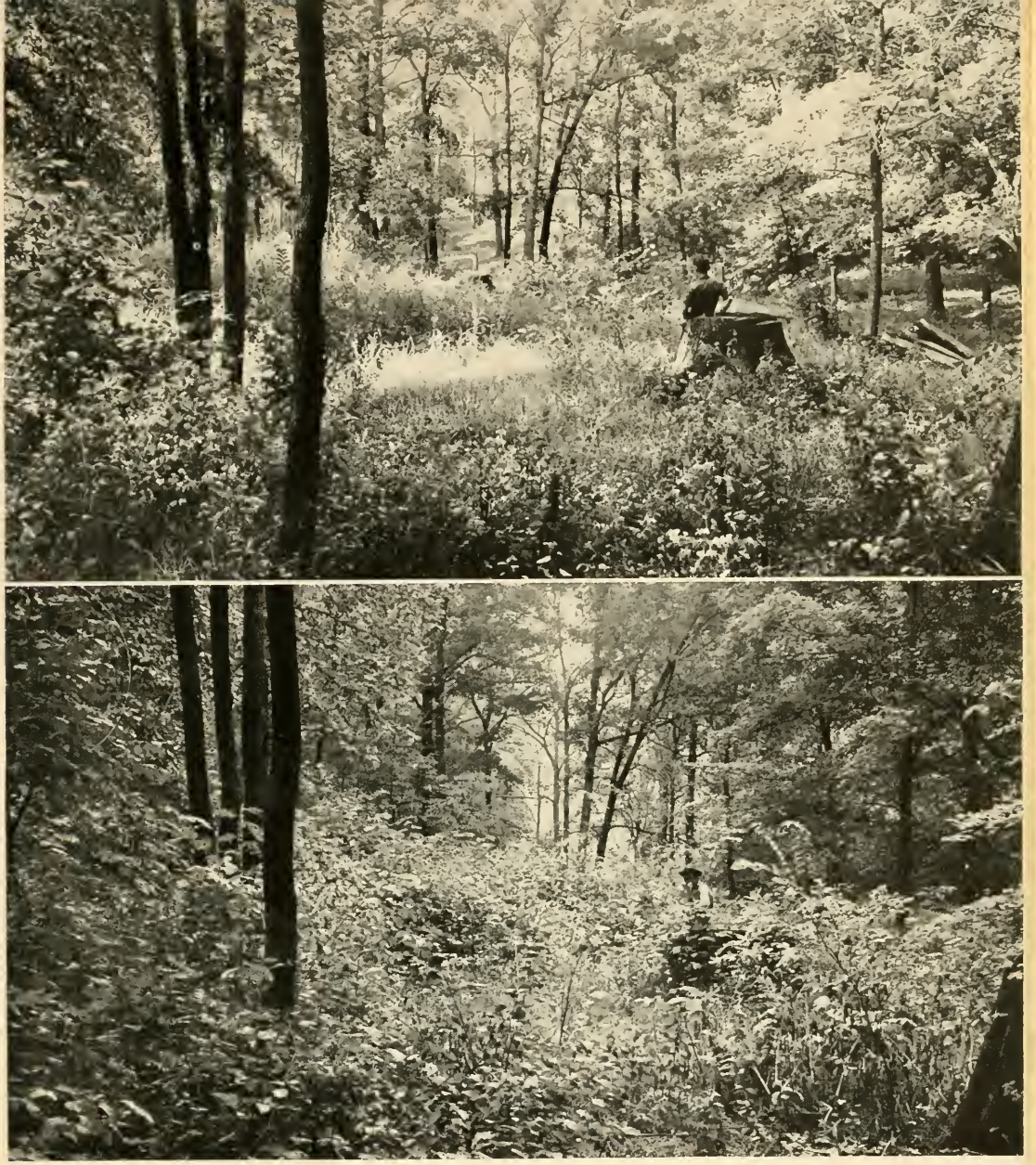


Plate 45. Group-selection harvest of timber provides small but valuable openings for grouse. Here we see a quarter-acre clearing resulting from the removal of three large crop trees. A (Upper). Just after cutting, showing stumps, and sunshine reaching the ground. B (Lower). Same after two years, showing thicket development of shrubs, and tree sprouts and seedlings.

PLATE 46. Slashings, or clear-cuttings, offer a means of improving and managing woodlands for the benefit of ruffed grouse. A (Upper). Aerial view of a Connecticut Hill woodland showing both unit and lane cuttings. B (Lower left). Close-up of a one-acre clear-cutting grown to briars, elderberry and other shrubs and trees. C (Lower right). A lane slashing, thirty feet wide, providing needed brush cover and valuable edges.

PLATE 47. A (Upper). Clear-cut areas provide edges, so needed by game. Lanes give much edge for the area cut. B (Lower left). An experimental slashing unit created by poisoning the trees, leaving the dead trees standing. Note the Virginia creeper climbing the dead trees upon receiving full sunlight. C (Lower right). The edge of a unit slashing showing the change in the character of the cover.

PLATE 48. Wherever the terrain permits, it is desirable to plant in contour-ploughed furrows. Survival and growth are both improved, especially for hardwoods. A (Upper). Contour-furrowed field being planted. B (Lower). The same plantation five years later.

PLATE 49. Selection of species that are adapted to the planting site is vital to success. A (Upper). In this ten-year-old plantation, the arborvitae (being pointed out), while surviving, has grown but a very few inches due to an unsatisfactory site. B (Lower). In this shrub border planting, the first (on right, next to grain field), third and fourth rows are a success, but the second row is a failure because of the use of a species unsuited to the soil. In this instance, the misplaced plant was winterberry in a well-drained soil.

PLATE 50. Reforestation provides interspersion of cover types by arrangement of species. A (Upper left). An aerial view of two fields on Connecticut Hill showing pattern of conifer and hardwood plantings (shrub bands cannot be distinguished from hardwood trees). B & C (Upper right and lower left). Same two fields from the ground, left and right respectively. D (Lower right). Field planting showing alternate bands of conifers and hardwoods.

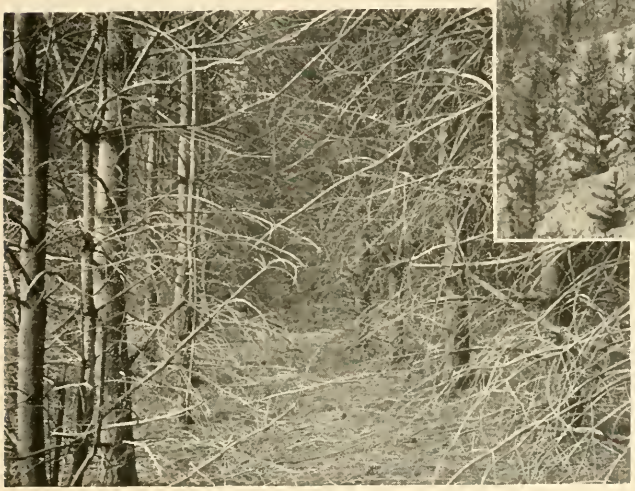


PLATE 51. Coniferous reforestation, or natural pure stands of pines and other conifers, vary greatly in value to grouse according to age. A (Upper). For the first few years the young trees affect the old field complex very little. B (Center). From about five to fifteen years of age the stand is mixed with natural reproduction, usually hardwoods, and serves as overgrown land. It may be of considerable value as a feeding area, is likely to be excellent cover for cottontails. C (Lower). After the crown closes, often between fifteen and twenty-five years of age, the competing natural vegetation is rapidly driven out. As the lower limbs die, the shelter value is reduced. Food is practically non-existent.

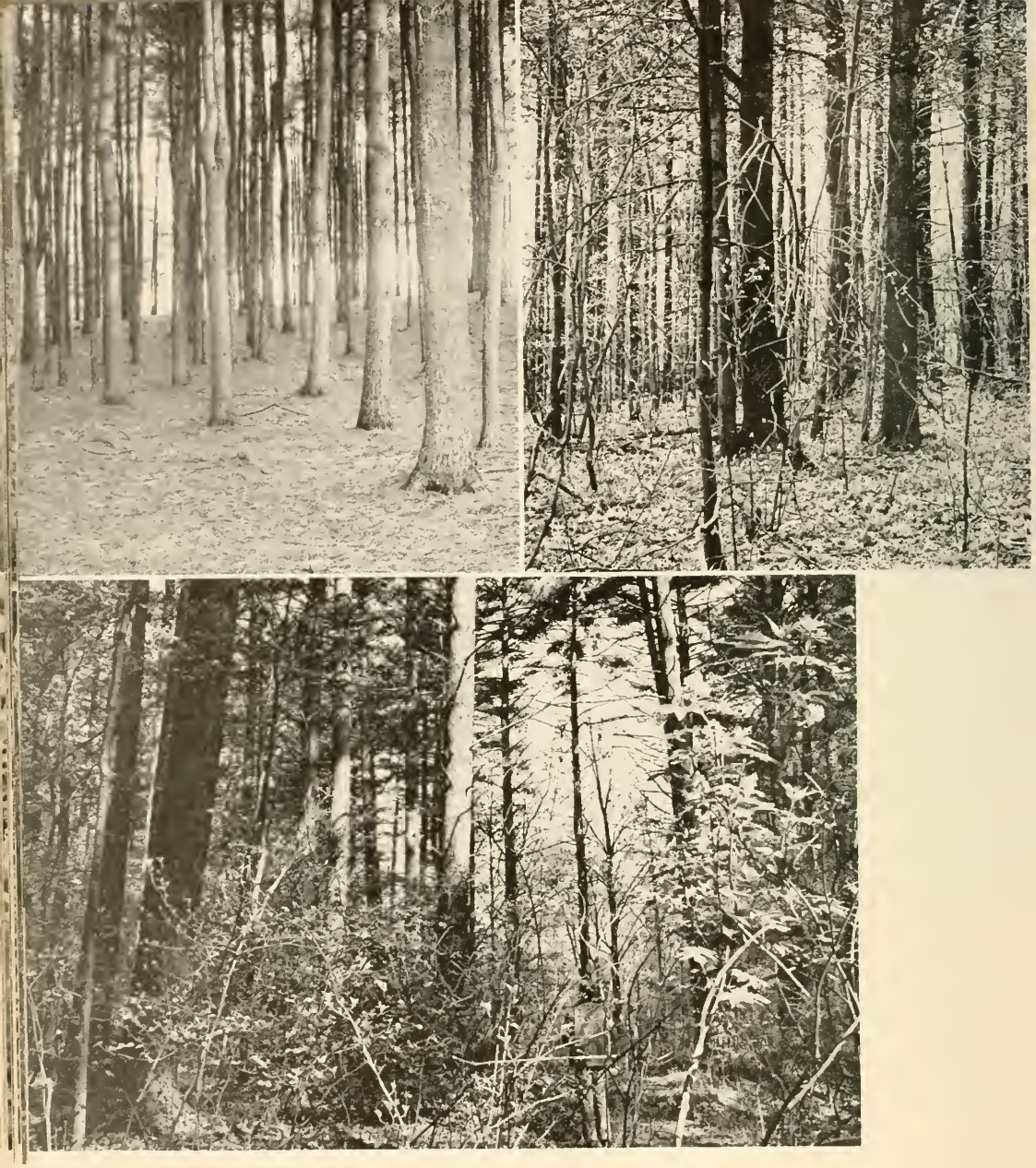


PLATE 52. A (Upper left). The trees gradually prune themselves and the tightly closed canopy prevents any germination of ground cover. It is this stage, lasting from twenty to thirty years, that is sometimes referred to as a "biological desert." B (Upper right). At around the forty-to-fifty-year age period, the crown begins to open and the return of herbs and hardwoods begins on the woodland floor. C (Lower). At maturity we find a top crown of pine, partially broken, with a complete hardwood-shrub-herb stand underneath. The shelter is out of reach, but food has now returned.

PLATE 53. Field plantations should strive for a balanced habitat. A (Upper). Mixed planting of conifers and hardwoods to provide both food and cover. B (Lower). Border of shrubs provides a desirable thicket type next to a pine planting.

PLATE 54. A ten-year-old planting of northern red oak.

PLATE 55. Nursery beds of seedling bayberry, one of the shrubs recommended for planting. These plants are in a nursery of the U. S. Soil Conservation Service.

PLATE 56. A (Upper). Game refuges are generally associated with public shooting ground areas when established on public lands. The type of marker shown here is used in New York. B (Lower). Trapping fur-bearers for their pelts on a sustained-yield basis is the only predator control recommended on grouse range. The red fox shown is one of the most important ruffed grouse enemies.

TABLE 8.

THE MORE IMPORTANT PREDATORS OF RUFFED GROUSE IN THE NORTHEAST [1]

Species of predator [2]	*Important as Destroyers of:* *Eggs*	*Chicks*	*Adults*
I. *Those of Primary Importance*			
Foxes (red and gray)	x		x
Great horned owl			x
Weasels (New York and small brown)	x		
Skunk	x		
Goshawk		x	x
Cooper's hawk		x	x
Sharp-shinned hawk		x	
II. *Those of Secondary Importance*			
Crow	x		
Raccoon	x		
Red squirrel	x		
Weasels		x	x
Great horned owl	x [3]	x	
Foxes		x	
III. *Occasional Predators*			
Bobcat			x
Woodchuck	x		
Chipmunk	x		
Dog	x		
Barred owl		x	x
Black snake	x	x	
Red-tailed hawk		x	x
Crow		x	
House cat		x	x
Marsh hawk		x	x
Porcupine (rarely)	x		

[1] "Importance" as used in this section is based on the relative number of grouse destroyed by one predator as compared to other predators, and does not imply the same significance as a limiting factor. See Chapter X for relative significance of all factors.

[2] Man is intentionally omitted as he is treated elsewhere.

[3] The horned owl does not touch the eggs but sometimes causes their loss by killing the nesting female. The other hawks listed may occasionally do the same.

ondary predators are of primary importance in local areas, and vice versa.

The question of the importance of the grouse in the diet of a given predator, or of a predator as a destroyer of grouse, may be approached from two directions. Both are needed to bring out the

complete story. From the standpoint of the prey species, the percentage of its population that the predator takes is all that counts, regardless of its ranking in the predator's diet. As a problem in the food habits of a predator, the volume of food that a prey species furnishes is all that matters at the moment, aside from the effect on the status of the prey species. To illustrate let us take a hypothetical case. We have two situations. In the first we have one family of foxes and one hundred grouse in a covert. In the second we have one family of foxes and ten grouse. Let us assume in each case that the foxes take ten grouse. In the first instance the prey species is little affected, losing only ten per cent of its numbers; in the second it is entirely wiped out. Yet in both cases the grouse furnished the same part of a fox family's diet. Let us assume it was two per cent. It was relatively unimportant to the predator, but to the prey species in one covert it was fatal.

Now let us begin over and take a different course with the same data. Say the foxes take fifty grouse in the first situation and none in the second. Then the grouse becomes a big item of food, ten per cent, to the fox in case I, without critically damaging the prey species, while in the second case, though the fox has not gained, there are fewer grouse than are left from the preyed-on population.

Thus the importance of prey species as food and the importance of predators as enemies are relative matters that must be correlated with other food habits and with population data to be properly appraised. Since we are concerned primarily with the grouse, we will examine the effect of the predatory species on this species, even if grouse is not an important item in their diets. We will also give some information on the part that grouse play in the subsistence of the various predators. It can be said categorically, however, that the grouse is rarely an item of vital importance in the diet of any predatory species, except possibly the goshawk.

Red and Gray Foxes. Both species of foxes native to the Northeast commonly take grouse. As predators, one is about as efficient as the other, and the relative importance of either one is generally in proportion to its abundance. The red fox is common throughout the Northeast, whereas the gray is found mainly from central-New York southward. So far as we know, their effects on grouse are much the same, therefore we will discuss them together.

The foxes probably warrant the title of "number one grouse enemy" over most of the Northeast. In the northernmost range they may sometimes be displaced by the goshawk, and in occasional localities by the great horned owl. Their leading position derives from their adeptness at taking grouse in all stages from the egg to the adult. As a nest predator they are by far the most destructive, and as an enemy of adult grouse they are outranked only by the horned owl and, in the northern range, by the goshawk. They are unimportant as destroyers of young grouse in summer, although they do take some.

Our experience indicates that a fox is not only a connoisseur of grouse eggs but is also quite skillful in finding them. On one occasion an observer had been placed in a house built in a tree at some distance from an incubating grouse to make a twenty-four-hour record of her activities. Near dawn on one morning a red fox was observed at some distance coming through the woods. It disappeared from sight and returned to view several times as it coursed the cover back and forth a-hunting. Gradually it approached closer to the observer and likewise closer and closer to the setting grouse. In time it came to within a few feet of the hen, and she flushed with the usual whir of leaves. The fox sprang after her but missed and ran swiftly in the direction the bird had disappeared. Presently it returned to approximately the place of action and with deliberate efficiency sniffed the base of every tree and stump in the vicinity until it found the nest of eggs.

That fox knew what it was doing. It obviously had flushed grouse before, had eaten grouse eggs before, and knew the relation between them. We had evidence that a single fox broke up seven grouse nests in a woodland of about two hundred acres in one spring. Whether or not this particular evidence may be taken as the full truth, it is certain that the fox as a species is a rather efficient nest hunter and that some individuals become particularly adept. On the other hand, I recall a grouse that successfully brought off a clutch of eggs within fifty feet of a red fox den in active use. The fox kits had played within twenty feet of the setting hen as evidenced by bones and skin of kills that they had dropped there. That did not seem to indicate predatory efficiency.

Foxes consistently destroy more grouse nests than do any other predators in New York. The proportion of all grouse nests taken by

foxes on Connecticut Hill has averaged about one in five. The percentage of predator-destroyed nests attributable to foxes varied much from year to year but averaged forty-three and five-tenths per cent over the whole state as summarized for two hundred and thirty-nine such nests observed from 1930 to 1934 (*N. Y. S. Cons. Dept. Ann. Rep., 1934*).

The records of foxes taking young grouse have been very few. It should be noted that until the birds are nearly half grown they are probably eaten whole, thus leaving no evidence. But even though summer food habits of the fox have not been well studied from stomach contents, circumstances indicate that foxes are not important as predators on grouse chicks at this season when other food is plentiful.

With the advent of winter the fox once again becomes a serious enemy. From autumn through spring the toll of adult grouse taken by foxes is significant, the greatest numbers being captured from midwinter to midspring. The number of grouse that are killed by foxes in the winter is somewhat dependent upon the weather. With deep snows, the grouse resort more to the snow for roosting; there some of them will certainly be found by foxes. The vulnerability of grouse in snow roosts is great. One of our observers, upon noticing one day that many birds in snow roosts flushed at very close range, determined to try to catch one by hand. Of the next three birds he saw in snow roosts he was able to stalk and catch two, and the third barely escaped. A fox too can learn to locate the bird by the slight snow mound at the end of a grouse track, and surely it can outdo a man at stalking.

The proportion of grouse lost through predation on Connecticut Hill that is attributed to foxes averaged twenty-one and four-tenths per cent of one hundred and ninety-one remains for which the enemy was identified (*N. Y. S. Cons. Dep. Ann. Rep., 1933*). The proportion of adult mortality [1] resulting from predation is about ninety-five per cent. As grouse mortality averages some forty per cent for the same period, foxes kill nearly ten per cent of the total population. In considering these figures we should not overlook the possibility that some of this apparent prey may have been carrion, or crippled or sick birds. However, it is our considered opinion that making such an allowance would not affect the figures materially.

[1] Aside from human destruction.

We have seen how important the foxes are in grouse mortality. How important is the grouse to the fox? The answer is that it represents a food delicacy, even as to you and me, but not a staple item of food. In following fox tracks (mostly red) for nearly three hundred miles on Connecticut Hill, no evidence was found of grouse being caught, and apparently only one attempt to catch a grouse had been made. The event, though rare, does occur. The accumulated animal remains at four fox dens on Connecticut Hill occupied by one pair of red foxes from March through May contained four grouse among thirty items of prey (*N. Y. S. Cons. Dept. Ann. Rep., 1934*). But all comprehensive records of fox food habits show the ruffed grouse to be a negligible item in the year-round food supply.

Before we review some typical records of fox food habits, it may be well to consider certain factors that affect the interpretation of these records. In the first place, the fox is most destructive as a nest predator in the month of May, but few indeed are the fox stomach records representing that season. Further, as the fox eats the egg contents, taking little if any shell, the stomach and scat records do not fully bring out the extent of this food habit.[1] Another important factor in food habits records that often leads to misinterpretation, is the source of material. It is obvious that foxes taken from areas that have no grouse will have no grouse remains in their stomachs. To interpret properly the importance of grouse in fox diet, we must give weight to these facts: Stomach or fecal analysis will not reveal the extent of egg-eating, even in specimens collected during the nesting season; summaries of stomach or fecal analyses will ordinarily be conservative in revealing grouse in the diet, as a part or all of the specimens may have been taken in localities where there were no grouse.

Hamilton (1937) summarizes the food of the red fox as follows: "Investigations in the Midwest, Michigan, New England, New York, and Virginia are all in essential agreement. The studies indicate that the fox feeds chiefly upon fruit and berries, small mammals—chief among which are mice—carrion, insects, and an occasional bird. I do not doubt it prefers a tender grouse to a half-dozen mice, but the fact remains that mice are far more abundant than grouse, and much easier to catch." Examination of five hundred and thirty-seven scats

[1] Of two fox scats collected in June in Centre County, Pa., one contained remains of grouse eggs (Kozicky, 1943).

of red foxes from eastern New York (Cook and Hamilton, 1944) revealed a frequency of occurrence of grouse averaging one and five-tenths per cent for the whole year; increasing to four per cent in winter and five per cent in April, by June the incidence fell to three per cent. No grouse parts were found in summer specimens but in autumn one per cent of the scats included some grouse remains. Dearborn (1932), writing of Michigan conditions, says of the ruffed grouse in the red fox diet: "Opposition to foxes is based largely on the belief that they are very destructive to game, especially to game birds. The only game bird of importance where most of this fox material was gathered is the partridge, or ruffed grouse, *Bonasa umbellus,* which was common there both years. According to the evidence collected in this investigation, the average fox eats not more than two grouse per year." Handley (1934), in reporting on the analyses of both red and gray foxes in Virginia, lists no grouse remains in twenty-seven summer and fall collected specimens and eighty-four winter specimens. As quail were recorded in these records, it may well be that the specimens were not taken in grouse range. Errington (1935) reported on fox stomach analyses from Wisconsin and Iowa specimens. He found no ruffed grouse in the forty-six red foxes taken in fall and winter, and but one in the seventy-two gray foxes taken from fall to spring. Likewise, Errington found no ruffed grouse remains at the one hundred and thirteen red fox dens studied or in one-thousand, one hundred and seventy-five feces samples. Here again the records indicate that the majority of the specimens were taken from farm land and not in grouse range.

Analyses of one hundred and forty-eight stomachs (those that contained food out of a total of two hundred and twenty) from Pennsylvania (English & Bennett, 1942) showed grouse to be a fairly common item of food for the red fox. Of one hundred and thirty-six late summer and fall specimens, five contained grouse, amounting to four and four-tenths per cent of the total volume of food. In this group, grouse were exceeded in volume by six other foods, all mammals, except grasshoppers. Only eleven winter stomachs were examined, and one of these contained a trace of grouse remains. Two of the five grouse captured from late summer to fall were in the twenty August records and constituted fifteen and six-tenths per cent of the food, ranking second to remains of woodchuck. Two more grouse were among the forty-two October speci-

mens and were ninth in volume of food eaten. One November stomach out of fourteen had grouse remains, and no grouse were in the fifty-six September specimens. Bennett & English (1942) also reported on analyses of twenty-nine gray fox stomachs taken from August to February. Only one, a winter specimen, contained a trace of grouse.

Of one hundred and eighty-six fox scats gathered in Huntingdon County, Pa., in the fall months, three contained grouse remains, constituting eight per cent of the volume (Kozicky, 1943).

The food of the red fox in southern New Hampshire was studied through examination of two hundred and six scats covering the period from October 1 to April 30 and two hundred and seven for the May 1 to September 30 period (Eadie, 1943). The author concludes, in reference to the use of grouse by the fox, "Ruffed grouse were abundant during the period of collection but were only sparingly represented in the scats (three per cent, winter; two per cent, summer)."

An examination of food eaten by forty-one gray foxes in Ohio revealed that only one stomach contained ruffed grouse (Bezdek, 1943).

From these references we can see that the ruffed grouse does not rate a high place in the scale of fox foods, even considering the conservative nature of these records. Nevertheless, foxes are a very important enemy of the grouse.

Great Horned Owl. The horned owl (see Plate 33C) is probably the most efficient of all grouse predators. With very powerful talons, soundless flight, a twilight-to-dawn attack, and adequate weight, it is the most capable of all the common predatory birds in taking grouse. It is widely distributed throughout the Northeast, and is generally the most serious predator on adult grouse. It ranks second to the foxes only because it is responsible for the loss of relatively few clutches of grouse eggs.

On the Connecticut Hill area the great horned owl was by a wide margin the most deadly of the adult grouse predators. More than half [1] of the mature grouse killed by predators each year were taken

[1] The figures given for proportions of grouse killed by the various winged predators are conservative, since a considerable number of remains were the work of hawk or owl, with the evidence inconclusive as to species. The total proportion of kills was 75 per cent by avian species, and 25 per cent by mammals.

by this bird. Since many of the signs could not be distinguished with complete accuracy from those of other hawks and owls, this figure is only approximate. It is regularly somewhat over fifty per cent of grouse adult losses from all causes.

While the prominence of the horned owl as a predator of grown grouse far overshadows its indirect effect on nests, a considerable number of grouse eggs are lost due to the owls killing the mother bird. On Connecticut Hill about one in twenty-five of the nests destroyed was attributed to avian predators, largely this species of owl.

We have already noted that predators are not a primary cause of mortality among the young grouse in the summer. No doubt the horned owl takes a small toll then, but the fact that feathers of very young grouse are not left in the woods but are consumed with the birds, makes an accurate survey of the owl predation impossible. Some remains of immature grouse have been found in horned owl pellets and the feather remains of a few have been taken as evidence of horned owl killings. It is probable that this species ranks next, after the sharp-shinned and Cooper's hawks, as a destroyer of young grouse.

We have seen that the foxes, though very important as grouse predators, do not depend upon them for a high proportion of their food. This is also true of the great horned owl. Although first among the predators upon adult ruffed grouse, it still does not make a very high percentage of its food of grouse. We must again conclude, therefore, that the proportion of a predator's food composed of a given prey species does not necessarily measure, or even indicate, the place that that predator plays in the ecology of the prey species.

Typical of the records of horned owl food habits are those summarized by McDowell (1940). Ruffed grouse made up one and nine-tenths per cent of the whole diet of the nine hundred and eighty-three owls examined. They were taken between November and May. The grouse were found in only fourteen of the stomachs, or one and four-tenths per cent of the total, and were far outranked by a number of other prey species, mainly rodents. Errington, Hamerstrom and Hamerstrom (1940) examined four thousand, eight hundred and thirty-eight pellets from Iowa and Wisconsin and found twenty-two of them, or five-tenths of one per cent, to contain remains of ruffed grouse. They say: "Ruffed grouse . . . populations in the

north-central region seem to be in many ways vulnerable to, or relatively secure from, predation much as are bobwhite populations," referring to the fact that predation primarily affects that portion of a population in excess of the carrying capacity of the range.

New York and Small Brown Weasels. We presume that both species of weasels common in the Northeast are capable of taking grouse eggs, and occasionally grouse, although evidence is lacking to identify the work of each. The New York weasel is probably the more destructive, owing to its larger size. Most important in grouse ecology as nest predators, the weasel is also of some significance in taking the birds too.

The weasels ranked third only to the foxes and skunk in nest destruction on Connecticut Hill. They were accounted responsible for ten per cent of the nests rifled by predators. Only three and one-tenth per cent, as an average, of the loss of adult grouse from predators was attributed to weasels (*N. Y. S. Cons. Dept. Ann. Rep., 1933*). These animals are no doubt responsible also for the loss of a few young birds in the summer.

All scientific writings on the food habits of weasels show that their food is largely rodents, mainly mice. Hamilton (1937) found that ninety-five per cent of their fall and winter food consisted of small mammals, and he does not mention grouse at all as a part of their diet.

Skunk. The common skunk (see Plate 33B) is a remarkable, though not an efficient, predator of grouse. It is unable to prey upon the birds themselves, but often stumbles upon and robs a nest. When these animals are abundant, the number of nests broken up by them may be quite large. On Connecticut Hill the skunk ranked second among grouse nest predators, and was adjudged responsible for eleven per cent of all nests destroyed by predators (*op. cit.*).

As might be expected, studies of skunk stomachs and feces have not revealed this habit. Skunks crush the eggs thoroughly when eating them and swallow bits of shell only by accident. The probability of recovering egg shells in these specimens is limited also by the short time in the spring during which they are taken. Hamilton (1936) examined five hundred and seventy fecal specimens and thirty stomachs representing the spring and summer seasons and found no remains of grouse eggs. Likewise, Dearborn (1932) says

"Not a trace of a game bird egg was found." In both of these studies no grouse either were noted. The grouse eggs that skunks eat are to them merely an occasional treat, not a dependable or sizable item of food.

Goshawk. This magnificent hawk is the only one that might dispute the horned owl's pre-eminence as a killer of grown grouse. A daytime hunter, it has a different type of attack; it simply overtakes the grouse by superior speed and maneuverability. This is all the proof needed of this bird's hunting prowess.

It may be fortunate for the grouse that the goshawk is not more generally plentiful. It is primarily found from northern New England and New York northward, although it occurs locally southward into Pennsylvania. It visited the Connecticut Hill area only in winter and then only in occasional years. From 1930 through 1933 it was not recorded at all; then a few were observed each winter for the next three years. In these winters, the goshawks levied a high toll of grouse, considering their own numbers. The proportion of all grouse killed by predators that were taken by goshawks averaged only about four per cent the first four years (*op. cit.*). Thus it ranked fourth among predators of adult grouse, behind the horned owl, foxes, and Cooper's hawk. But in its more year-round range, the goshawk probably is the most destructive of all adult grouse enemies. No doubt where the hawks breed, they take young grouse in the summer too.

The goshawk is the one species of predator for which the ruffed grouse furnishes a really big proportion of the food. McAtee (1935) says: Grouse, chiefly ruffed grouse, were determined in thirty-one of the stomachs out of two hundred and forty-three examined, or twelve and eight-tenths per cent. McDowell (1941), in examining one hundred and one goshawk stomachs taken from November through May in Pennsylvania, records an incidence of thirteen and nine-tenths per cent of grouse, which amounted to thirteen and two-tenths per cent of this predator's whole diet. Mendall (1944) found remains of grouse in five of thirty-one (sixteen and one-tenth per cent) of these hawks taken in Maine throughout the year. McAtee concludes: "On the economic side, there is comparatively little that can be said in its favor." In spite of its destructiveness, I still have a great admiration for the goshawk. In it, and the duck hawk, nature

has evolved the "Spitfires," "Mustangs," and "Messerschmitts" of the bird world.

Cooper's and Sharp-shinned Hawks. These two "blue darters," or "bird hawks" are generally common over the Northeast. They are substantially smaller editions of the goshawk, less powerful, and hence less able to take large prey. The Cooper's is the larger of the two and the only one that as a rule can kill an adult grouse. Both birds are notable predators of the young grouse, the sharpshin being the more important on Connecticut Hill due to its greater numbers. McAtee (1935) recorded the Cooper's hawk as having taken grouse in a few cases, but reported no grouse in the nine hundred and forty-four stomachs of the sharpshin examined. McDowell (1941) found the remains of two grouse in one hundred and eight stomachs of Cooper's hawks from Pennsylvania, these constituting one and eight-tenths per cent of the total food. On Connecticut Hill, the Cooper's hawk was third among the predators of adult grouse, averaging over five per cent of the kills made by predators (*N. Y. S. Cons. Dept. Ann. Rep., 1933*).

The data on mortality of the young grouse caused by these hawks are too meager to summarize. The number of chicks taken by them is of some significance. They were clearly the first-ranking predators of the chicks on the study area. The number of remains found increased towards late July and in August, but this was at least partly due to the larger size and more substantial nature of the feathers at that time.

It is unlikely that grouse ever compose a very high proportion of the diet of the sharpshin, and only in occasional local instances of that of the Cooper's hawk.

Crow. This "black marauder" is widely renowned as an egg eater. There is little doubt but that crows will raid any nest of eggs they discover, that of the grouse being no exception. The number of grouse nests broken up by crows on Connecticut Hill from 1930–34 averaged six per cent of the predator-destroyed nests, but this proportion declined somewhat in later years. This record entitles the crow to a place of rather limited importance as a grouse predator.

On one occasion a flying crow was seen carrying a very young grouse chick. We must thus list the species among predators of the young grouse too, although this habit is surely of small importance.

While eggs of all kinds may be an appreciable part of the crow's spring food, it would be rare indeed for grouse eggs alone to amount to a very significant item.

Other Mammalian Grouse Predators. Both the raccoon and the red squirrel have in some years been of considerable significance as grouse nest predators on the Connecticut Hill area. On the average, the raccoon was responsible for the destruction of about eight per cent of the nests taken by all predators, and the red squirrel for only about two per cent. The bobcat, and no doubt the Canada lynx where it occurs, are of some importance as grouse predators, primarily in winter. Neither of these wild cats occurred on Connecticut Hill, however. Of one hundred and forty bobcat stomachs examined by Hamilton and Hunter (1939) from animals taken from fall to late winter in Vermont, twelve contained grouse. These composed five and five-tenths per cent of the bulk of the food. The authors conclude: "It is evident the bobcat has little trouble in catching grouse. Dearborn found 'no evidence of grouse remains in more than three hundred feces, although grouse were abundant around the swamps where the wildcats live.'" A trace of grouse remains was found in the intestine of one mink from among one hundred and two specimens examined from southern Michigan (Sealandt, 1943). Woodchucks are known to have broken up a few nests, and the porcupine has been recorded as eating grouse eggs (*Pennsylvania Game News,* May, 1933). Chipmunks have a habit of stealing grouse eggs and storing them in holes. King (1937) found this to be of considerable significance in Minnesota and noted that playful chipmunks used the eggs like marbles. House cats that roam grouse coverts no doubt take some grouse. Dogs, likewise, will occasionally break up a grouse nest, but rarely will catch a grown grouse. It is at least possible that shrews (*Blarina*) may take grouse eggs occasionally, since they have been recorded to have eaten whippoorwill eggs.

Other Avian Grouse Predators. Several species of hawks in addition to the accipitrine trio already discussed occasionally take a grouse. None are of much significance. McAtee (1935) reported grouse in three of seven hundred and fifty-four stomachs of red-tailed hawks, in four of six hundred and one marsh hawks, and, surprisingly enough, in one stomach of a broad-winged hawk. Mendall (1944) reports the remains of one bird, "apparently a ruffed

grouse," in one stomach of the fourteen from red-shouldered hawks taken in Maine, and one grouse in thirty-six stomachs of marsh hawks. It is likely that duck hawks and pigeon hawks may also occasionally get a grouse. Among the owls, the barred and snowy owls take an occasional grouse. Gross (1944) records the occurrence of grouse remains in five of one hundred and twenty-seven stomachs of snowy owls examined from birds taken in the northeastern states during winter incursions. However, none of these species are of any significance as grouse enemies.

It should be noted here that while no specific instances of this latter group of hawks and owls taking grouse on Connecticut Hill were noted, it is reasonable to suppose that a few of the cases attributed to the horned owl and the accipitrine hawks may have been misidentified and actually were the work of some other species.

Reptilian Grouse Predators. The black snake is the only reptile that has been recorded as a grouse predator. Records of nests being destroyed by black snakes are not uncommon, and two cases of grouse chicks being killed by black snakes have been recorded (*Pennsylvania Game News,* August, 1935; West Virginia Conservation, Dec., 1941). It is probable that other snakes too may take grouse eggs, even though no records are available. In the southern Appalachians where snakes are numerous, they might even be of some significance in connection with grouse egg losses. T. E. Clark of Virginia advised me that snakes, including the pilot black, black racer, timber rattler, and pine snake, are important grouse nest predators there and occasionally take young grouse.

RELATION OF PREDATION TO COVER TYPES

The concept of "escape cover" used in wild-life management indicates that certain cover conditions are better in preventing attack, or successful attack, by predators than others. Generally, it has been thought that dense shelter, such as that of thorny thickets and coniferous types, served this purpose best for game birds. The types of cover in which grouse remains left by predators are found as compared with the incidence of grouse in the same cover indicates that mixed woodland is the most hazardous type of cover. It is somewhat ironical that the mixed-woodland type also is the

best all-use cover for grouse. Apparently it may also serve a like purpose for some predatory animals, and in any event they would tend to hunt wherever their prey is most plentiful. Least hazardous are coniferous woods and overgrown lands, including thickets. The usual concept of safe cover, therefore, seems to hold for ruffed grouse. However, it must be remembered that factors that benefit grouse, such as escape cover, are effective only for populations well accommodated by the environment (that is, below the threshold of security).

PREDATORS AS AN AGENT OF SANITATION

It is generally recognized that predators take the prey that is easiest to get—limited, of course, by the range of their food habits. This being the case, it is reasoned that sick, injured, and weak individuals of a prey species will be the first to succumb, other things being equal. Thus the predator acts to maintain or increase the virility of its prey species. Likewise, many predators are also scavengers to a degree. They clean the range of dead animals that escaped attack before dying from some cause other than predation. How do these ideas stand analysis with respect to grouse?

The ruffed grouse normally maintains its full vitality in the face of affliction until very near death. By the time a bird shows weakness of flight, or sluggishness of activity, it is ordinarily very near death. The time during which a predator might take a sick grouse easier than a well one is very limited. Although not very significant, the sanitation principle probably does hold with grouse within this limitation. Probably of greater significance than physical weakness, is the vulnerability of birds that are in unfamiliar habitat. Similarly, grouse living under strain of intolerance by confreres may fall victim to an enemy more readily than would otherwise have been the case.

When it comes to cleaning up carcasses of birds that have met death through means other than enemy attack, the scavengers are very efficient. For example, three birds that were shot and left lying without being handled by man, were taken the first, second, and fourth nights of exposure. It is rare indeed for a grouse to lie on the ground long enough for the flesh to rot appreciably.

THE EFFECT OF PREDATOR CONTROL ON RUFFED GROUSE POPULATIONS [1]

We have already observed that any discussion covering the relations of predators and game is most delicate. That phase of the subject dealing with control of the predators, and its value, is probably the most delicate of all. Our object, therefore, must be to evaluate dispassionately the effectiveness of control on the prevalence of the predatory species themselves and the resulting effects on the ruffed grouse populations.

Predator control studies were made on the Connecticut Hill area, New York, in 1930–32, and continued in 1933–35. Two types of control experiments were made: complete control, where all predatory species were taken; and selective control, under which foxes (two species) and weasels (two species) were taken.

The initial experiment in 1930–32 was designed to appraise the effects of complete predator elimination. Of course this was far from accomplished, the degree of success with any species depending upon its mobility and its susceptibility to trapping. The trapped area consisted of one thousand, four hundred and twenty-five acres of grouse coverts while the untrapped check-area covered one thousand, two hundred and twenty-three acres. The fact that these two tracts lay adjacent to each other, one being the northern, the other the southern part of the whole study area, unquestionably acted to reduce differentials in both grouse populations and mortality. Hence, any conclusions as to positive effectiveness of predator control in improving grouse numbers would probably be conservative.

A total of five hundred and fifty-seven predators were taken by trap and shot during the first two-year period, three hundred and twenty-one the first year (October 1, 1930–September 30, 1931) and two hundred and thirty-six the second year (October 1, 1931–August 31, 1932), including fifty-six horned owls, twenty-five foxes, sixty-six skunks, forty-three weasels and twenty-two accipitrine hawks.

Records of the numbers taken the second year indicate that reduction was markedly successful with respect to the long-eared owl, red-tailed hawk, and small brown weasel; and moderately success-

[1] This account is taken largely from an article of the same title, by the author, in the *Journal of Wildlife Management*, October, 1939.

ful with the horned owl, marsh hawk, and crow.[1] Species which showed little or no reduction the second year included the Cooper's hawk, sharp-shinned hawk, sparrow hawk, red fox, gray fox, skunk, domestic cat, red squirrel, and raccoon. Considering only the more important grouse predators, control apparently showed some effect on the horned owl, crow and small brown weasel; but made little dent in the Cooper's hawk, sharp-shinned hawk, red fox, gray fox, skunk, and raccoon numbers.

Even though some of the most important grouse predators remained as abundant the second year as the first, there may have been an immediate effect on the grouse by the temporary reduction.

The data indicate that the predator control reduced the nest mortality markedly both years. During the first year the brood- and adult-mortality records show a small differential favoring the trapped sections, but in the second year the brood mortality was practically identical on the two tracts and the adult mortality was actually higher on the controlled portion. But even though the predator control proved unable consistently to lower the brood or adult losses, the reduction in nest loss accomplished might produce a higher shootable fall population.

In the fall of 1931, while the grouse population of the area was still well below carrying capacity, the predator-controlled portion had a markedly higher population density. These additional grouse, twenty-five per cent more than on the check area, may reasonably be credited to the control of predators. Then the second year, with a nearly peak population at hand, the effect of the predator control was negligible, although still producing a slightly more dense population than developed on the untrapped subarea. It appears then that the increase in adult mortality on the controlled portion the second year, presumably brought on by the higher population density the first fall, almost completely offset the saving in nests. That is to say, the inevitable inverse relationship of productivity to breeding density canceled any possible benefits of predator control. Thus the vital part that population level plays in determining grouse losses indicates the futility of attempts to regulate them.

The value of predator control in high population seems, from this test, to be negligible.

[1] Since these species are migratory, the indicated results may have resulted merely from variations in the annual flights.

Following the two-years' study of predator control in 1931 and 1932, a year was allowed to elapse and then the experiments were resumed. With the possibility in mind that the results of the first experiments may have been affected by factors peculiar to the two subareas, the trapped and untrapped areas were reversed in the second series of tests beginning late in 1933.

Trapping and shooting were carried on from October 1, 1933, to April 30, 1934, rather than for the full year as previously. The 1934 experiments continued the complete control with a no-trapping check area. A total of one hundred and one birds and ninety-four mammals were taken, including thirty-seven horned owls, fourteen foxes, nineteen skunks, ten weasels, and twenty accipitrine hawks.

As in the earlier experiments, the outstanding species taken was the horned owl, which is probably the most efficient (if not always most important) of the common grouse predators. The mammalian predators showed practically the same abundance as in the first experiments, with the two species of foxes being most important.

The nest mortality on the subareas for 1934 was twenty per cent for the trapped portion and forty per cent for the untrapped. The following summer, the brood mortalities were fifty-two and three-tenths per cent and fifty-six and three-tenths per cent respectively. By calculation, the loss of adults on the trapped area was twenty-three and seven-tenths per cent and that on the untrapped thirty-two and two-tenths per cent.

In reversing the trapped and untrapped areas the results, too, have been reversed. Nest mortality was decreased by one half, brood mortality slightly lessened, and adult losses lowered appreciably. We conclude that the predator-control-effect data were not seriously confused by other factors, although detailed accuracy of the results cannot be claimed. If comparability of the results of the two experiments was maintained, the 1934 fall population densities on the two subareas should have shown little difference, as was the case in 1932, since 1934 was another peak year. The density on September 1 on the trapped area proved to be a bird to five and six-tenths acres while on the untrapped portion the ratio was five and five-tenths acres per grouse. Thus, we find the result repeated that in a peak year even effective reduction of the nest mortality by predator control does not appreciably increase the fall population on unshot areas.

The main objective of the 1935 experiments on Connecticut Hill was to learn the effectiveness of fox-weasel control, these animals being the most destructive nest predators. But with the fall of 1934, a situation arose that seemed to present an unusual opportunity to get further valuable data on complete control. One section on Connecticut Hill attained a September density of two and five-tenths acres per grouse (equivalent of one and eight-tenths acres per grouse of actual coverts, including no open land). This represented the highest population density any covert had attained. It was decided to subject this section alone to complete predator control to determine if by so doing this saturated population density could be maintained. Indirectly, it gave a better opportunity to obtain data on dispersion or disease that might result from this heavy population.

The predatory species taken during the 1935 trapping and shooting period, October 1, 1934 to April 30, 1935, totaled one hundred and twenty-one individuals, of which ninety-seven were from the complete control subarea and twenty-four from the selective control subarea. These included sixteen horned owls, twenty-five foxes, and thirteen weasels. Most significant in this record are the takes of horned owls and foxes.

While the analysis of the data for 1935 is complicated by additional factors, the broad effects followed the same course as in previous years. Both complete and selective predator control proved effective in reducing nest losses. The selective control brought a reduction of about forty per cent in the nest mortality. Again, little or no reduction of brood losses was accomplished by either type of control—complete or selective.

The adult losses ran exactly opposite to the objectives, being greatest on the complete control subarea, least on the non-control sections. Because the losses on the complete-control section were accentuated by a marked dispersal of birds from the high population of the fall of 1934, examination of the predator decimation would seem to give a fairer comparison. Based on grouse remains found, we find that nearly twenty per cent of the 1934 fall population were picked up on the complete control subarea, nearly twenty-two per cent on the selective control and only thirteen per cent on the no-control sections. Thus, despite drastic control of predators, the high population density still induced a higher rate of predation

than occurred without control on the areas used as a check but which had much lower populations to start with. Thus, the high decimation expected in peak populations occurred regardless of elimination of predators.

From all the data on hand, we must conclude that intensive predator control of any type, while it may be markedly effective in reducing nesting loss, will not produce a higher shootable fall population of grouse during years of high abundance. During years of low grouse numbers, the evidence shows that predator control may increase appreciably the fall grouse population. But even under these conditions, with the grouse population increasing anyway, the justification for deliberate predator control is very doubtful.

Control measures designed to benefit game populations often take the form of bounties. In this connection, Gerstell (1937), in reporting upon the experience of the Pennsylvania Game Commission, concludes:". . . as a predator-control measure the payment of bounties has proven grossly inefficient . . . it has been impossible to prove that the operation of the bounty system over a relatively long period of years has improved game conditions. Furthermore, it was shown that the annual amount of money expended for bounty payments was controlled not by the abundance of predators, but principally by climatic and general economic conditions." What more need be added? There is no substantial evidence to justify intensive predator control for the benefit of grouse populations.

THE ABUNDANCE OF BUFFER SPECIES AS IT AFFECTS PREDATOR FOOD HABITS AND GROUSE MORTALITY

Buffer species are those animals that furnish the bulk of food for predatory animals. They are generally abundant, sometimes exceedingly so, have a high-reproductive rate, and wide distribution. They are the staple animal foods of the foxes, weasels, owls, hawks, etc. Predominantly they are rodents, and they are markedly cyclic in their population trends. In the Northeast the more prominent ones are: rabbits (cottontail rabbit, snowshoe hare) (see Plate 34A, B), squirrels (red and gray) (see Plate 34C), mice—field (*Microtus*), wood (*Peromyscus*), red-backed (*Evotomys*), and others—shrews, and woodchuck. Since they are relatively easy to catch, because of their abundance, their slowness afoot, or inability to protect

themselves, they tend to act as buffers in reducing predator pressure on other prey. If, because of a scarcity of buffers, the predatory population pursues the game birds more intensively, more game birds will succumb. Thus there is a close theoretical relationship between the rodents and grouse. How does it work out actually?

Determination of populations of rodent and predatory species on extensive areas is a trick still to be mastered. However, methods for determining population trends are available and, we believe, are reasonably accurate. These include state game kill records; "sign" recorded on field censuses, reduced to a number-per-man-day basis; sample-track counts taken over marked trails of standard length under as nearly uniform conditions as possible. All of these methods have their shortcomings, but using all of them some trends appear.

Several interesting trends come to light. Beginning with the early 1930's, all of these rodents increased to an irruptive peak in numbers in 1935. Then from 1935 to 1936 they all suffered a catastrophic decline. Three out of four rabbits died, four of five field mice, and nine out of every ten red and gray squirrels. This fact is supported by general census data, by the game kill reports (see Fig. 9) for cottontails and gray squirrels (although the general decline in cottontails apparently began two years before), and by the well-defined and much-publicized migration and die-off of gray squirrels in the fall of 1935.

The decline in cottontails was not so complete from 1935 to 1936 as that of the other animals, but it continued for two more years while recovery of all the others began. This three-year period of cottontail decline is substantiated by the state game kill records.

The uniformity of the rise and fall of these species from 1930 to 1936 is notable. But very significant variations in the recovery rate followed. As already pointed out, the cottontails continued to decline for another two years; the mice began a rapid recovery the next year, and the red squirrels a gradual one. The recovery in gray squirrels began the second year, as the mice and red squirrels completed their recovery to normal abundance. Then from 1938 to 1939, as the cottontails began their increase, the others again declined, the squirrels only moderately and for a single year, the mice significantly and for at least two years. The cottontails also showed some loss in the second year of the latter period.

From the standpoint of the effect of these fluctuations on the

predatory species that depend upon them for food, and the indirect effects upon the ruffed grouse, two very significant facts are pertinent. In spite of the great coincidence of the periods of major decline of these rodents, there is enough dissimilarity in their population drops so that they are not all very scarce at once. Thus, in 1936, the cottontails had only declined part way when the others "hit bottom."

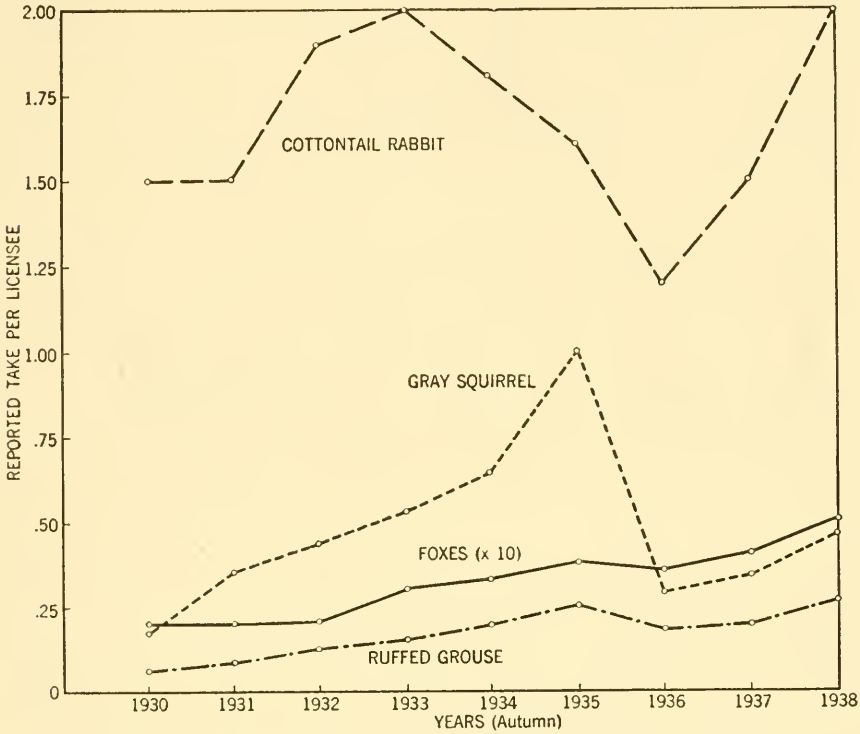


Fig. 9. New York State Game Kill Records 1930–1938.

In 1937, the mice had increased considerably above their low point and the cottontails had still not reached their low. In these two worst years for buffer foods, there were still some species in fair relative abundance. The second significant point is that even when the rodents reached the trough of their population trends there were still a lot of them, enough to support a fair number of predators.

The only one of the predator groups that is recorded in the state game kill take is the foxes. We find a slight decrease indicated in these records for 1935 (see Fig. 9).

We may fairly conclude that the numbers of several of the predatory animals are responsive to changes in the numbers of their chief prey species. The response in decline of predators may take up to two years following marked changes in rodent numbers to become significantly apparent.

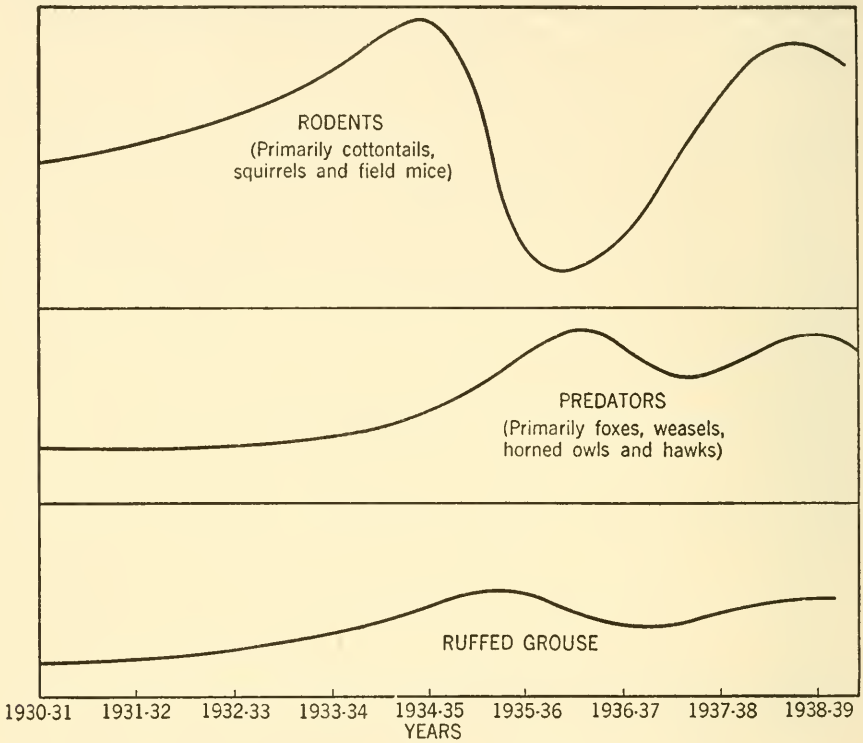


Fig. 10. Generalized Population Trends of Ruffed Grouse, certain Predators, and certain Rodents New York State 1930–1939 (Based on State Game Kill Records and field data)

Turning now to the trends in ruffed grouse in comparison with those of rodents and predators, there are both correlations and lack of correlations. We find that the Connecticut Hill trends indicate that the population drop in 1933 was probably not associated with predator-buffer trends, the 1935 decline is definitely not so associated, while the 1937 decline is quite probably linked with these trends. In examining the state-wide game kill records [1] there appears

[1] These records are well-known to be inaccurate; but since the sources of error are the same each year, the trends indicated may be quite reliable.

to be a possible correlation in the 1936 decline in grouse take, which coincided with decreases in the take of foxes and gray squirrels and with the completion of the reduction in take of cottontails that had begun two years prior (see Fig. 9).

So many factors enter into these population trends, and they are of such varying importance, that it would not be expected that the population curves of so many animals would agree in details. There is enough evidence from the data, though, to support the interrelation theory among these populations. In Fig. 10 we have tried to generalize the data in order to illustrate what appears to be the correlation. The rodents lead the parade, and change most violently; the predators and grouse follow with less marked changes.

OTHER ANIMALS THAT AFFECT THE GROUSE WELFARE

Predators and their usual prey, the buffer species, are not the only mammals that influence grouse. Many mammals, and birds too, compete with grouse for food, although this does not ordinarily cause much trouble (see page 178). However, those mammals that graze or browse can have a seriously detrimental effect on the woodland cover. Over most of the grouse range, the white-tailed deer is the only one that becomes abundant enough to damage the range. The Pennsylvania deer problem, much publicized in the past two decades, will serve as an example. Leopold (1943) in discussing this situation says: "Many plants important to other game species were also depleted; thus greenbrier, on which ruffed grouse depend for cover, was nearly annihilated. Snowshoe hare and wild turkey likewise felt the pressure of excess deer."

PREDATION AS A LIMITING FACTOR

Throughout the discussion of the relations of grouse populations to other animals, it has been apparent that predation is normally a constant and immediate medium of reduction of grouse, either as eggs or birds. The manifestation of predation does not, however, necessarily measure its status as a limiting factor, or potential limiting factor. However, it does deserve the most careful analysis in comparison with other major factors. Any group of organisms that normally destroy two eggs out of every five laid by a prey species,

and half the birds that reach maturity—and that may, under certain conditions, far exceed these rates of destruction—cannot be dismissed lightly, even though a part of the losses be conditioned by other factors.

It may be well for us at this time to review the meaning of "limiting factor." It is that element which ultimately prevents any more of a given species from existing or surviving than actually do. To clarify the matter let us take a couple of simple, and factual, examples.

The Lancaster County region of southeastern Pennsylvania is an intensively farmed area. The vegetation on the land is mainly crops (corn, wheat, oats, tobacco, hay) and pastures. The woodlands are small, scattered, and lacking in conifers. This range contains no grouse. Clearly the limiting factor is a lack of suitable habitat, shelter first, and food also but probably to a lesser degree. It is obvious that predation is not limiting the grouse here, since there are no grouse for them to capture.

There are cases in the Northeast where good grouse habitat exists almost literally in the shadow of the tall buildings of large cities. Unless this habitat is protected as a virtual sanctuary, it will ordinarily contain no grouse. Man's interference, as a hunter, or in seeking recreation, or cutting the underbrush for a park, or in other pursuits, eliminates grouse from this potentially habitable range.

These are two cases where a single element serves definitely and continuously to act as a limiting factor upon grouse—in both cases an excluding type of action. Under more normal circumstances, recognition of the limiting factor is more difficult. Moreover it may change from one year to the next. It is very likely to change as the grouse population itself fluctuates. There may be times and places that predation will act as the ultimate determinant of the level of grouse population, but these will not be general. They will most commonly be where the number of birds is well below both carrying capacity and saturation point. There will be times at almost any density of grouse when weather conditions will act as the major brake to increase. This may merely condition predation, as in severe winters, or may act more directly, through chick mortality. When populations are high, disease may limit the birds or condition an increase in predation, or the natural intolerance of the birds for their own kind (each requiring so much territory) may be the factor that

prevents a higher degree of survival so that further increases are prevented.

We have already seen that drastic control of predators may bring about an increase of grouse when the density is quite low, and that it fails to have that result when populations are high. When the number of grouse is more than the environment can safely accommodate, decline is inevitable. The conclusion seems to be that predators may limit grouse populations when below the peak of their upward trend, but still do not ordinarily prevent them from increasing to a greater density that permits another limiting factor to bring about declines beyond expected seasonal losses. These relations of population densities to changes in population level are fundamental and override all others including predator-prey relationship.

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8

The Diseases and Parasites of Wild Ruffed Grouse

Most species of vertebrate animals are subject to infection by a variety of parasites, and the grouse is no exception. The proportion of grouse playing host to one or more forms of parasites varies with the seasons, in different regions or localities, and changes from one year to another. The presence of parasites is not necessarily an ill omen. How serious the infection is to the bird depends upon the kind of parasite, the number present, and the destructiveness of the species.

As disease is a serious factor in the mortality rate of many animals, it has long been suspected that many grouse may die from this cause. Particular attention has been directed at the possible connection between epizootic diseases and population fluctuations, or cycles. Epizootics among the red grouse (*Lagopus lagopus scoticus*) in England have been shown to be caused by a nematode worm (*Trichostrongylus pergracilis*) and Coccidia (Leslie and Shipley, 1911). One of the early reports attributing disease as a cause of ruffed grouse scarcity was that of Woodruff (1908) in New York. Of nine theories "offered as a possible explanation of the grouse scarcity," three related to disease: "(5) An epidemic disease . . . (6) An internal parasite. (7) An external parasite ('ticks')." He concluded "that it was due to an unhappy combination of three separate factors, each one of which alone was serious in its effects." Following winter predation and adverse spring weather in 1907, number three is "an epidemic of some disease or parasite, or both, just which we cannot now determine."

However, the report on the next die-off in New York (Stoddart, 1918) deprecated disease as an important factor. After recalling the importance that Woodruff attached to disease in the earlier report, Stoddart says: "There is nothing in Mr. Woodruff's report that is

conclusive on this subject. Those who answered the Commission's questionnaire are convinced that these agencies (*i.e.* diseases and parasites) are playing little or no part in the present grouse shortage —'disease' being placed last on the list of causes . . ."

It was not long though before the matter of grouse disease again received considerable attention. Following the secondary grouse decline in 1924, the American Game Association arranged a study of the grouse which from the start gave primary emphasis to the disease factor. Led by two eminent ornithologists, A. A. Allen and A. O. Gross, this study inaugurated an era of research in the field of wild life ecology and management. In their first report Allen and Gross (1926), after a year's work including examination of nine hundred and twenty-three birds, stated that ". . . no definite conclusions or recommendations can yet be advanced." Nevertheless, considerable progress was made. "The common belief is that there is one disease responsible for the disappearance of the grouse. The investigation this year uncovered no evidence to support the belief. On the contrary over twenty different parasites and diseases were found, any one of which may prove to be important in different localities. Some are abundant and of general distribution, others seem to be of only local importance as yet." Later, evidence indicated that the stomach worm (*Dispharynx spiralis*) might be the cause of local grouse declines. Gross (1930) found that "this parasite was responsible for the death of a large proportion of the birds found dead in Massachusetts and Connecticut and sent to us . . ." No other diseases or parasites of the wild birds showed any likelihood of causing serious mortality. When Gross reported again a year later (Gross, 1931) he said that "not a single bird was received (during the past year) which had met death through diseases or parasites."

Thus was indicated the periodic nature of grouse disease as a lethal agent. In the early years of the New York study, 1930–32, not a bird found gave any indication of having serious trouble arising from disease. Then, in 1933, the first indications of possible trouble showed up at Connecticut Hill. The author found two grouse dead and in full flesh which proved to have died from *Dispharynx* infection. Soon another bird was found which, while killed and decapitated by a predator, was found to have been severely affected with aspergillosis, which very likely had weakened it before the predator attack. The grouse population was high and the incidence of parasitic infections was much higher than during the previous year. The

bird population declined that winter more than usual, but recovered quickly the next year, and there was no conclusive evidence of disease being a major decimating agency. And so it has been each succeeding year since in New York.

During the 1930's the results of three other investigations on the grouse disease factor were reported. Working in Ontario, Canada, Clarke (1936) concluded that a protozoan blood parasite, *Leucocytozoon bonasae* ". . . is most probably the organism responsible for the dying-off of grouse." Boughton (1937) reported on examinations of five hundred and sixty grouse, mainly from Minnesota, and was unable to draw definite conclusions as to the part played by disease in causing grouse mortality. He did feel that ". . . none of the parasites found during the present survey (which does not include examinations of adult grouse during the months of June, July and August) have been directly responsible for the mortality among the adult ruffed grouse during the year 1933–34, when a decrease in the grouse population was reported." However, he added that "the possibility still exists that parasitism is the cause of 'epidemics' in adult grouse during the summer months . . . It appears more probable . . . , however, that any mortality that did take place might have occurred in the young grouse . . ." More than three hundred grouse were autopsied in connection with the Michigan grouse study by Fisher (1939). He concluded ". . . that parasites and diseases of the ruffed grouse appear to be a major factor in the decimation of these birds in Michigan. It is evident that in order to account, if possible, for the periodic fluctuation in the population of the ruffed grouse in Michigan, it will be necessary to continue laboratory studies and field observations on these parasites that infest the species."

It seems apparent that the several investigators each feel that there is something vital in the grouse's disease relationships but they are not quite sure what it is or how it works. Before considering further the epidemiology of these diseases, let us review those that are the more prevalent.

CHARACTERISTICS AND OCCURRENCE OF DISEASE AGENTS

The diseases and parasitic conditions in the ruffed grouse, and their causative agents, may conveniently be grouped in the following categories:

Helminths, which are internal, parasitic worms, divided into three classes, the roundworms (Nematodes), tapeworms (Cestodes), and the flukes (Trematodes).

Protozoa, microscopic, single-celled animals.

Bacteria, viruses, and fungi.

Ectoparasites, including flies, lice, ticks, fleas, and mites.

The Nematode Worms (roundworms). At least fourteen species of roundworms have been found in the ruffed grouse, of which nine are known to occur in the eastern seaboard states. In the listing below, those of most significance are placed first.

Dispharynx spiralis (Molin, 1858) Skrjabin 1916 b. This stomach worm (see Plate 35) attacks the bird's proventriculus or glandular stomach, but is also occasionally found in the gullet and the intestine. It affects a number of hosts in addition to the grouse, including the domestic chicken, dove, robin, turkey, and guinea fowl.

It is a small, whitish worm a little less than half an inch long, which attaches itself by its head to the mucosa of the stomach, and usually rolls its body in a spiral.[1] There is usually a swelling of the organ, the degree depending upon the severity of the infection. There is a small, bloody lesion of the epithelial tissue, which spreads to redden the entire mucous surface if many worms are present. In such cases the lumen (passage) is reduced by swelling of the walls. In the most serious cases, the worms penetrate and destroy the gastric glands. This is accompanied by an excessive secretion of a white, glary mucus. In some cases the proventriculus is perforated, resulting in a fatal peritonitis.

In severe infections, the digestion is severely impaired and emaciation results. Death commonly results from the primary tissue destruction and starvation. Most of the infections are produced by a few worms. Allen and Gross (1926) found the usual infection to be "from three or four up to a dozen." However, they recorded one case of two hundred and twenty-eight parasites. Evidence indicates that infections with twenty to thirty worms are sufficient to affect the bird's health and those more severe may prove fatal.

The life history of the parasite begins with the eggs passing out of the grouse in its droppings. These are eaten by sowbugs (*Porcellio laevis*) which are the intermediate hosts. Here the embryos escape

[1] See Cram (1927) for full description.

and develop into infective larvae in the body cavity. The sowbugs are then eaten by grouse (or other primary host species). In the bird's digestive tract, the larvae mature and attach themselves to the proventricular wall. When mature, they lay eggs free in the digestive tract to be carried out in the droppings, thus completing the round.

The occurrence of Dispharynx is quite local, and varies greatly in different years. So far as is now known, it has been a serious grouse parasite only in the area from New York and New Jersey through southern New England. Of four hundred and forty-three birds examined by Allen and Gross (1926) from five states, several of which had been picked up dead, forty-nine (eleven per cent) had Dispharynx infestations. None of these stomach worms were found in four hundred and four birds from ten other states and provinces. Of 2,059 adult wild grouse examined during the New York study (*N. Y. S. Cons. Dept. Ann. Reports 1932–42*) about three hundred and fifty contained Dispharynx, an average infection of seventeen per cent. The rate of infection varied from six and five-tenths per cent in 1933 and seven and seven-tenths per cent in 1932 (and probably less in 1931 and 1930) to twenty-eight and two-tenths per cent in 1942. The rate increased generally from 1932 to 1938 when it reached twenty per cent. Then it declined to six and five-tenths per cent in 1939, whence it again increased each year until 1942. Serious cases were not uncommon, as in 1934 when eight out of eighteen cases "were thought serious enough to have caused death in due time."

The parasite occurs in young grouse too. The *New York State Conservation Department Annual Reports* from 1933 to 1941 (except 1936) summarize the examinations of nine hundred and thirty-two chicks, of which fifty-four or five and eight-tenths per cent had Dispharynx. The annual rates of infection varied from zero (1933 and 1934) to ten and two-tenths per cent in 1940.

Since these birds were collected from various parts of the state and at all seasons (chicks only in summer, of course), the probability of obtaining a true estimate of the rate of infection from the number of cases is slight. However, there is some indication, particularly as indicated from the records of the adults, that the incidence of this parasitism fluctuates more or less periodically, building up to a large number of cases, then falling off, and so on. Further, the high in-

cidence reached in 1937 coincides with a minor decline in grouse populations. How much significance this may have is conjectural.

Except for the records in New York and New England, the only instance of Dispharynx in grouse is in a single bird recorded by Fisher (1939) from Michigan. It was very heavily infected. In domestic fowl this parasite is known from many parts of the world.

Ascaridia bonasae (Wehr, 1940). This is an intestinal worm that may be found almost anywhere in the alimentary tract, although primarily in the small gut, and occasionally free in the body cavity. Closely related species are parasites of the domestic duck and chicken.

The parasite is one of the largest infecting the grouse, varying from about two to four inches in length; it is yellowish in color.[1] Ordinarily it does not affect the host seriously and no gross lesions are produced in most of the cases. The life history probably parallels that of a close relative in the chicken. Infection is acquired directly, no intermediate host being necessary. Its primary effect is to deprive the host of nutrients from the digested food in the intestine.

Infections often are high, two hundred or more worms occasionally being found in a single bird. Such numbers do not seem to affect the grouse seriously although it has been observed that in domestic chickens there may be a large enough number of worms to prevent food from moving through the intestine. If this does occur in grouse, it has not been observed and surely is rare.

Allen and Gross (1926) found from one-quarter to one-third of all birds they examined from various states to be affected with from one to fifteen worms per bird. Clarke (1936) found this species to be the commonest endoparasite of Ontario grouse, with incidence ranging from zero to forty per cent in different areas and averaging twenty-one per cent. Boughton (1937) records an incidence of thirty-seven per cent in five hundred and thirty-three Minnesota grouse, with an average number of six worms per infected bird.[2]

Erickson (1944) found eleven of twenty-six birds from Minnesota to contain this parasite. Fisher (1939) gives the rate of occurrence in Michigan grouse as from twenty to thirty-seven per cent in different years, with the number of worms averaging one to three.

[1] See Cram (1927) for complete description.

[2] Boughton lists the species as *A. galli* in the text although he gives it the name *A. lineata* in the first instance on page 7.

The records of the autopsies performed by the New York study from 1932 to 1942 on 2,059 adult grouse showed a great variation in incidence of *Ascaridia,* ranging from nine to seventy-one per cent in different years and averaging forty-one per cent. The incidence of twenty-five per cent in 1932 (and probably less in the preceding two or more years) increased to the highest rate in 1935 and then decreased steadily each year to the lowest rate in 1942. This steady trend may have some significance as an indicator of population relationships.

These worms are commonly found in grouse chicks too, but are not nearly as prevalent in them as in the adults. The average incidence in nine hundred and thirty-two chicks reported by the New York study in their annual reports from 1933 to 1941 was ten and four-tenths per cent, with variations of from zero to twenty-five per cent in different years. The highest incidence of infection with this parasite in the chicks occurred in the same year that it reached a high in the adults, a year of high grouse density (1935).

Thus, while its distribution is general and its incidence high, *Ascaridia* is not normally a parasite of much consequence. However, as several authors have indicated, it might conceivably cause serious trouble, and may be one of the numerous parasitisms of the grouse that are associated with high population densities and may contribute to their decimation.

Heterakis bonasae (Cram, 1927). This parasite infects the caeca, or blind gut, that forms an appendage to the intestine. It is a little less than half an inch in length. Its development is direct, eggs discharged from the host embryonating and infecting other birds.

The occurrence of this worm has been recorded most commonly from New York and the species found here and named *H. bonasae* is somewhat different from the species, *H. gallinae*, reported as common to many domestic and wild gallinaceous birds and certain others throughout the world.

It was found in one bird from Rhode Island and one from Nova Scotia among four hundred and seventeen examined by Dr. E. E. Tyzzer and in ten per cent of the birds from New York and fifty per cent of those from Pennsylvania studied at Ithaca (Allen and Gross, 1926). Neither Fisher nor Clarke reported any occurrences from their studies but Boughton (1937) reported three from among

five hundred and thirty-three birds (one to three worms each); he identified the species as *H. gallinae*.

In the adult birds examined during the New York study, six hundred and thirty-two or thirty-one per cent had this parasite present. The incidence varied from zero to seventy-three per cent in different years, with 1935 to 1937 being the high period. This worm was found in only four of nine hundred and thirty-two chicks examined over a nine-year period.

There is no indication that this parasite is of serious consequence to the ruffed grouse.

Cheilospirura spinosa (Cram, 1927[1]). This is a slender, whitish worm that inhabits the gizzard between the muscular walls and chitinous lining. Its length varies from about three-quarters to one and one-half inches, and the body usually assumes a twisted shape. Its life history involves an intermediate stage in a grasshopper (Cram, 1931).

Its distribution appears to be quite general in the range of the ruffed grouse. First discovered in 1925 by Stafseth and Kotlan in Michigan specimens, it was found commonly in the birds examined by Allen and Gross (1926) except in those from New England. They reported the highest incidence of infection from Michigan birds (forty-two per cent) and twenty-one per cent of those from Minnesota, twenty-two per cent of Pennsylvania grouse, nineteen per cent of Wisconsin specimens, fourteen per cent of those from New York, and three out of eight birds examined from New Jersey, revealed them. The average number of worms was about twelve to sixteen but in some cases varied up to forty. Only in the most severe infections was any damage apparent—an abnormal thickening of the muscular wall, and even this seemed to cause little damage.

Gross (1930) reported that "This parasite was found to be common, particularly in specimens received from New England." Mueller (1941) again recorded its occurrence in New Hampshire. Clarke's (1936) records from Ontario showed an average infection of *Cheilospirura* of nine and two-tenths per cent, with variations at different locations of from none to fourteen and eight-tenths per cent. He found a few cases severe enough to cause serious lesions but noted that in these instances the bird's vitality must have been

[1] See Cram, 1927, for complete description.

impaired. His records showed no pronounced variation from year to year and he concluded that the parasite has no relation whatever with the cyclic dying-off.

Boughton (1937) recorded an infection rate of twenty-three per cent in Minnesota grouse with an average infection of three and eight-tenths worms and a maximum of thirty. Erickson (1944) reported four instances among twenty-six birds also taken in Minnesota. Boughton included this parasite among those that are potentially dangerous to the ruffed grouse but found no very serious cases among those examined. The grouse from Michigan reported upon by Fisher (1939) were more heavily infected than any recorded, except the Michigan specimens earlier examined by Allen and Gross. In the four years from 1933 to 1936 the rate of infection varied from twenty-eight per cent to fifty-one per cent. Fisher indicates that the species may be quite significant, for not only was it the most prevalent parasite but "many of the grouse were so heavily infected with these parasites that part of the lining of the gizzard had been destroyed and there was destruction of the surrounding tissue."

The autopsies of the New York study over the eleven-year period, 1932–1942, show it to have very minor importance in that state. The average infection rate for adult birds was eight per cent and for chicks two and six-tenths per cent. The annual extremes were two per cent (1932) to sixteen per cent (1941) for the adults and zero (1933, 38, 39) to four and five-tenths per cent (1941) for the young birds. This parasite cannot be considered to be of significance to grouse in New York on the basis of present evidence, but may be so locally, and possibly quite generally, in Michigan in some years.

Capillaria annulata (Molin). A hair-thin worm found beneath the epithelial lining in the bird's crop and gullet, this parasite is about two to three inches long. It can do serious damage by causing the walls of the crop and gullet to thicken. An anemia in a grouse parasitized by *C. annulata* was described by Allen and Gross (1926).

The specimens examined by these authors did not reveal this species commonly for they say "Fortunately these are apparently comparatively rare parasites, only five wild birds, all from southern New England and Columbia County, New York, were found with them."

The species was not common in the birds examined during the

New York study in most years, but did reach a high incidence from 1935 to 1937. From an occasional case in the years up to 1934, the incidence rose to twenty per cent in 1935 and to forty-nine per cent in 1936. Then the rate declined to thirty-four per cent in 1937 and to unimportant numbers thereafter, with no cases at all recorded from 1940 to 1942. In the chicks, it is not common. Only in 1935, when six cases were found in one hundred and twenty-two specimens, did it make its appearance in more than a single bird.

Except for these New York and New England records, the only other record is a single bird from Michigan (Fisher, 1939). It is another one of the parasites having a limited range and is not normally a serious threat to its host.

Oxyspirura petrowi (Skrjabin, 1929). An eyeworm that is found under the nictitating membrane, this parasite has been reported only from Michigan (Fisher, 1939). Here it seems to be a rather prevalent and possibly serious pest. In the three years, 1934 to 1936, the incidence in ruffed grouse examined was twenty-eight, twenty-two and five-tenths and fifteen per cent respectively. "As many as seventeen of these worms have been taken from one eye, and a number of birds developed marked cases of conjunctivitis" (*op. cit.*).

Another species of eyeworm, *Oxyspirura mansoni* (Cobbold, 1879), Ransom, 1904, was found in three out of one hundred and fifty-five grouse examined by Boughton (1937), there being one worm found in each case. No significance was attached to their presence.

Microfilaria. These blood parasites have been found in a number of grouse, both old and young, by the New York study (*N. Y. S. Cons. Dept. Ann. Reports, 1933–39*). Their numbers are not significant and the incidence only reached eleven per cent one year (1936), seven per cent in 1933 and 1934, and less in other years. Only two cases were found in the chicks. Clarke (1936) reports one occurrence of these parasites in a ruffed grouse from Ontario. None of these instances indicated any serious pathological trouble.

Physaloptera larvae (Rudolphi, 1819). These larval nematodes have been reported by Boughton (1937) from Minnesota and Wisconsin grouse. They are described as, ". . . two to three millimeters long . . . encysted near the surface of the muscles of the breast and in the muscles of the legs. The cysts themselves usually were

yellowish in color, measuring about two millimeters long. The number found in an individual varied from one to many dozens." Only the larvae were found, and the primary host is not known.

Boughton found them present in three and twenty-five hundredths per cent of the birds examined from Minnesota. However, their presence was not considered serious to the birds for, when comparing grouse weights to analyze the effects of parasitism, those having only *Physaloptera* larvae ". . . were considered uninfected."

These parasites have not been reported in grouse farther east than Wisconsin.

Tetrameres americana (Cram, 1927). This parasite is found in the stomach (proventriculus). It was first reported from ruffed grouse by the New York study in 1936 (*N. Y. S. Cons. Dept. Ann. Rep., 1936*) although common in poultry in the South. In 1937, it had apparently increased somewhat in prevalence, being found in about nine per cent of the adult birds examined. Thereafter its occurrence fell off. "Of just what significance this parasite is to game birds is unknown, but since it is a great destroyer of tissue and causes heavy losses among poultry in the South and has been found in pheasants and Hungarian partridge also, it is possible it may become important" (*N. Y. S. Cons. Dept. Ann. Rep., 1937*).

Other Nematodes. Three other species of nematode worms have been found in ruffed grouse in the northeastern quarter of the United States and eastern Canada. None is common or of much ecological significance so far as known.

The gapeworm *Syngamus trachealis,* Montagu (1811), was reported in six adult grouse out of six hundred and sixty-two examined during the New York study from 1932 to 1935, none thereafter; and in seven young grouse out of six hundred and eighty-three specimens between 1933 and 1939, none thereafter. As the name implies this parasite infects the bird's windpipe, causing it to "gape" or choke in an effort to get rid of the cause of irritation.

Allen and Gross (1926) report a single case of an intestinal round worm of the genus *Contracaecum.*

A cecal worm, *Subulura strongylina* (Rudolphi, 1819) Raillet and Henry, 1912, was found in a single grouse examined by Boughton (1937). The specimen was from Minnesota but the parasite is

known to infect a number of other birds elsewhere in the Western Hemisphere.

The Cestodes (Tapeworms). At least seven species of tapeworms have been found in the ruffed grouse. Since many of these found in autopsies made in the course of the New York study have been listed in published [1] records only by genus or simply as "cecal cestoda" or "tapeworms," it has not been possible to analyze accurately the occurrence of the different species in each genus found in New York.

Hymenolepis microps (Diesing)

Hymenolepis carioca (Magalhaes, 1898) (?)

Hymenolepis sp.

Specimens of this genus of tapeworms have been reported from New England (New Hampshire), New York, Minnesota, and Ontario. They are found in the small intestine, primarily in the duodenum.

This is the only genus of tapeworms identified in the reports of the New York study. Only a portion of the tapeworms reported were determined as *Hymenolepis sp.* but it seems likely that at least the majority of those identified as "intestinal cestoda," or merely "tapeworms," were of this group.

The prevalence of these intestinal tapeworms in adult grouse varied greatly in different years, the incidence varying from zero to twenty-three per cent, with no clear-cut trends. The average incidence was seven per cent; but none at all were found in four years out of eleven.

The record is quite different with the chicks in which these parasites were found every year and in consistently higher proportions. The incidence of infection averaged nineteen per cent over a nine-year period, 1933–41, with extremes of thirty-seven per cent in 1933 (based on only eight specimens, however), thirty-two per cent in 1934, and ten and eleven per cent respectively in 1938 and 1939. The records indicate a consistency of occurrence not usual with grouse parasites. It is notable that the greatest incidence occurred in a period when most parasites of grouse were at a low ebb.

Clarke (1936) found nine cases of *H. microps* in Ontario grouse, eight of which were in young birds and one from an adult. All of

[1] N. Y. S. Cons. Dept. Ann. Rep., 1932–42.

the eight youngsters had minor infections and ". . . no apparent harm had resulted to the birds." The adult, however, was ". . . captured alive in a weakened condition . . . There was an enormous abundance of *Hymenolepis* in the duodenum and the bird would probably have perished eventually from this cause." Erickson (1944) found a single ". . . cestode fragment, possibly *Hymenolepis sp.* in one bird" from Minnesota.

Mueller (1941) reported the occurrence of *H. carioca* in New Hampshire grouse, but gave no details.

These parasites are thus occasionally pathogenic but are normally not a serious source of mortality as far as can now be determined. Considerable evidence indicates the group to be more prevalent in immature grouse than in adults. This may be because of the young eating more insects, which undoubtedly act as intermediate hosts.

Davainea tetraoensis (Fuhrmann, 1919) Stafseth and Kotlan, 1925

Davainea proglottina (Davaine, 1860) Blanchard, 1891

These are almost-microscopic tapeworms that occur in the intestinal tract, especially in the duodenal region. They have been found in grouse from New England to Minnesota.

Allen and Gross (1926) mentioned two specimens from New York that contained unidentified species of *Davainea.* At about the same time another species was described from Michigan, *D. tetraoensis.* Clarke (1936) found this in fifteen out of thirty-one young grouse in Ontario in three out of five locations. At one site twelve of thirteen chicks were infected. No serious lesions resulted and Clarke concluded that this, together with its local distribution, renders it of no importance in connection with the die-off.

Michigan grouse examined by Fisher (1939) proved to be commonly infected with *D. tetraoensis.* Of seventy-nine birds examined in 1934, fourteen contained it. Only a single case in eighty autopsies in 1935 and four out of eighty-six in 1936 completed this record. No importance was attached to these cases by the author.

Another species, *D. proglottina,*[1] was reported from three specimens from Minnesota by Boughton (1937), also in three birds from Minnesota by Erickson (1944), and from New Hampshire by Mueller (1941). It too is found in the small intestine and there is no

[1] See Boughton (1937) for complete description.

indication that it is a lethal factor. It is also found in the domestic chicken, and its intermediate hosts are several species of snails.

All authors in reporting on the species of *Davainea* note the minute size of these organisms and the likelihood of overlooking light infestations. Their prevalence may, therefore, be greater than is shown by the records.

Raillietina tetragona[1] (Molin, 1858) Joyeux, 1927. This species of tapeworm, from two-fifths to ten inches long, occurs primarily in the small intestine, occasionally in the ceca. It was identified (as *Davainea t.*) in three New England grouse by Dr. Tyzzer and recorded by Allen and Gross (1926). It was found in five out of fourteen young Minnesota grouse by Boughton (1937), aged from a few hours to ten days, and was reported from New Hampshire grouse by Mueller (1941). The species is also known from the bobwhite and other game birds, and infects a species of snail and the domestic fly as secondary hosts. No significance is indicated for this worm as a grouse parasite.

Choanotaenia infundibulum (Bloch, 1779) Cohn, 1899. Another intestinal tapeworm, from two to eight inches in length, was reported by Boughton (1937) as the most prevalent cestode in Minnesota grouse. The incidence of infection was about three per cent. It is also found in several other gallinaceous birds. The domestic fly serves as a secondary host. In spite of its widespread distribution, it has not been reported elsewhere in grouse.

The Trematodes (Flukes). At least five species of flukes occur in the ruffed grouse in the northeast quarter of the United States and eastern Canada. None are known to be of any significance as a lethal factor. These worms are probably more prevalent than is indicated by the records since they commonly escape notice in routine autopsies, imbedded as they are in the bird's tissues and assuming the same color. Mueller (1941) notes that his examination of forty-six New Hampshire grouse added two new species of trematodes to the one previously known from this region and suggests this finding resulted because his birds were taken largely from low ground where snails, the intermediate hosts, are abundant.

Harmostomum pellucidum[1] Werby, 1928

[1] See Boughton (1937) for complete description.

Harmostomum sp.

The fluke, *H. pellucidum*, is found in the ceca. It is about one-twentieth to one-tenth inch in length and one-fiftieth inch wide. Its life history is unknown. Boughton (1937) found it present in ten Minnesota grouse, or two and eight-hundredths per cent of the birds examined. The average number of parasites per bird was five and two-tenths and the maximum eighteen. This fluke has also been reported from New Hampshire grouse by Mueller (1941).

Another fluke of the genus *Harmostomum*, species not identified, was found in four young grouse in two locations in Ontario by Clarke (1936). The parasites were found in the anterior extremity of the rectum.

Leucochloridium pricei McIntosh, 1932. This fluke, first described from spruce grouse taken in Alaska, was first found in the ruffed grouse by Mueller (1941). It was present in over half the grouse he examined from New Hampshire (forty-six birds), and characterized one of the most frequently encountered parasitisms. The worms were located ". . . in the bursa Fabricii, cloaca, and lower rectum . . . Heavy infections were commoner in young birds, with as many as a hundred or more worms present in a single host." The individuals were about one thirty-sixth of an inch long. The author does not mention any pathogenic effects.

Prosthogonimus macrorchis Macy, 1934. This parasite was described from the lake states and had not been reported either outside that area or at all in ruffed grouse previous to the single case found by Mueller (1941) in New Hampshire. It is about one-fifth of an inch long and lives in the cloaca. The bird from which it was recovered was a male weighing two hundred and thirty-three grams, indicating it to be an immature.

Agamodistomum sp. Larval forms of these flukes were found encysted in the subcutaneous tissue of the bird's breast, imbedded in the chest muscles, or occasionally on the outer surface of the crop (Boughton, 1937). Its cysts were pearly white and about one-fiftieth of an inch in diameter. They were in eighty Minnesota grouse, or sixteen per cent of the birds examined, and were also found in one sharp-tailed grouse. The known range is from Minnesota east to Michigan.

Brachylaemus fuscatus. This fluke was reported in one grouse from Minnesota by Erickson (1944).

In the autopsies of Michigan grouse reported by Fisher (1939), trematodes were found only one year, 1933. Of seventy-three specimens, two and fifty-nine one hundredths per cent contained cysts of intestinal flukes.

Of all the hundreds of grouse examined by the New York study (*N. Y. S. Cons. Dept. Ann. Reports, 1932–42*) only one bird was found to have a fluke infection. In 1938, one bird of 69 had "cecal trematodes." However, it seems quite likely that in these studies these obscure worms may have been commonly overlooked. In no instance, however, has their presence given rise to serious pathogenic effects so far as is known.

The Protozoa. Protozoans are single-celled, microscopic animals, the parasitic forms of which are found in several parts of the body. Some of these parasites cause serious disease in gallinaceous birds. At least nine species are known to infect the ruffed grouse.

Eimeria angusta E. A. Allen, 1934

Eimeria bonasae E. A. Allen, 1934

Eimeria dispersa Tyzzer, 1929

These protozoans are known as coccidia, and the disease they cause is coccidiosis. Allen and Gross (1926) reported one wild grouse as having a few coccidia but they found these organisms to be a serious cause of loss in young grouse in captivity. A few years later Tyzzer (1929) described *E. dispersa* from wild ruffed grouse. This species is found in the small intestine. It ". . . is differentiated from any other species of coccidia in gallinaceous birds by the absence of any well-defined polar inclusions in the oöcyst" (Boughton, 1937). This author reports finding it in twenty-four Minnesota ruffed grouse, six and five-tenths per cent of those examined.

Two new species of coccidia in ruffed grouse were described by E. A. Allen (1934), as *E. angusta* and *E. bonasae.* The former lives in the ceca and has been recovered from grouse taken in Labrador, Alaska, and Minnesota. Allen says that "quite a number of the birds examined had heavy infections . . ." Boughton (1937) found it present in four ruffed grouse, or one and one-tenth per cent of those examined and in one sharp-tailed grouse.

E. bonasae occurs in the ceca, or rarely in the small intestine. It was reported by Allen (1934) from birds taken in Massachusetts, Quebec, Labrador, and Alaska. Few of the birds examined were found to harbor this species.

Coccidia were found in seventy-nine, or three and eight-tenths per cent, of the adult grouse examined during the New York study, as noted in their annual reports, but all were found between 1932 and 1937, none from 1938 to 1942. The highest rate of infection was ten and seven-tenths per cent in 1936, but this figure may have been affected by inclusion of some captive birds. Of the young grouse examined, forty, or four and three-tenths per cent, had coccidia. Again the record is erratic, varying from zero (three years out of eight) to seventeen per cent in 1934 and thirty-seven and five-tenths per cent in 1932 (three out of eight birds).

Infections of coccidia in wild grouse have not been proved to be of significance as a mortality factor. However, the possibilities of this disease assuming importance at times are real, especially among the young birds. Boughton (1937) concluded that it ". . . is undoubtedly a dangerous parasite. It is an intracellular parasite, developing chiefly in the epithelial cells of the small intestine, and when present in large numbers may give rise to acute enteritis, causing denudation of the intestinal epithelium, consequent digestive derangements and malnutrition, and the bird becomes emaciated and anemic." Coccidiosis has caused considerable trouble to grouse in captivity (Allen and Gross, 1926; Bump, 1935) although it does not necessarily follow that similar infections can occur in wild populations. The most that can be said is that these organisms are potentially dangerous to wild grouse, but are not yet proved to be so.

Leucocytozoon bonasae Clarke, 1935. This species is a blood parasite that causes a malaria-like disease. It is found in both adults and young but seems to be particularly pathogenic to the young. So far it has been found and identified only from Ontario, Minnesota, and Michigan.

So impressively did its occurrence correlate with the dying-off of grouse in Ontario in 1933 and 1934 that Clarke concluded it ". . . is most probably the organism responsible for the dying-off of grouse." It is quite possible that epizootics of this disease might

have caused local dying-off in the areas studied, but it is certain that they are not responsible for grouse declines in a broad geographical sense. As species of this genus are known to be peculiarly pathogenic to the young of turkeys, ducks, geese, and ostriches ". . . this fact, together with the high incidence of the disease, especially in the single case of . . . (a) sick bird . . . (he mentions) . . . and the lack of evidence of any other disease-producing organism or parasite . . ." (Clarke, 1936) led him to conclude that it was the organism responsible for sudden grouse declines. Even the assumption that the cause of grouse dying-off is some pathogenic organism is not known to be valid, even in restricted areas.

Regardless of any cyclic significance this disease might have, Clarke did find it in twenty-one out of twenty-four specimens examined for blood parasites [1] in the areas of dying-off in 1934. The previous year, the gametocytes of the *Leucoctozoon* were found in four of five grouse ". . . in which they might be expected." One of these was a sick youngster, half underweight, which apparently was a result of this disease. No other serious cases were noted.

The only other areas from which this organism has been reported are Michigan and Minnesota. Fisher (1939) records that five grouse out of seventy-nine examined in 1934 from Michigan showed its presence in blood samples. In July, 1935, two five-weeks-old chicks out of seven collected by Dr. O'Roke contained the parasite (Fisher, 1939). Erickson (1944) found the parasite prevalent in Minnesota. The incidence among 30 specimens in 1941 was sixty-three and three-tenths per cent; of 48 specimens examined in 1942, sixty and four-tenths per cent were infected; and of twenty-four grouse taken in 1943, eighty-three and three-tenths per cent had these protozoons present. These birds were collected from September to November.

Subsequent to Clarke's pronouncement on the importance of this protozoan in 1936, others conducted a diligent search for it in other areas. None at all was found by the New York study.

The Flagellates

Trypanosoma gallinarum Bruce et al.

Trypanosoma sp.

[1] Examination for blood parasites requires the preparation of fresh blood smears in the field at the time the bird is killed.

Ptychostoma bonasae Tyzzer, 1930

Cyathosoma striatum Tyzzer, 1930

These three (possibly four) species of flagellates have been described from the ruffed grouse. In no instance have they shown any indication that they might be seriously pathogenic. They apparently are a normal part of the bird's internal fauna and are not associated with any disease. They were found in a large proportion of the birds examined by Dr. Tyzzer and reported upon by Allen and Gross (1926). These flagellates they mentioned were probably the species later described by Tyzzer (1930). Clarke (1936) reported four birds from Ontario lightly infected with a flagellate tentatively identified as *Trypanosoma gallinarum.* He noted that the organism is probably more prevalent than would be indicated by the small number of cases, a suggestion borne out by the prevalence reported by Tyzzer, yet passing unnoticed in several other reports on grouse parasites. Fisher (1939) reported one grouse from Michigan containing flagellates of the genus *Trypanosoma,* identified by Stafseth and Kotlan.

Tyzzer (1930) found the two parasites he described as prevailing in the ceca, over the surface of the mucosa, and occasionally found in the contents of the large intestine. It appeared that of the two, *Ptychostoma* was preponderant near the outlet of the cecum while *Cyathosoma* occurred in the dilated portions. He noted that they may be in ". . . the nature of symbionts essential to the health of the mature bird . . ." but this is merely a conjecture.

Histomonas meleagridis (Smith, 1895) Tyzzer, 1920. This protozoan is the organism that causes the disease known as "blackhead," a scourge of the domestic turkey. It is a common cause of death of grouse in captivity (Allen and Gross, 1926; *N. Y. S. Cons. Dept. Ann. Reports, 1933–42*) but has not definitely been identified in wild grouse. Even though this chapter intends only to cover the diseases of wild grouse, this organism is included because of the great probability that it actually does affect the wild birds when they come into contact with poultry range. The action of the disease is so rapid that infected specimens in the wild would be exceedingly difficult to obtain.

Any poultry range is apt to be infected with blackhead even though the chickens or turkeys themselves do not show signs of

the disease. Chickens especially are likely to be carriers. Any grouse walking over infected range may pick up the organisms from the ground. Being exceedingly susceptible, the bird would die in a short time.

The organism first affects the ceca and later the liver, causing destruction of the liver parenchyma. According to Allen and Gross (1926) "One or both ceca gradually become filled with cheesy, necrotic material which is more or less bloodshot. Sometimes the young grouse and occasionally the old birds die at this stage before the typical lesions appear on the liver. These lesions on the liver appear as dark depressed areas with a central light area and an outer light fringe, at first appearing as watermarks but later the white areas grow until the dark portion is entirely obliterated. There is usually also a thick straw-colored fluid in the loose tissue about the heart and sometimes in the peritoneum covering the viscera."

Again it should be emphasized that this very serious disease has not yet been proved to occur in wild grouse, but the circumstances indicate that its occurrence is likely where grouse range borders the farm poultry yard. Any statement linking this disease with grouse declines would be purely conjectural.

Trichomonas, species. A protozoan parasite reported by Allen and Gross (1926) as "occasionally found in small numbers by Dr. Tyzzer." No significance was attached to its presence, nor any details given concerning its status as a grouse parasite.

Infectious Diseases. The grouse is occasionally subject to infectious disease of several sorts. The disease of captive grouse called "blackhead" (and likely to occur in wild birds) is caused by a protozoan parasite and has been discussed above. Several others known to occur in grouse are covered below. All are capable of causing death and some, as tularemia, blackhead, and aspergillosis, are potentially agents of serious epizootics.

Aspergillosis. This is a disease of the lungs and air sacs caused by a fungus, *Aspergillus fumigatus.* Its spores generally are distributed in the soil and in such material as moldy straw. The conditions required for its growth in the bird are not well understood.

It has been most prevalent in captive grouse (Allen and Gross,

1926; *N. Y. S. Cons. Dept. Ann. Rep., 1933–42*), but is also known to occur in wild individuals. Dr. Tyzzer found it in two such specimens in 1925 (Allen and Gross, 1926). The New York study reported twenty-seven cases in adult wild grouse from 1,816 specimens examined from 1935 to 1942 (*N. Y. S. Cons. Dept. Ann. Rep. 1935–42*). No cases were listed among birds examined from 1932 to 1934, although one bird found dead by the author on Connecticut Hill, N. Y., in 1933 after decapitation by a predator, proved to have suffered from aspergillosis.

Tularemia. This disease is caused by a bacterial organism, *Pasteurella tularense.* It has been found in wild ruffed grouse only in the Midwest, primarily in Minnesota. Green and Shillinger (1934) reported one case among eighty-seven birds (including some sharp-tails) collected in northern Minnesota in 1932; two instances were found among seventy-one grouse taken in September 1933 (again the total included some sharp-tails); in October 1933 three cases of tularemia were noted in ruffed grouse from among twenty-six grouse of three species. They concluded ". . . that tularemia is a common disease of both ruffed and sharp-tailed grouse." They could not ". . . however, give any decisive judgment as to the significance of the occurrence of tularemia in grouse as a mortality factor." These birds were all collected for the study by game wardens, were all able to fly, and showed no symptoms of disease, with a single exception. One of the infected birds was found in a dying condition. However, it was noted that there was little opportunity to locate sick or dead birds, hence the disease might well have been more prevalent than indicated.

The tularemia organism is spread by its alternate host, the tick (*Haemaphysalis cinnabarina*), and probably by other species of the same genus. These ticks infest numerous other birds and mammals and in some are known to spread tularemia, notably in the snowshoe hare. The number of ticks per animal varies greatly both by season and in different years, and may well be correlated with population fluctuations. As tick numbers rise, the disease increases until finally an epizoötic occurs. This reduces the host population and with it the disease, and from there the cycle builds again.

This hypothesis is still just that—a theory so far as grouse are con-

cerned. Despite diligent search, no tularemia has been found in eastern grouse. The true significance of this disease in ruffed grouse therefore remains unsolved. At least, it is potentially destructive.

Ulcerative Enteritis. This infection of the posterior part of the small intestine has been observed in captive ruffed grouse and bobwhite quail for several decades. Commonly called "grouse disease" or "quail disease," it caused great mortality in numerous bird-rearing ventures. Levine (1932) described an epizoötic in captive ruffed grouse and showed that the causative organism was transmitted on ground infected by the birds' droppings. Morley and Wetmore (1936) proved that the organism was bacterial, similar to that which causes human diphtheria, and named it *Corynebacterium perdicium.* Bass (1941) later identified the organism in quail as a ". . . gram-negative, anaerobic bacillus . . . ," transmittable by coprophagy. He was able to immunize quail with killed cultures of the specific organism.

It was suspected that a disease that would infect grouse so rapidly as ulcerative enteritis, would likely occur in wild birds, possibly becoming a serious mortality factor. Green and Shillinger (1934) found it among wild grouse in Minnesota, and noted that "Occurring as a natural infection, it stands out as a disease which may play a devastating role in the periodic destruction of ruffed grouse at peak abundance." They reported three cases of the disease, one of the birds being greatly emaciated and weighing only 210 grams.

For the present, we must list this disease along with tularemia as a potentially destructive force, but not yet demonstrated to be effective in wild grouse populations.

Other Diseases. Wild ruffed grouse are occasional victims of various other diseases. A number of these are secondary afflictions following wounds from accidents or gunshot. Among these may be enteritis, peritonitis, pneumonia, hepatitis, ventriculitis, ruptures, tumors, lead poisoning, septicemia, and so forth; all of these have been reported by the New York study (*N. Y. S. Cons. Dept. Ann. Rep., 1932–41*). Other abnormalities reported as a result of that investigation include tuberculosis (three cases in 1937–38), cloacal infection, egg-binding, and malnutrition.

Allen and Gross (1926) recorded two cases of bird pox in grouse from Massachusetts. They described it as causing warty growths

about the head, mouth, and tongue. Recovery probably takes place unless feeding is so interfered with as to result in starvation.

Green and Shillinger (1936) have reported the occurrence of the bacterium, *Pasteurella aviseptica*, in wild grouse. This organism is the cause of fowl cholera in chickens. The discoverers note that "if this organism is as destructive in grouse as it is in domestic fowl, it may well be an important factor in grouse mortality." No evidence of its widespread occurrence has as yet been demonstrated.

External Parasites. Ruffed grouse are known to be infested by five different types of ectoparasites, creatures which live on the body surface and mostly derive their sustenance from biting or piercing the bird's skin to take its blood. An exception are the feather mites which live on the feather substance. The other four types are ticks, fleas, lice, and flies. It is also likely that grouse are attacked by "bite-and-run" insects such as mosquitoes that remain on the body only long enough to take one load of blood.

These external parasites are not normally a serious threat to the bird's health. However, some carry other diseases which may be serious (see under tularemia, p. 243), and occasionally the infestation may be so heavy as to be a serious drain on the vitality. In these instances it is commonly found that the bird has been weakened by other afflictions as well as the ectoparasites.

Ticks (*Ixodoidea*). Four species of ticks of the genus *Haemaphysalis* are known to infest ruffed grouse. They are found on the bird in all three stages: larva, nymph, and adult. The degree of prevalence decreases with each older stage, the larvae being most abundant, nymphs next, and the adults relatively scarce. The reason for this is not wholly clear but is probably due to reduction in numbers of ticks with each stage from mortality and progressively increased difficulty in locating hosts. Ticks drop off a grouse quickly upon the bird's death. The adults probably leave most quickly, due to greater agility, and this helps to explain the difference in numbers of each stage of ticks found on birds freshly killed.

They are found on the host from spring to fall, and pass the winter in the ground in the egg stage. Abundance seems to be greatest in late summer. Further, there is apparently a marked geographic variation in abundance, the ticks being most prevalent in midwestern lake states, less in the East.

Probably the most prevalent species is *H. cinnabarina* Koch (1844), the common rabbit tick, found on numerous mammals, gallinaceous birds, and man. It is a carrier of the dread disease, tularemia. Its range is wide and it is known to infest grouse in the eastern United States and Canada from Minnesota and Alberta to New England and Labrador.

Another species attacking grouse over a wide range is *H. leporispalustris.* Gross (1930) reported it ". . . present in considerable numbers on most of the birds collected and examined at Matamek (in Labrador, eastern Canada) in 1929." Fisher (1939) recorded 1,172 specimens taken from thirty ruffed grouse from Michigan and examined by Dr. R. G. Green of Minnesota. The average number of ticks per grouse was one hundred and sixty-seven. This species also carries tularemia. Fisher also reported one grouse from Michigan examined by Dr. H. J. Stafseth that had the tick *H. punctata punctata,* a species found on a number of mammals and birds. The fourth species, *H. chordeilis,* was reported from New York in 1941 (*N. Y. S. Cons. Dept. Ann. Rep., 1941*).

The heaviest infestations of ticks have been reported by Green from Minnesota. The average number on all Minnesota grouse examined during September was six hundred and forty and in October it was one hundred and eighty (Green and Shillinger, 1934). The heaviest infestations were on two birds that yielded 2,985 and 2,468 ticks, respectively. The authors believed that the average figures were lower than the actual owing to ticks escaping before the birds were picked up and sealed in bags.

Fisher (1939) quoted Green on the examinations of Michigan grouse and their ticks: "Nineteen samples of a hundred ticks each were injected into a corresponding number of guinea pigs. Two of the nineteen guinea pigs died with lesions typical of tularemia, showing that the samples of ticks obtained from grouse specimens were infected with tularemia to the extent of ten per cent. This figure is probably to be considered a normal finding and does not represent an unusual situation for the present stage of the game cycle, as similar findings have been obtained in Minnesota."

Infestation of ticks varies greatly in different years and probably follows a rather well-marked cycle. However, there is often marked variation in nearby localities at any given time. Numbers of ticks present are, of course, correlated with grouse abundance, there be-

ing an increase in the rate of infestation and in the degree of infestation as the birds become more numerous. The correlation is also connected with the abundance of other tick host animals, notably hares and rabbits.

Clarke (1936) said that "Ticks were found on most of the specimens collected . . ." in Ontario. Allen and Gross (1926) recorded heavy infestations on eight of fifteen birds taken in northern Maine, and stated that ticks ". . . were likewise reported on birds in Alberta, Canada."

Ticks have been found more commonly on the chicks than on the adults in the New York study (*N. Y. S. Cons. Dept. Ann. Reps., 1932–42*). With both age-classes tick occurrence has varied greatly in different years, and is low judging by Midwest standards. The first instance was that of a single adult bird in 1933. No further cases of ticks infesting adults were noted until 1939. Sixteen instances in the three years, 1939–41, a negligibly low incidence, were all. None was found in 1942. The first ticks on grouse chicks were twenty-five cases in 1934, representing an incidence of fifteen per cent. They were identified as *H. leporis-palustris.* Next year the incidence dropped to six per cent (seven cases); then for two years the record was incomplete, although there were numerous cases of tick infestation in 1937. No chicks were found infested in 1938, but for the next three years the incidence increased yearly. From a six per cent (ten cases) rate of infestation in 1939, it rose to twenty per cent in 1940 (twenty-eight cases) and twenty-one per cent in 1941 (twenty-four cases). The next year none was reported. From 1935 to 1940 the species was called *H. cinnabarina;* in 1941 it was determined as *H. chordeilis.*

In addition to the possibility of transmitting tularemia to grouse, ticks may cause the birds considerable discomfort, and occasionally ill health. The ticks tend to congregate about the head and neck and may cause this area to be almost completely denuded of feathers. With the young birds especially, the drain of blood as the ticks engorge themselves may reduce the bird's vitality, and sometimes result in death.

Louse Flies. A single species of the true flies (Diptera) is of fairly common occurrence on grouse, both young and adult. It is a hippoboscid, *Lynchia americana* (Leach). Allen and Gross (1926)

commented: ". . . reported rather generally distributed but few specimens sent in." This may have been because the insects left the birds quickly after death, and were not caught by the collectors. Clarke (1936) reported a single case in Ontario.

Nine scattered instances in eleven years were reported by the New York study on adult grouse, and twenty-two cases in ten years on chicks (*N. Y. S. Cons. Dept. Ann. Reps., 1932–42*). These are blood-sucking flies, but no serious significance is attached to their presence on grouse.

Lice (Mallophaga). Mallophagous insects of at least two species are occasional on grouse. Allen and Gross (1926) reported several on birds sent in during winter and spring. Clarke (1936) collected them ". . . in numbers from many of the specimens taken at the field stations." They were identified as *Degeeriella camerata* (Nitz).

Of seventy-one occurrences of lice on adult grouse reported by the New York study, all but one were in the period 1935 to 1937. In 1936 the incidence was thirteen per cent. Only one case was reported for chicks, that in 1935. Whether this erratic occurrence is actual, or the result of different methods of analysis is not clear. It hardly seems that an infestation of this type would be so highly erratic.

Lice are a source of irritation to grouse but are not known to be of any significance as a mortality factor.

Fleas (Siphonaptera). Two grouse having fleas were reported by Clarke (1936). One of the parasites was identified as *Ceratophyllus* species. No importance was attached to its occurrence.

Mites (Acarina). Feather mites of the family Analgesidae, and belonging to the genus *Megninia*, ". . . were found in greatly varying abundance on most of the specimens examined in the field. On some young birds they were very numerous, but except as a possible source of irritation, cannot be considered as of pathological importance." So reported Clarke (1936) concerning Ontario grouse. He also recorded larvae of the mite *Trombicula microti*, of the family Trombidiidae, on grouse, particularly in Algonquin Park, Ontario. They were not found in great numbers, and were sporadic in occurrence.

Air-sac mites (*Cytoleichus nudus*) were reported in seventeen

grouse by the New York study (*N. Y. S. Cons. Dept. Ann. Reps., 1935–37*) in the three years 1935 to 1937. None was found in other years. No indication was given of any importance attached to these infestations.

TOTAL PARASITE INFESTATION

In discussing each organism that parasitizes the ruffed grouse, the conclusion was almost always reached that the species was not a very serious mortality factor. Most have not been demonstrated to be lethal even when prevalent and widespread in occurrence. None of the afflictions known to cause death commonly is widely distributed. The stomach worm (*Dispharynx spiralis*) is apparently restricted to parts of New England and the middle Atlantic states, the blood parasite (*Leucocytozoon bonasae*) primarily to Ontario, and tularemia to the north-central states. No one disease-producing organism has been shown to cause major grouse declines over a wide range.

Possibly of more significance as an indicator of the importance of disease as a mortality factor than each parasite by itself is the total prevalence of all parasites and diseases. It is entirely logical that there would be a cumulative effect when more than one organism is attacking an individual bird. The effect of several species could result in death whereas any one of them alone might not have caused trouble.

The proportion of grouse having one or more parasites or disease organisms has varied with a clear-cut trend in New York in the period 1930–42. The autopsy records are not available to corroborate the belief that parasitism was at a low ebb in 1930 and 1931 but circumstances indicate it to be true. Beginning with 1932 the incidence of parasitism increased steadily; forty-eight per cent in 1932; sixty-four per cent in 1933 and sixty-one per cent in 1934; then ninety-five per cent, ninety-two per cent and ninety-four per cent in 1935, 1936 and 1937, respectively. Then followed a decline in parasite incidence beginning with a seventy per cent rate in 1938, followed by fifty-five per cent in 1939 and forty per cent in 1940. The next two years indicate another period of increase, the 1941 rate being fifty per cent and that of 1942, sixty per cent.

The periods of increase exactly parallel these of growth in the

grouse population, and the break in the increase phase, in 1938, came immediately after a significant reduction in grouse numbers generally in New York. While these are admittedly rough correlations, they almost surely carry considerable significance.

With the grouse chicks, the trend of parasite incidence is not so pronounced, but rather is more consistent from year to year. Further, though there is much evidence that disease is a more effective mortality factor among chicks than with adult grouse, the incidence of parasitism is notably lower in the young birds. This probably reflects the fact that many of the chicks were collected when but a few days old, a time when few parasites are likely to be found. The nine-year record of nine hundred and thirty-two autopsies of grouse chicks from 1933 to 1941 (1936 excluded) shows the incidence of total parasitism as follows: 1933—thirty-eight per cent; 1934—fifty-eight per cent; 1935—thirty-four per cent; 1937—forty-four per cent; 1938—seventy-five per cent; 1939—thirty-three per cent; 1940—fifty-one per cent; 1941—fifty-two per cent. The grand average was forty-three per cent, compared with an average of seventy-two per cent for all 2,059 adult birds examined (*N. Y. S. Cons. Dept. Ann. Reps., 1932–42*).

DISEASE AS A LIMITING FACTOR

Interpretation of the disease factor is among the more difficult of all the facets of grouse ecology. It is manifestly impossible to gather the vast amount of factual information that would be necessary to render a well-substantiated judgment. Not only must the dead and dying grouse be gathered in considerable numbers during a die-off period, an achievement never attained by any grouse investigation, but the related factors must be placed in their proper perspective too. Geographical distribution of disease-caused mortality, and its direction and spread are important. Correlations with grouse populations must be made, and hence widespread censuses must have been made, another impossible task. The part played by secondary hosts of the parasites, their population, condition and distribution, the relation of weather (and possibly other meteorological conditions) to grouse health and to the disease organisms, the part played by predation and hunting (or lack of them), these and other matters may be fundamental to an adequate understanding of grouse popu-

lation changes. So it is no wonder that we cannot yet paint a very clear picture of the significance of disease among grouse.

Despite all of the defects in our knowledge, certain conclusions can be made with fair accuracy and other probabilities can be suggested.

During most years, disease is not a primary mortality agency of grouse in any given area. A considerable incidence of most of the parasitic organisms that affect grouse may be considered normal and not a serious threat.

The incidence of disease organisms and the intensity of the individual infections and infestations are directly related to the population density of the grouse. When grouse are scarce, they will have little disease; as the numbers of grouse increase, parasitism and disease will increase, and when grouse are abundant, disease will generally become more virulent and an important cause of mortality in local areas.

When grouse are abundant over a wide range, losses from disease will probably occur from a combination of several species of parasites; and when epizoötics do occur from a single species of parasitic organism, the effects are likely to be very local and unevenly distributed.

It is probable that there is a significant relationship between disease mortality in grouse and weather conditions. It is well-known that some parasites reproduce more abundantly under certain meteorological conditions than under others, as for example in wet weather as contrasted to dry. Boughton (1937) discussed this matter at some length. He concluded, ". . . a definite correlation between the degree of parasitism and the meteorological and topographical factors appears to occur."

When disease becomes an important mortality factor of grouse, it probably is primarily effective in killing the young birds during the summer.

When serious declines in grouse populations occur over considerable areas, declines of the type that have been called cyclic, disease almost certainly plays a part, and just as certainly shares the responsibility for causing the losses with other major factors as weather conditions and predation.

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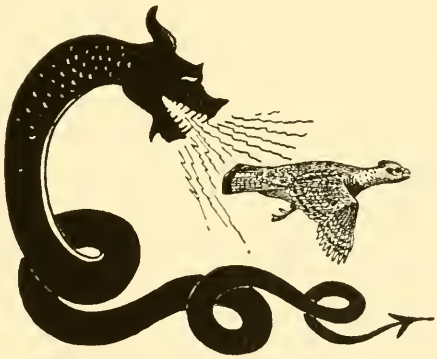

9

Man's Relation to the Grouse

The effect of man upon the grouse depends upon the kind of man. The American aborigines lived their lives almost literally with these birds, in their own habitat. The numbers taken by them for food probably was no more than the excess above the winter carrying capacity, and a healthy thing for the birds. The clearings and trails made by the Amerindians were improvements to the grouse range. And the bird was a fairly important item of food to these men.

The early white settlers also depended upon the "partridge" for a considerable amount of food. For a time the pioneer's land clearing provided a beneficial interspersion of cover types over the grouse range. But in most areas it outgrew this effect and more and more excluded the grouse from the land, restricting it to the regions and cover that could not be profitably and extensively cleared. Complete extermination was the fate of this magnificent bird over much of its original range. More than half of the northeastern states comes within this category. Such is the march of civilization.

Surely no further elaboration is needed to indicate the importance of man in grouse ecology. In fact it may be said that the bird's future rests with him. Man's relations with grouse are many faceted, as man in the mass is many-sided. As a hunter he kills grouse; as a trapper he kills the enemies of the grouse, or the food of the grouse's enemies, thus possibly adding pressure on the grouse itself. As a woodsman he sometimes improves and at other times destroys the bird's home with saw, ax, and fire. As a farmer he protects the woods with fence or he grazes it with livestock, he clears the land and keeps it cleared, he keeps livestock and pets which may kill the grouse, trample its eggs, or transmit disease to it. As a conservationist he enacts laws, manages the land, and does other things that sometimes benefit and sometimes injure the grouse. In all these and other ways man's impact is felt, however unwittingly, by *Bonasa umbellus.*

AS A HUNTER AND TRAPPER

To the early settler, the grouse was one of several game species that helped fill the family larder. Its role was purely utilitarian. As agriculture grew and cities developed, the taking of grouse turned into a commercial venture. There was little sport in hunting the "fool hen" grouse of those days. Wilson (1812) speaks of the advantages of a "good" dog thus ". . . the more noise he keeps up seems the more to confuse and stupify them, so that they may be shot down, one by one, till the whole are killed."

It is difficult from the records of the era of commercialization of grouse to gauge how many were taken, what the populations might have been, and other relevant information. Audubon (1856) records their sale in the Cincinnati markets for twelve and one-half cents each in 1820, which might indicate that large numbers were available. Elliott (1864), condemning the slaughter of the young, relates: "I know of one firm that receives sometimes, on many Saturdays in succession, five hundred pairs of these birds." Market hunting flourished through most of the nineteenth century, varying in intensity with the abundance of the birds, but gradually waning with the more limited range, the more and more restrictive laws, and the slow change in emphasis toward hunting as a sport Monon (1875) indicated the resentment toward this business when he says: "The whole north country, from Amsterdam to Northville (New York), is infested with pot shooters who hunt (out of season) for the Saratoga market." By the turn of the century the shift to grouse hunting as a sport was about complete, although some illegal market hunting continues even today.

Forbush (1912) gives one of the few records that indicate former grouse abundance when he quotes E. F. Staples of Taunton, Mass., that in the early 1880's about one thousand birds were taken in a season on twenty thousand acres that he ranged. He comments that these were "real good" years, the last good ones that he had observed up to the time he was interviewed in 1908. With densities only equal to those of the 1930's (and former peak periods may have been higher) there could have been on such an area from four thousand to five thousand birds on the basis of a twenty to twenty-five per cent kill.

Effect of Hunting on Grouse Populations. Since hunting has been attributed by many to be a serious factor in reducing grouse numbers ("Its arch enemy, man, has shot and snared it almost to extinction," Bent, 1927), an analysis of this problem is of utmost importance. Among the means of analysis is the reported game take required of each hunter annually in some states, including New York and Pennsylvania. While these figures are open to many criticisms, they are consistently arrived at and are valuable in showing trends.

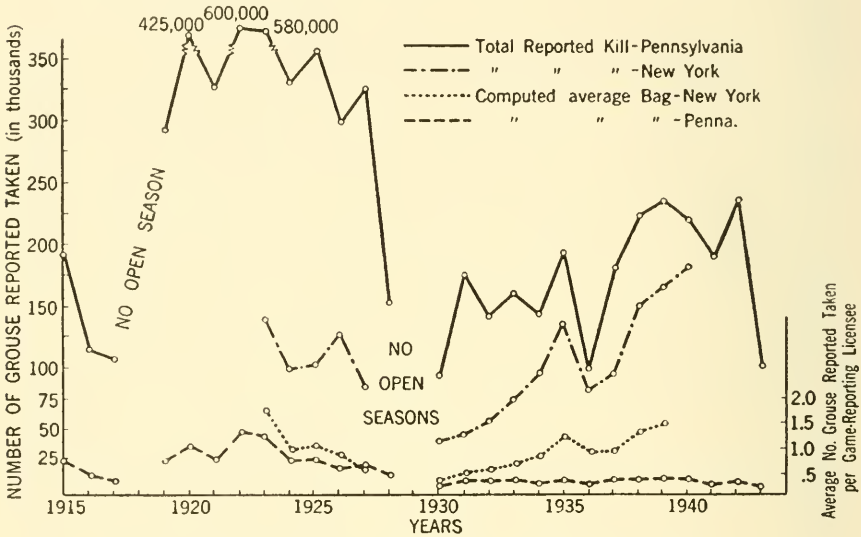

Fig. 11. Reported Take of Ruffed Grouse by Hunters
Pennsylvania 1915–1943
New York 1923–1940

(The New York figures used for average seasonal bag for the years 1923–1931 obtained by multiplying take-per-licensee by 3.5 to get an estimated take-per-game-reporting licensee. Those for 1923–1925 are based on hunting licensee figures; those for 1926–1940 are based on 80 per cent of combined hunting, fishing and trapping licenses. Pennsylvania figures are based on numbers of hunting licenses.)

These records are shown in Fig. 11 for the years 1915–43 in Pennsylvania (taken from Ryder, 1944) and 1923–40 in New York (taken from N. Y. S. Cons. Dept. Ann. Reports).

Any interpretation of these figures must weigh several pertinent relations. The daily and seasonal bag limits were three per day and fifteen per season in New York, two and ten generally in Pennsyl-

vania. The number of licenses varied from less than three hundred thousand to nearly seven hundred thousand in each state in different years. Reports in New York are ordinarily received from only about three-fifths of licensees and are taken by local clerks when a new year's license is issued, which is anywhere from one to ten or more months after the game was taken. From 1923 to 1925, specific hunting licenses were issued. From 1926 to 1939 the licenses covered hunting, fishing, and trapping and no separate hunting license was issued. In Pennsylvania, the figures were based on field estimates from 1915 through 1936, and on hunters' game-kill reports from 1937 through 1943, received from almost all hunters. Landowners were not required to be licensed to hunt on their own lands, nor were licenses required of women. Thus the actual total take is very much higher than that reported, probably about double. But the trends should be accurately reflected in these statistics.

It has been thought by some "old timers" that the peaks of grouse abundance have gradually lessened over each previous height. This is not borne out by a comparison of the New York kill between 1923 and 1926 with those of 1935 to 1940. The author was about convinced of this contention in 1936 when the tabulation of the 1934 hunter reports was completed. It is indicated in the Pennsylvania records.

From all evidence the grouse populations had been generally as high in New York from 1932 to 1934 as in 1935 to 1938. This is not reflected in the kill records. Apparently this is a product of social factors: the change in number of hunters; the unwillingness of many hunters to shoot grouse for a few years after the closed seasons of 1928–29 and the extermination scare that accompanied the major decline of that period; the shift of bird hunters to the pheasant, particularly of the younger men who never knew grouse hunting, etc. Apparently these factors are gradually overcome as the good grouse years continue, and thus produce a definite lag in the grouse kill trend (as indicated by state records during the years of grouse increase) behind the actual population trend.

When hunting is normal, and grouse are plentiful, hunting nowadays in the Northeast (from Virginia northward) results in a legal bag of about eight hundred thousand birds. In the United States, all grouse were estimated to have contributed 3,864,000 pounds of meat in 1942 (S.A.F. Comm. Report, 1944).

Further efforts at evaluating the importance of hunting in grouse

ecology were undertaken by field studies in 1930, 1931, and 1936. Several areas of average quality grouse coverts running from about one hundred to three hundred acres each in size in Tompkins County, N. Y. (six of them in 1930 and thirteen in 1931), were censused and the hunting results checked. The kill averaged ten per cent of the birds in 1930 and sixteen per cent in 1931 (Edminster, 1933), individual units of cover lost from zero to fifty per cent of their birds to the hunters. The very low return in the first year probably reflects the reluctance of the hunters to pursue grouse during the first open season after two years of closure and grouse scarcity. This feeling was somewhat abated the next year although it apparently took several years to disappear entirely.

Another check on the hunting take was made in the fall of 1936 on a portion of the Connecticut Hill area not devoted to the regular studies. On a total of 1,379 acres of coverts, the hunters took fourteen per cent of the October grouse population (*N. Y. S. Cons. Dept. Ann. Rep., 1937*). The highest kill on any of the three cover units involved was twenty-three per cent.

During 1932 to 1935 two studies bearing on this subject were made in Minnesota and Michigan. While done under different ecological conditions, the results are interesting for comparison. Trippensee (1935) found the hunting take on national forest land in Minnesota in 1934 to vary widely. On one unit of two sections of land the kill was only nine and four-tenths per cent; on another unit of four sections it was thirty-eight and two-tenths per cent. A summary of his figures for all of the 6,400 acres involved gives an average take of nineteen and seven-tenths per cent of the fall population.

The study in Michigan in 1932 and in 1935 was summarized in a letter from Harry Ruhl to me in 1936. The 1932 results on the Pigeon River State Forest showed a hunter take of six and seven-tenths per cent of the September population (probably somewhat higher for the prehunting season population of mid-October) on the four square miles censused. The 1935 studies were made on two areas, Pigeon River State Forest and Escanaba River Tract (*Mich. St. Cons. Dept., Biennial Rep., 1935–36*). The hunter bag on the Pigeon River area was seventeen and three-tenths per cent and on the Escanaba tract seventeen and four-tenths per cent. The Pigeon River data when developed on the basis of a September census gave a kill of only ten per cent, thus indicating that the 1932 records

were much lower than the actual kill. In Pennsylvania in 1940, Studholme (1941) found the hunting season loss to be twenty-three and two-tenths per cent, of which at least seventeen per cent was attributable to hunting by man.

These Midwest and Pennsylvania records corroborate the New York results remarkably closely. We may conclude that the normal hunter kill is in the neighborhood of fifteen to twenty per cent of the prehunting season population.

We have discussed the total kill. Now let us see what this means to the individual hunter. What is the average daily and seasonal bag of grouse? This will be a discouraging revelation to those who are considering becoming grouse hunters—and reassurance for the experienced shot who may still be smarting from being unable to get his eye on 'em the last time out, for there are multitudes who have fared worse. Before revealing the shockingly low effectiveness of hunters it may be well to pause and note again that the grouse presents as hard a wingshot as any American game bird. (I know quail, woodcock, and duck hunters will rise up in wrath at that statement!) That this creature could so develop from a "fool hen" in the space of a century is a remarkable tribute to its adaptability.

High daily and seasonal bags of individual hunters are plentifully recorded in the old literature. Forbush (1912) lists a number of such occurrences from Massachusetts thus: "I can remember when a market hunter going out from the city of Worcester by train each day, walking to the covers and returning at night, killed from ten to fifteen birds daily. . . . Mr. George Howes shot and marketed three hundred and ninety-eight birds in one shooting season. . . ." With the disappearance of the market hunter went the story of large individual kills. The very limit of the present-day laws, as for example two per day, ten per season in Pennsylvania, three and fifteen in New York, makes large bags legally impossible. But the hunter who attains these figures is rare indeed.

On Fig. 11 is shown the seasonal take per hunter based on the number of hunters who reported taking some game.[1] Of course this is very conservative since many of these hunters who reported taking game did not pursue grouse at all. For what it is worth, the average game-taking hunter in New York has bagged an annual total of from

[1] This is based on actual data beginning 1932, on computed data 1923–31 using the 1932–38 average of 3.5 times as many licenses reporting as reported taking game.

less than 0.3 grouse to 1.7 grouse, not an alarming record to say the least. Leopold (1933) gives 0.3 grouse per hunter for the seasonal average in Wisconsin, which checks well, since all of the Wisconsin hunters are not grouse hunters either.

Other grouse-hunting states show similar records. For example, in 1938, Pennsylvania hunters averaged .3 grouse, Connecticut hunters .4, each for the season. For honest-to-goodness, dyed-in-the-wool grouse hunters, the average is very much higher. Many of my grouse-hunting friends make their daily limit several times each season, and regularly take their seasonal limit. Van Coevering (1931), in speaking of the miraculous recovery of the bird, noted that two hundred and sixty-five grouse hunters in 1930 put up 11,000 birds, and took 1,248. The average kill per hunter was 4.7, less than half the legal seasonal limit.

Data on daily hunters' bags was gathered in the field studies of grouse hunting, already discussed. In New York in the 1930 and 1931 studies, it took 19.0 and 12.6 hours of hunting, respectively, to bag a grouse. The average hunting "day" was 5.75 hours in 1930 and 3.4 hours in 1931. Adjusting the take to the basis of an eight-hour day, the average daily hunter bag was .42 grouse per man in 1930 and .63 in 1931. The actual daily bag on the short hunting days was .33 and .37 respectively. This daily bag probably increased some in successive years as both grouse and grouse hunting increased. However, the tendency is more marked in the increased total take than it is in the individual take; that is, the increase is mainly in more hunters taking grouse rather than the same hunters taking more grouse (see comparison of graphs in Fig. 11).

The distribution of hunting take is of interest too. Only about one-quarter of the hunters took any grouse at all. Again we see that relatively few hunters get grouse, even among those who are hunting in grouse cover. If we convert our figures to include only the approximately twenty-five per cent of hunters who can hit grouse, the daily eight-hour-day bag per hunter would range from 1.6 to 2.8 birds per day. Half of these figures would give the approximate take on the basis of the length of day actually hunted.

The records in Michigan in 1932 (Ruhl) indicate an average daily bag of 0.7 grouse per hunter. It may be noted that this is considerably lower than Van Coevering's (*op. cit.*) record of 4.7 birds per average three days' hunting in Michigan in 1930, or 1.6 birds per man day.

The complete losses in grouse that are attributable to hunting by men are larger than the actual take by the amount of the loss from crippling. This factor is difficult to evaluate and has been the subject of wide differences of opinions, some observers depreciating it while others believe it to be as important as the bag itself.

An exaggerated estimate of the crippling loss may be derived by deducting the hunter kill from the difference between the posthunting season and prehunting season populations as determined by censuses. This figure will include losses from predation, disease, and accident, as well as from hunter crippling or losing. This total loss has been about equal to the hunter-take figure. The corresponding figure for the 1932 Michigan work (Ruhl), was nine per cent, which was 136 per cent of the hunter take. Trippensee (1935) indicates a rather different result, his other losses amounting to only 21.6 per cent of the hunter kill for the hunting period.

The proportion of other-than-hunting-take losses of the New York studies that is actually the crippling loss cannot be accurately determined, since these areas were not under intensive study. They indicate only the upper limit of such losses. Some information on these losses may be inferred from experience of expert hunters, aided by trained dogs. The crippling loss averaged about one-seventh of the grouse bagged. These may be considered as minimum figures since the hunters, being experts, probably left less than the average proportion of cripples.

Some additional light may be shed on this problem by a consideration of the fall losses on census areas that were not hunted. This is from natural causes but not from gunshot. The loss during hunting season on no-hunting areas is about equal to the hunter kill on a hunted area; and the loss from all causes on a hunted area about double the hunter take. Thus the losses other than the hunter take, whether crippling may be involved or not, are about the same. This indicates that the crippling loss is probably nearer the minimum suggested above rather than the maximum. It is my estimate that the true average loss from crippling will approximate twenty-five per cent of the hunter take, or about four per cent of the prehunting season grouse population.

The total hunting kill is the hunter take plus the crippling loss. By applying the twenty-five per cent of take rule derived above for the New York figures we find the estimated total hunter kill to be: 1930—twelve per cent; 1931—twenty per cent; 1936—seventeen per

cent. Since these samples are only indicators of a general condition we may conveniently use twenty per cent of the prehunting season population as the normal anticipated loss from hunting.

An interesting sidelight on grouse hunting is the success ratio—the proportion of flushed birds brought to bag by the hunters. About one grouse in a dozen flushed was retrieved. This is considerably less than the success ratio of birds actually shot at, which is a more correct indication of shooting skill. This was from two to three times the ratio of flushed birds bagged, or about one bird in four or five shot at was taken.

The effect of hunting on grouse populations varies with the density of the population, as well as with the local intensity of hunting pressure. Whether the hunters kill twenty per cent of the grouse, or more or less, is important mainly as it affects the continued abundance of the species. During the years of moderate-to-high abundance, the twenty per cent of kill effected is of little importance in changing the trend of grouse abundance.

Ordinarily there are about two and a half grouse produced for each pair of grouse in the spring. Thus two and a half birds from each four and a half living in the fall may be removed and still maintain the normal number of spring breeders. If there were no other sources of loss, the hunter could thus safely take fifty-five per cent of the fall population. This represents the upper potential safe limit of kill, but actually it cannot safely be approached owing to unavoidable losses from other causes. It has already been noted that winter losses from predation are low when fall populations are low, other things being equal. Under such circumstances the probability of predation may be twenty-five per cent or less, even where no hunting has taken place. Following Errington's theory of vulnerability, which seems to hold fairly well with grouse, hunter take would displace a loss from some other cause for all birds in an insecure position. This becomes effective only in years of high abundance. From both theory and practice we may conclude that a hunter kill of twenty-five per cent is safe in all but years of scarcity, and that this figure may be increased somewhat in years of abundance. Surely the record of increased take and increased populations in New York from 1930 to 1938, along with specific field data, show that hunting as currently practiced has not been a factor in causing serious grouse declines.

The rather small part that hunting plays in total grouse mortality

may be gathered by considering the fate of an average hundred grouse eggs in the spring (see page 285). Of eighty-two which may perish the first year, hunters are responsible for only five. Obviously this five per cent of eggs accounted for by hunting is the same as the twenty per cent of adults. It should be noted though that the number of mature birds lost are of far greater importance than an equal number in the egg and immature stages.

Predator Reduction by Hunters and Trappers. It is a sad commentary on our progress in conservation education that the average American hunter still considers all hawks as bad hawks, can see no good in skunks or weasels, continues to believe that if there weren't so blankety-blank many foxes there would surely be more game for him to shoot. This attitude results in the actual loss of conservation values. John Q. Hunter still takes a pot shot at every hawk, owl, fox, crow, turtle, snake, red squirrel, or whatnot that crosses his path, and believes himself to be a worker for "the cause" when he does so. Worse, he is often encouraged by the payment of bounties, or prizes offered in "vermin control" contests. As a fur trapper he also takes species that affect grouse populations, and some of the legitimate game animals are also in this class.

The haphazard shooting of predators cannot be evaluated in its effects on grouse. We only know that by far the greater portion of this take is of species that do not prey on the grouse at all or are of no real importance to grouse. Probably the best insight into man's endeavors with respect to grouse enemies may be gained by analyzing the organized efforts which have produced tangible records. Notable among these are bounty systems, and of particular significance in the Northeast is the story of the Pennsylvania bounties.

Gerstell (1937) has written a fine analysis and summary of the results of bounty payments in the Keystone state, from which we will quote freely. Bounties of one kind or another have been given there since 1683 but the modern bounties that are aimed at game management began in 1915. Most of the species on which bounties have been paid in recent years are important grouse predators—red and gray foxes, weasels, goshawks, and horned owls. The bobcat and mink have also been subject to bounty but owing to their low numbers are not of great importance to grouse.

The goshawk's bounty record indicates that: (1) The hunter kill

does not reduce the abundance of goshawks in the succeeding winter; (2) the number taken is but a small part of their population; (3) the kill depends mainly upon the degree of southward winter migration of the species. Gerstell summarizes: ". . . the payment of bounties for the destruction of goshawks in Pennsylvania will never result in the control of the species . . . it appears most advisable to discontinue. . . ."

With respect to the red fox which was removed from the list in 1929, he concludes that the record "seems to indicate that the species was not controlled by the bounty." On gray foxes, "an increase in the bounty rate (from $2 to $4 in 1923) has increased the number of gray foxes annually presented for bounty, but as yet the species shows no evidence of being controlled by the bounty." Likewise in New York, in spite of constant persecution, the gray fox continues to increase its range and its numbers. During the twenty-one years prior to Gerstell's writing, an average of over fifty-two thousand weasels had been presented in claim for bounty, yet "the bounty system has not to any noticeable extent, if at all, controlled the weasel even though two thirds of the system's cost has been expended in payments on the species."

The bobcat has reacted differently. Subject to bounty almost continually since 1819, "bounty has brought the wildcat under absolute control in Pennsylvania." In fact, it became so scarce that it was removed from the bounty list in 1937 in order to afford it some chance of preservation.

"As a predator control measure, the payment of bounties has proven generally inefficient as it has placed under control only one relatively small species population, while its effect on five others has been negligible. . . . It has been impossible to prove that the operation of the bounty system over a relatively long period of years has improved game conditions. Furthermore . . . the annual amount of money expended for bounty payments was controlled not by the abundance of predators, but principally by climatic and general economic conditions."

Trapping for fur, while undertaken as an economic enterprise, affects several important grouse predators. Of these, the take of several species in New York is reported annually. Most significant in grouse ecology are the foxes, skunk, and raccoon. Only the weasels among the more important mammalian grouse enemies are not re-

ported. Analysis of these records, available since 1926, fails to reveal either: (1) control of the furbearer, or (2) any correlation with grouse abundance. The take depends considerably on fur prices. Since the additional economic incentive of a bounty has failed to show game management results, it seems unlikely that trapping or shooting of predators for fur will have any appreciable effect on grouse populations.

Organized "vermin hunts" reflect the character of the results of predator control efforts by hunters not engaged in taking furs. They are far from being a systematic control over species that may actually warrant some reduction in numbers. In the first place the average hunter is not very selective, especially with respect to hawks. He is unable readily to identify many kinds of predators, particularly the birds. He takes those easiest to get, which are usually the beneficial rather than the "bad" kinds. The need for control must be based on a careful knowledge of the populations of both predators and game—something which the hunter rarely has.

An analysis of the returns of ten sportsmen's club predator campaigns taken at random from published records in New York and Pennsylvania showed: (1) Three and six-tenths per cent of the victims were identified as species which are important grouse predators (crows not included); (2) seventy-five per cent of the hawks were either unidentified or were identified as beneficial species, and this assumes that the Cooper's and sharp-shinned hawks were correctly named, which is doubtful; (3) of the three and six-tenths per cent identified as among important grouse enemies, forty-eight per cent were submitted for bounty; (4) sixty-four per cent of all kinds taken were crows, seven per cent were starlings, seven per cent water snakes, four and five-tenths per cent rats, five per cent red squirrels; (5) of over 7,700 specimens only three were foxes, the most important grouse enemy, and thirty-six were horned owls, the runner-up. We can only conclude that the greatest benefit from the sportsmen's nongame hunting is his own self-satisfaction, the economics of shotgun shell sales and the recreation derived. He would aid conservation more by shooting clay pigeons.

Use of Guns, Traps, Snares, Dogs, Autos, and Roads. Man's tools of pursuit have been an interesting sidelight to his relations with the ruffed grouse, and in some respects have influenced its abundance.

Considered somewhat in chronological order, we might discuss the snare, net, deadfall, and various types of traps ahead of guns. But for the early white man all methods were fair and effective. The variety of implements utilized to catch the then unwary grouse were almost endless. Most of these tools would be quite inefficient on the "smarter" grouse of today but helped to bring untold thousands to the markets of the past two centuries. In the sporting era, the gun, primarily the shotgun, has been the only weapon of significance.

There has been a great improvement in the effectiveness of sporting guns in recent decades. However there have also been changes in the hunter and in the grouse itself. Phillips (1937) says: "Technical improvements in the past forty years we can set aside, for the early hammer guns, in skillful hands, were nearly as effective as the more dainty modern weapons." He goes on, ". . . if we compare the average skill of the present-day brush shooter with the average of the market shooter of fifty years ago, the result would be highly amusing and very disastrous to the pride of the modern edition." Phillips then points out that what the modern hunter lacks in skill, he makes up for in numbers. It has taken increased protection as well as a constantly growing wariness on the part of the bird itself to make up for the modern army of hunters that annually takes to the field.

Dogs have been used to aid man in the pursuit of grouse for a long time, but in two quite dissimilar forms. We have already noted (see page 21) the early use of a yipping cur dog to hold the attention of a covey of treed "fool hen" grouse while the hunter picked them off one at a time, from the lowermost up. Such a mutt is a far cry from the magnificent, staunch, and silent setters and pointers of the twentieth century. To many a sportsman the most enjoyable part of hunting is working with a good dog, and the supreme thrill is in seeing a perfect point on a closely held bird. In the northern states, bird dogs were mainly trained on grouse up to the last fifteen or twenty years. With the coming of a completely closed season in a period of pronounced scarcity (1928–29 in New York) and the great increase in interest in pheasant hunting, it is rare today to find a really well-trained grouse dog. Most of the pointing dogs are "spoiled" on pheasants. So we find that the far-famed grouse dog, not long ago the pride and joy of the dyed-in-the-wool grouse hunter,

is but a fond memory in the lore of the old timers, any one of whom will delight in "pouring it on" in front of a crackling hearth on a cold winter's night, recreating the exploits of "good old Pooch," known in more dignified circles as "Royal Master Skylark of Worthingdon."

One of the most significant of recent changes in hunting problems is the advent of fast transportation for the general public—good highways and motorcars. Only three decades ago, grouse hunting by any individual was confined to the few square miles that he could reach from home on foot, or from the terminus of a short buggy or train ride. How vastly different it is today. We jump in the car and in an hour we are at coverts forty miles away. An hour's try at this locale and we are off again, and in a single day we have taken a quick course through several coverts scattered over a hundred miles or more. This increased mobility has aided materially in adding to the number of hunters, hence to the problem of finding good hunting for all.

At the same time that so many roads were becoming arterial highways in the Northeast, other dirt roads that proved to be back roads have become abandoned and inaccessible to modern automobiles. Thus the hunter's ability to get around to the coverts has increased in the broad sense while actually decreasing locally in many areas where there is good grouse range.

The net effect of the changes in transportation are hard to sum up, but are probably not seriously affecting the grouse. Whereas formerly each hunter traveled in his own back yard, he's now in someone else's. And the increase in grouse hunters has not kept pace with that of hunters in general, thanks to the pheasant and rabbit.

AS A FARMER AND LUMBERMAN

Land Clearing and Farming. When the white man first began hacking at the forest wilderness in the eastern states, he found game generally plentiful around the new clearings. This caused the fallacious belief in the supposed abundance of game throughout the wilderness, for it seemed "self-evident that if wild life was abundant around the settlers' clearings, it must have been more abundant where man had not intruded" (Edminster, 1941). It did not occur to him that his very clearings were aiding in producing this game supply.

As land clearing progressed, the grouse range was generally improved even though the quantity of woodland was being reduced. But in the more fertile and level regions the extent of land clearing soon passed the optimum for grouse and the birds were then gradually exterminated from these parts of their range, except for occasional islands of wooded swamp or rough land that remained to support some grouse. In areas of poorer fertility and steeper slopes, as in southern New York and northern Pennsylvania, only from one third to two thirds of the woodland was ever cleared. Here the remaining grouse range is about the best in the Northeast. It is about half again as productive of grouse as the Adirondack wilderness range even when all the open land is included, and the birds are produced on only about half the total land area.

It is probable that the optimum amount of open land for grouse range would be from ten to twenty-five per cent, if it were well distributed. This would not be found ordinarily in a regular farming setup. Hence man's land-clearing activity ordinarily falls short of meeting grouse needs in mountainous country and far exceeds it in agricultural areas.

As a farmer, man maintains his open fields by cultural operations with plough, harrow, mowing machine, etc. (see Plate 37). This work serves to prevent grouse range from expanding, and at the same time it maintains the valuable woodland edges. On intensely farmed areas, cultivation prevents the grouse from reclaiming its former range; on the hill farms it maintains the land in a higher-productive condition for grouse than would ultimately result if the area were abandoned to continuous forest. Many of the poorer of the hill farms in the Northeast are being abandoned as unsuited for profitable agriculture. In New York alone there are five million acres of such lands—one sixth of the whole state. After abandonment, the open fields grow into brush and for a period better grouse range results. As natural afforestation progresses the range loses much of its grouse productivity and becomes a more extensive forest area.

Relations of Livestock and Pets to Grouse. Wherever livestock farming, either for meat or dairy products, is found on areas of grouse range there is apt to be a conflict of interests. Fortunately, much of the livestock that does occur in grouse country is fenced out of the woodland areas, and much of the grazed woods are not

in suitable grouse range anyway. When woodlands are pastured it is detrimental to grouse and when this pasturing is intense enough to create a visible "cattle line" it renders the woods practically non-inhabitable to grouse regardless of its other attributes.

It should be pointed out that open-field pasturing is a means of maintenance of balanced conditions almost as effective as cultural operations. When accompanied by proper pasture management measures for the prevention of woody plant encroachment, it is fully effective in excluding grouse and in maintaining woodland edges outside the pasture fence.

Man's pets, particularly dogs and cats, are of some slight significance as grouse predators. His poultry may conceivably play a part in aiding the spread of disease in grouse but contacts between grouse and chickens are not common. In many small ways, the animals that are particularly associated with man affect the lives and homes of the grouse.

Man's Woodcutting Activities. Beginning after the land-clearing work has been completed and the extent of potential grouse range thus delimited, man's most significant consequence to the grouse is his work in the woods with ax and saw. Potentially he can make the area most unproductive by clearing the remainder of the woods; or poorly productive by allowing all the land to return to mature forest (see Plate 6B). Actually he does neither of these things, but many of his activities between these extremes determine the types of cover, hence the character of the grouse range. With respect to man as a woodcutter even more than man as a hunter may it be said that the future of the grouse rests with him.

As a lumberman he may clear out extensive forest areas; or he may cut selectively by species, by size limit, or for certain products as tanning bark, alcohol wood, mine props, etc. Each of these methods affects the grouse range differently. As a farmer he may take out fuel wood, fence posts, or barn lumber, or he may contract with an operator to skin the area. Again he may be interested in the trees for themselves and not cut anything. Whatever he does fixes the value of the cover which supports the birds. We have discussed these shelter and food values in the cover in Chapters IV and V. We will consider the deliberate use of woodcutting methods as a tool in managing grouse in the last chapter. But since the ordinary

farmer or woodland operator does not make his woodland cutting plans with regard for grouse needs, it is a fact that most grouse range is the product of the haphazard results of lumbering for various and sundry individual reasons. For better or for worse, the grouse will largely depend upon man as a woodcutter for the character of its cover.

Use of Fire. For various reasons men sometimes set fire to the land's vegetation. Ofttimes he does so accidentally. It takes no stretching of the imagination to realize that fire in grouse cover will materially affect the birds whatever the cause. It may burn up a nest; quite often does. It may drive the birds out of important units of range for a considerable period of time. Referring to conditions in parts of Missouri, Woodruff (1908) says that the annual burning over of forest floors has removed all the suitable cover and caused rapid diminution of the grouse. Forbush (1927) includes "prevalence of forest fires" among the important factors having much to do with the decrease of this bird. Describing a forest fire, Krieble (1941) said, "Grouse were incubating their eggs, and time after time we saw birds fly out ahead of the flames utterly frantic; then, completely bewildered they would wheel around and fly headlong back into the flames and perish. How many grouse, and how many clutches of grouse eggs were destroyed that day would be difficult to estimate, but it's certain a severe toll was taken."

Forest fires in the Northeast today are generally so few, so well controlled and so small that they do not greatly affect grouse populations. In fact small woods fires are not all on the red side of the ledger so far as grouse are concerned. After a year or two of barrenness, burns usually grow up to briars, cherry, popple, and other shrubs and trees valuable to the grouse. A change in grouse cover bringing good summer range and brood cover is effected. If not too extensive this may actually improve the grouse cover conditions. Phillips (1937) noted that the largest grouse population he had ever encountered was on a tract of land in western Quebec, in the autumn of 1895, which had been burned about seven or eight years previously.

To sum up, small fires ordinarily do grouse little damage, often benefit them materially. Large and hot fires are apt to be quite destructive and the benefits they bring in cover change are rela-

tively unimportant because too extensive for the birds to fully use. In some areas, such as the Adirondack Forest Park in northern New York, where fire is rigidly controlled and lumbering of any kind prohibited on public land, a little forest fire now and then is literally a godsend to the game of the area.

AS A CONSERVATIONIST

Laws as a Means of Conserving Grouse. Laws, like the proverbial poor, we always have with us. This is no less true of game laws than of others. For a time after the first colonists arrived in the Northeast, the social organization was so loose and the supply of game so plentiful for the few men there to harvest it, that there was no need for formal laws to restrict man's pursuit of wild animals. But as the settlements expanded and game occasionally became scarce locally, restrictive laws were quickly enacted. Understanding man's part in reducing game populations, it was only natural that they should feel that the losses might be checked by restricting man's liberties.

There were probably very local, and less formal laws in parts of the Northeast in the seventeenth century, but the first law on grouse that became a matter of permanent record was a partial closed season in New York in 1708. However an earlier law in New York in 1629 first set up the control of the hunting privilege on all game in the state. (These and most of the subsequent references to dates of laws are taken from Palmer, 1912).

The spread and jurisdiction of laws increased rapidly throughout the nineteenth century. Restricted seasons, curtailed bag limits, limitations on use of certain types of weapons, and the prevention of sale followed one after the other. The chronology of some of the more important of these events affecting grouse in the Northeast is as follows:

1818: Massachusetts—season closed March 1—September 1.
1820: New Jersey—season closed February 1—September 1.
1837: New York (Kings, Queens, New York, and Westchester counties)—purchase or sale prohibited out of season.
1838: New Jersey—closed season extended to January 10—November 1.
1846: Rhode Island—season closed February 1—October 1.

1851: Delaware—season closed March 1—July 1.
1858: Maine—season closed March 1—July 1.
1862: New York—sale prohibited during closed season, whole state.
1867: New York—possession permit required to keep them alive over winter.
1869: Pennsylvania—prohibited baiting, trapping, snaring; West Virginia—season closed February 14—September 1; Maine —closed season extended to February 1—September 1.
1878: District of Columbia—season closed and sale prohibited February 1—August 1.
1887: Delaware—no hunting when snow on ground.
1897: Pennsylvania—sale prohibited.
1911: New York—sale prohibited.
1928: New York—first completely closed season (effective for two years).

This list is far from a complete record of the attention given to grouse by the legislatures, but it gives the trend of events by periods from complete freedom to complete closure.

For a long time it was felt that game abundance could be accomplished by the simple procedure of legislating it. As more and more restrictions successively failed to accomplish this end, various supplementary efforts were one by one brought into play. But it should be clearly recognized that even though legislation and law enforcement are not synonymous with game management, they are, if adequate, the essential foundation of any sound system of game management. To say that our present laws are not adequate is to state the obvious. Their immense variation from state to state is ample evidence of this.

Probably the greatest weakness in the grouse laws (as well as all other game laws) of most of our states today is the lack of authority in the executive conservation officer to adjust seasons and bag limits without resorting to specific legislation. Legislative machinery is notoriously slow, and grouse do not wait on the good senators to undergo marked increases and decreases in numbers. If lack of confidence in the executive setup deters the legislature from delegating this authority, then they should readjust the system so that there are adequate safeguards. Most important, the authority is direly needed somewhere if good game management is to result.

Except for the ability to adjust the annual take to the population conditions each year, the laws relating to the grouse are generally just and adequate. Restriction of weapons to modern guns and long bows, prohibition of sale and elimination of commercialization are about complete. The major field for future improvement lies with regulation of land use.

Land Management for Wildlife Conservation. Within the framework of his laws, and apart from his control of the hunting harvest, man's primary efforts as a conservationist are applied on the land itself: plantings or seedings to add durable elements to the habitat; cuttings to improve the existing cover and induce the growth of other desirable plants; and supplementary practices such as protection from grazing, establishment of posted refuges, control of other animal populations as deer and fur-bearers (see Plate 38). For the most part we have already discussed the effects of these practices on the grouse. Plantings, cuttings, and protection result in various changes in cover conditions. These we have discussed at some length. The relations of grouse to predators and other animals has also been covered. We may now discuss the value of refuges and sanctuaries. The application of all of the principles involved in these relations will be treated in the chapter on management of the ruffed grouse. But before we consider the practice of establishing refuges and sanctuaries, we may pause to say that man's highest accomplishment as a conservationist is his care of the land. The degree to which he does this well is the measure of his success and of the endurance of his customs, his pleasures, and of his very civilization.

Refuges and Sanctuaries for Grouse. In the history of man's efforts to protect and increase game for hunting, the idea of leaving certain areas unhunted in order to assure the survival of at least some individuals came early. But it has become a public policy in the United States only in recent years. Pioneering in this work have been the Audubon Societies and the U. S. Biological Survey (now Fish and Wildlife Service) in establishing sanctuaries for persecuted birds, notably those threatened with extinction by the feather trade. Of recent years the Fish and Wildlife Service has undertaken a big program of refuges for migratory waterfowl. These have been improved and managed (in contrast to a sanctuary which is merely protected) both for resting areas and breeding grounds. The state

of Pennsylvania has pioneered in establishment of refuges for upland game, notably deer, on lands acquired for game purposes. The fever for acquiring public game lands for refuges hit New York in the mid-twenties (see Plate 40A). The slogan was "A game refuge for every county." While not the panacea it was hoped to be, the refuge still is a valuable tool of game management.

The idea of the use and value of game refuges has been considerably confused, particularly in the minds of sportsmen. It was conceived that a game species, such as grouse, within the confines of a refuge would increase greatly and overflow the refuge boundaries. This excess would be shot in the surrounding public hunting grounds while the breeding stock would be preserved. It was also contended that game in open-shooting cover near a refuge would seek protection there when hunted. As it turns out, these theories do not apply very well to grouse.

In the first place, a clear distinction is needed between the breeding refuge and the protection, or "seed-stock" refuge. Breeding refuges are needed only when the breeding facilities of a species are hampered or endangered. Such a case is the well-known destruction of waterfowl breeding grounds by drainage activities. This is not the case with grouse. The change of land ownership and placing of signs and a boundary wire do not help the birds' breeding one iota. Furthermore, the principle of protection refuges assumes that hunting is a vital factor in the survival of the species. Under existing practice this is not true with the ruffed grouse in most areas.

The questionability of the value of refuges for ruffed grouse induced an evaluation of the principle in New York by censusing a 2,120-acre refuge area and a comparable public shooting area from 1935 to 1937 (Edminster, 1937). ". . . instead of producing a greater supply of grouse, (the refuge) actually had fewer birds than the check area in two of the three years . . . while analysis of the effect of the small differences in the areas may serve to explain some of the variations in grouse numbers, the fact still remains that the protection afforded by the refuge . . . did not serve to enlarge the crop of grouse." The study concluded that refuges were not of value in increasing grouse in normally hunted areas in years when grouse are at least fairly plentiful. It indicated that refuges might be more useful in times of scarcity, and that areas of

abnormally heavy hunting might well have some refuges as insurance against total local extermination. However, it may be desirable to establish game refuges for other species in areas inhabited by grouse.

MAN AS A LIMITING FACTOR

In a direct sense, as a destroyer of grouse, man is seldom the limiting factor under modern conditions of hunting. Locally this may occur, and potentially he might be generally over-destructive if the legal restrictions and the restraints of hunting ethics were lifted. In an indirect sense he is the dominant limiting factor in all but wilderness areas. More vital to the grouse than man's hunting are his use of the ax, saw, plow, fence, fire, and livestock which in various combinations determine what shall constitute the grouse's "home on the range."

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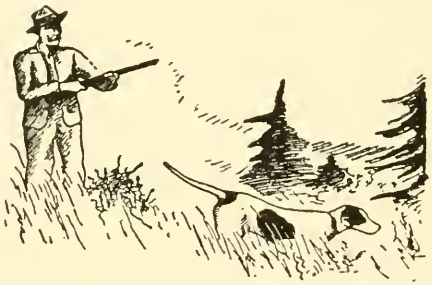

10

Productivity and Populations

POTENTIAL AND ACTUAL PRODUCTIVITY[1]

Productivity is defined by Leopold (1933) as "the rate at which mature breeding stock produces other mature stock." Before an appraisal is made of this, the actual productivity, let us consider the potential productivity—that constant property of the species which is the theoretical rate at which the species could increase if no mortality occurred. From this base line, we may examine the factors that affect this theoretical possibility and derive the actual result. Being promiscuous, breeding the first year after birth and laying a large clutch of eggs (averaging over eleven eggs per clutch), the ruffed grouse has a high-breeding potential. Like the plant aphid that we learned about in elementary biology, it would overpopulate the earth in relatively few years if nothing checked its increase. Assuming a balanced sex ratio, which is normal, a pair of perfectly healthy grouse producing twelve eggs would result in fourteen birds the first season; continuing with equally successful progeny, this original pair of birds becomes 110 the second year, 782 the third, 5,486 the fourth, and so on.

That such productivity is never even remotely approached is due to the perpetual interplay of numerous delimiting conditions, environmental influences, and decimating factors. To begin with, universal breeding is rarely attained; the occurrence of a few nonnesting females, nonbreeding males, or infertile eggs makes an initial reduction in the potential. Then losses in the egg, immature and adult stages result from a never-ending gamut of hazards.

Subtracting these losses from the potential productivity, we have remaining the actual. When the fall and winter losses bring the population back to the original number of breeders, we have a

[1] The first portion of this chapter is taken largely from *Productivity of the Ruffed Grouse in New York*, Edminster (1938).

stable population. When the annual increment is higher we have an increasing population; and when the losses exceed the increment, the population declines. In the long run, it cannot continue to increase, nor can it continue to decrease without risk of extermination.

The wild-life manager strives to manipulate controlling factors so that annual losses equal the annual increment in an environment populated to its carrying capacity. Further, he aims to have the greatest possible part of these inevitable losses occur from hunting by man rather than from other causes.

This objective is not regularly attainable in the grouse for it does not have a stable productivity. Its numbers vary so widely that it has been termed a cyclic species. But even apart from its general fluctuations, the variation in the effect of many of the decimating agencies year by year cause other variations in the productivity. Marked irregularity was noted in areas and on individual coverts within areas. But it is noteworthy that the early attributes of productivity—sex ratio, breeding, number of eggs, fertility, viability of eggs, nest survival—have remained remarkably constant, while great variation occurred in both brood and adult survival.

ANNUAL FLUCTUATIONS IN GROUSE NUMBERS

The most complete and continuous productivity record of the New York grouse investigation was obtained on the Connecticut Hill Survey Area. The regular census units totalled two thousand three hundred four acres of coverts (other portions of the survey area which were utilized for special studies are not included here due to interruptions in the census records). The population changes taking place on this area for the nine-year period 1929 into 1938 are shown in Table 9.

For five years out of nine the productivity resulted in a larger breeding population than the previous year and for four years in an increased crop. At the outset, shortly after the low ebb of numbers in 1928, the population was far below carrying capacity. After three years of very low populations, conditions favored a big increase: Predator pressure was relatively low, disease incidence was near zero and hunting pressure was eliminated for purposes of this study. Weather conditions proved favorable too.

An increase of ninety-three per cent from breeding stock took place in 1930 with little reduction the following winter, leaving a net increase of fifty-seven per cent in the spring of 1931. The seasons of 1931 and 1932 also had high productivity, one hundred nine per cent and one hundred twenty per cent respectively, but owing to mounting winter losses the net yearly gains in breeding population dropped to fifty-three per cent in 1932 and to only twenty-six per cent in 1933. The forces of decimation were catching up, both predation and disease having increased notably. Then productivity in 1933 fell way off owing to a very high brood mortality of unknown cause, resulting in a summer increase of only eighteen per cent of the spring population. This was followed by a thirty-seven per cent winter loss which, while somewhat lower both in number of birds and percentage of September population than that of the previous year, resulted for the first time in a reduction in breeding stock, amounting to a twenty-six per cent net loss for the year.

TABLE 9

POPULATION CHANGES ON 2,304 ACRES OF GROUSE COVER, CONNECTICUT HILL AREA—1929–1938 [1]

Year	*No. Adult Breeders*		*No. Young Maturing*		*Loss of Adults in Summer*		*Grouse Population (September)*		*Fall & Winter Loss of Adults*	
1929	—		—		—		123		40	(32%)
1930	83	+	77	—		=	160	—	30	(19%)
1931	130	+	146	—	4	=	272	—	73	(23%)
1932	199	+	253	—	15	=	437	—	187	(43%)
1933 [2]	250	+	65	—	20	=	295	—	110	(37%)
1934	185	+	265	—	33	=	417	—	176	(42%)
1935	241	+	99	—	53	=	287	—	132	(46%)
1936	155	+	153	—	23	=	285	—	175	(61%)
1937	110	+	143	—	5	=	248	—	108	(44%)
1938	140									

[1] Figures taken from Edminster (1938) and derived from data in *N. Y. S. Cons. Dept. Ann. Reports, 1930–38.*

[2] 1933 figures calculated from sample data.

Recovery in 1934 reached a high rate again with a productivity of one hundred twenty-five per cent, the highest noted in any year except 1938. This brought the fall population nearly up to the high level of 1932. A normal winter loss (42 per cent) for a dense popu-

lation left a breeding stock for 1935 which was thirty per cent higher than that of the year before. In the ensuing summer, brood survival again fell disastrously as it had in 1933, giving a recovery of only nineteen per cent for 1935. This time the abnormal loss was apparently largely caused by extreme precipitation, ten inches of rain in forty-eight hours, which also provided the worst floods in the history of the region. With the fall population thus lowered to two hundred eighty-seven birds, we would expect a reduction in winter loss. The number of birds lost was lower than in the previous winter, but the percentage lost remained high. In fact the forty-six per cent reduction was the highest in the first seven years. So also was the net loss in breeding stock—thirty-six per cent from 1935. Again we find the immediate explanation in local environmental conditions—adverse winter weather that resulted in abnormally high vulnerability to predation. And I pause to note that any excellence of habitat would not prevent an increase of predation under those extreme conditions of snow and low temperatures.

From the relatively low population carrying into the spring of 1936, recovery was effected for the third time in the period of the survey. Productivity was good although not as high as in some years.

Survival through the winter of 1937 proved to be the lowest yet observed, sixty-one per cent of the September, 1936, population being lost by the next April. This reduced the breeding population to the lowest level since 1930. Once more, however, a productivity of one hundred twenty-five per cent brought a quick recovery which continued with increasing fall and spring populations until the summer of 1940. Then, as had occurred twice before, the productivity fell to a low level, only fifty-two per cent, this time the result of an abnormally high nesting loss.

From this record, we may conclude that during periods of grouse increase, the net summer productivity is normally about one hundred twenty per cent of the breeding population. At the peak, occasional disasters, affecting brood mortality primarily, may reduce this expectation practically to the vanishing point. The summary of the actual productivity rates on the Connecticut Hill area, together with the subsequent changes in breeding populations as compared with the preceding year, are given in Table 10.

There is a direct relationship between yearly recovery, or productivity rate, and population density. This same relationship car-

TABLE 10

PRODUCTIVITY RATES AND CHANGES IN BREEDING POPULATIONS—CONNECTICUT HILL AREA—1930–1941 [1]

Year	*Percentage Increase of September Population over That in April* [2]	*Percentage Change in Breeding Population from Previous Spring*
1930	93	—
1931	109	+ 57
1932	120	+ 53
1933	18	+ 26
1934	125	− 26
1935	19	+ 30
1936	84	− 36
1937	125	− 29
1938	(High)	+ 27
1939	114	
1940	52	
1941	122	

[1] Figures taken from Edminster (1938) and from data in *N. Y. S. Cons. Dept. Ann. Reports, 1930–41.*

[2] Also referred to as the "recovery rate."

ries through to the changes in the subsequent breeding population. Productivity increased annually for three years until the population reached a total of four hundred thirty-seven birds (5.3 acres per bird) in the fall of 1932 and held two hundred fifty birds (9.2 acres per bird) into the 1933 breeding season. With the population at this high level, recovery in 1933 fell to the exceedingly low rate of eighteen per cent. This change in trend resulted in the first decrease in breeding stock, in 1934. However, productivity then returned to a high rate and another irruptive peak was reached. The 1933 situation was repeated in the spring of 1935, and the summer productivity also repeated the pattern of two years before. The reduction in both breeding and fall populations reached their low for this decline in 1937, which was the largest decline witnessed. Both figures fell to a point below any year except 1930. However, this decline cannot be compared in intensity with that of 1926–27. The full decline in breeding population from 1935 to 1937 was fifty-four per cent; the decline in the early fall population for the same period was forty-one per cent. From 1937 to 1940 the breeding population increased to another peak in 1939–40, dropping again

in 1941. Productivity was normal from 1937 to 1939 for increasing populations. The very low productivity in the summer of 1940 preceded a moderate decline in 1941.

Reviewing the trends of the whole twelve-year period, the correlation between breeding density and subsequent recovery seems to be of basic importance. They appear to fall into three groups: (1) low breeding populations that have a low recovery rate; (2) low breeding populations that are followed by a high recovery rate, or moderately high populations having a high recovery; and (3) high populations (or occasionally only moderately high ones) that are followed by poor recovery rates (see Fig. 12).

Generalizing these correlations, we may regroup them into two series in order to illustrate the inverse ratio between breeding density and productivity in its two opposite phases. Combining the first two groups as those having low-to-moderate breeding densities (1931 almost falls with the second group anyway and 1930 had so low a population that it was not yet able to attain a high reproductive rate, thus making it an exception to the principle involved), we see the contrast with the other group of years having high breeding populations that lead to low recoveries.

Errington's records on marginal grouse populations at Prairie du Sac, Wis., suggest the same three phases, but here too the details are somewhat obscured by inadequate data (letter from Errington, January 21, 1942).

The inverse ratio between breeding density and productivity is also shown for gallinaceous species other than ruffed grouse. Errington's data on bobwhite quail (a noncyclic species) in southern Wisconsin, R. E. Yeatter's work on prairie chickens and bobwhite in Illinois, and that of Arthur Hawkins and others on mixed populations of bobwhite, Hungarian partridge, ring-necked pheasant, and prairie chicken in Wisconsin, all illustrate the principle (Aldo Leopold and Paul L. Errington, MS).

From the consistent evidence we may conclude that the losses of birds that succumb following seasons of high-breeding density are destined to happen from some cause as a result of the population condition regardless of what the actual and immediate cause of death may be. They are vulnerable as a result of their own numbers and the adjustment in population level is in the cards, irrespective of the operation of the various mortality factors. However, one

should be cautioned against looking upon these inverse ratios as ends in themselves. They are merely the manifestation of population mechanics.

If density of population should prove to be instrumental in setting the stage for catastrophic losses, prevention of such densities might

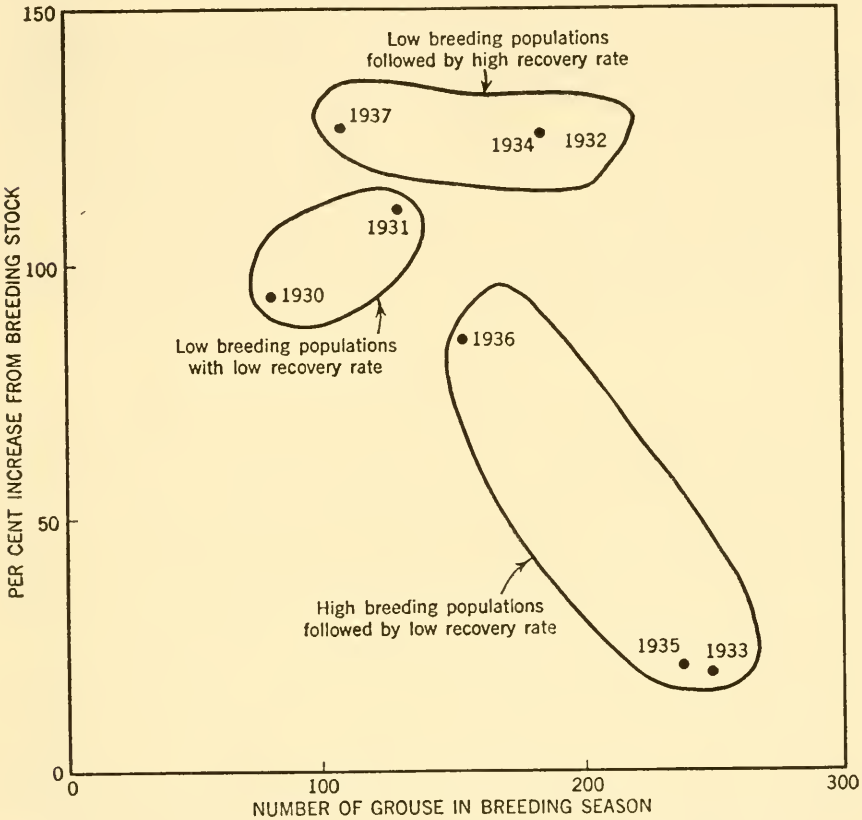

Fig. 12. Correlation of Grouse Recovery Rate with Breeding Density Connecticut Hill, N.Y., 1930–1937

(Based on data from *New York State Cons. Dep't Ann. Reports* and Edminster, 1938.)

conceivably prevent these losses. Then the recovery rate might be maintained at a consistently high level. Because of these possibilities this subject received particular attention in the New York studies. (Edminster, 1938; *N. Y. S. Cons. Dept. Ann. Reports, 1935–37*). Two coverts (apart from the regular work area on Connecticut

Hill) totaling 777 acres were subjected to artificial control of the grouse population beginning the winter of 1933–34. All but four grouse were collected after the public hunting season. With this beginning, the population was deliberately reduced each successive winter to about half normal survival in order to maintain a breeding population well below carrying capacity.

The productivity rates for 1935, 1936, and 1937, from moderately sparse breeding populations were one hundred per cent, one hundred sixteen per cent and one hundred sixty-one per cent compared with nineteen per cent, eighty-four per cent and one hundred twenty-five per cent, respectively, on the uncontrolled portion of the survey area in the same periods. Thus, additional evidence supports the contention that as populations approach the range-carrying capacity, their productivity declines, and that productivity is higher in breeding populations well below carrying capacity.

LIFE EQUATION

In terms of populations, rather than the individual, the life story of the grouse tends toward an equation—the population at any given period of the year resulting from a balance of the losses on the one side of the scale and the gains on the other during the preceding year. Actually this yearly circle of events on any given unit of range almost invariably leads to an inequation—with the gains sometimes exceeding the losses and other times the reverse. This equation might be expressed as: $BP + MY - AL = B'P'$ where BP = breeding population, MY = maturing young, AL = adult losses and $B'P'$ = breeding population of the succeeding year. If the yearly changes actually result in a stable population, the equation may be simplified to $BP = B'P'$ in which case $MY = AL$. When the population increases from one year to the next, $B'P'$ exceeds BP and hence MY exceeds AL. This condition may be expressed graphically as follows (Fig. 13) for eighteen grouse breeders (nine pairs) producing one hundred eggs.

Such an inequation cannot long continue. The trend must be toward an actual equation, but oscillating first to one side and then to the other of a true balance. From 1932 through 1941 in New York, the balance has been nearly true. This theoretically true equation is illustrated in Fig. 14, again for nine pairs of breeders producing one hundred eggs.

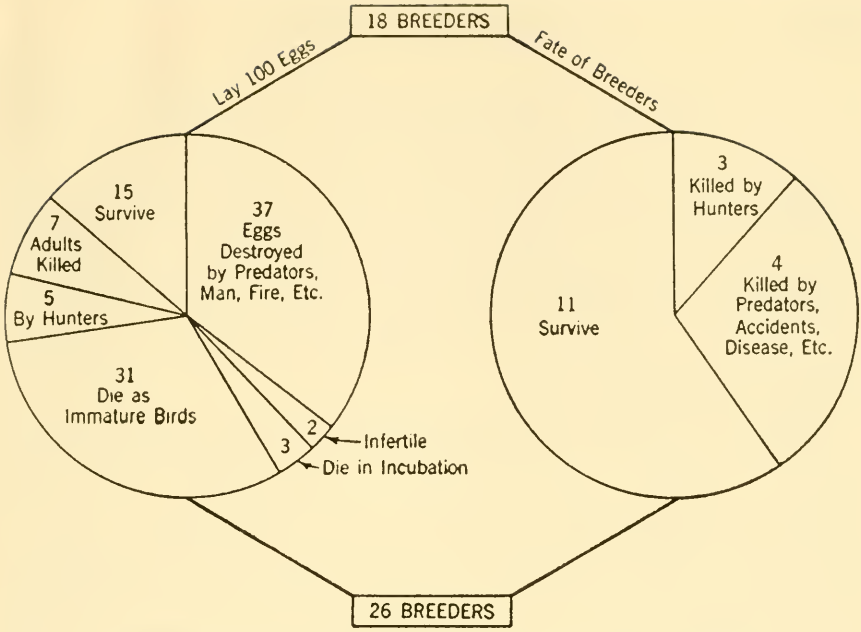

FIG. 13. Life Equation of Grouse for an Increasing Population

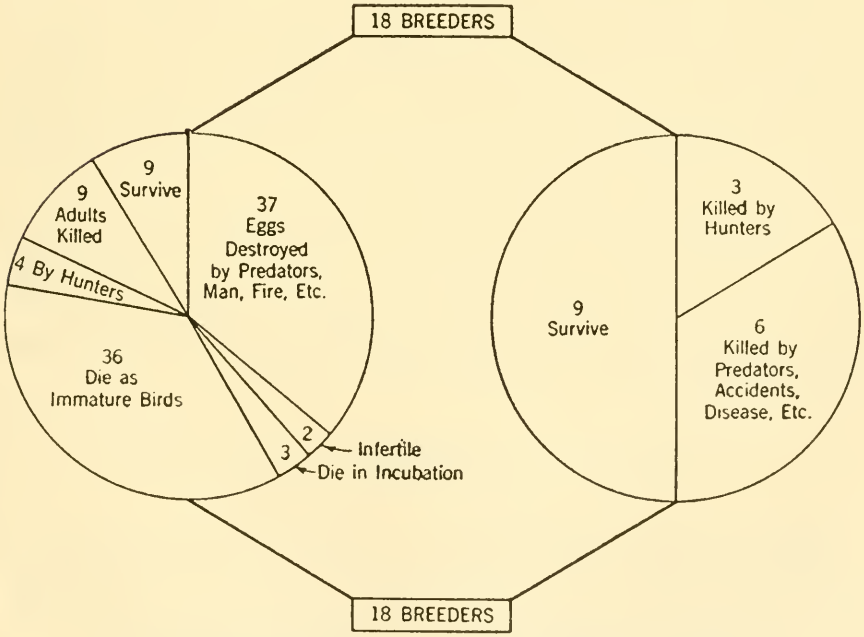

FIG. 14. Life Equation of Grouse for a Stable Population

VARIATIONS IN DIFFERENT HABITS

We have considered the actual productivity of the grouse population on one area, which is typical of the disconnected coverts in the submarginal farm region of southern New York and northern Pennsylvania. Productivity in wilderness range of connected coverts was studied in New York's investigation on an area in the eastern Adirondack mountain region. (*N. Y. S. Cons. Dept. Ann. Reports, 1932–37;* Edminster, 1938).

There is an outstanding difference in the Adirondack record as compared to that of Connecticut Hill—a seemingly greater instability of population. The first year of the Adirondack area survey, 1932, was apparently a peak year, and winter mortality data indicate that 1931 also was a year of high population for this range. Then in 1933 a marked drop occurred as a result of low brood survival. It will be noted that this same condition prevailed on Connecticut Hill that year. Then followed a recovery in 1934 to the same level as 1932. This also took place on both areas. In 1935 we again note a very low survival of young which brought a drop in population in both areas. Recovery began here in 1936 and was continued on the Adirondack area in 1937 while Connecticut Hill receded. Thus the trends in productivity on the connected covert area were somewhat synchronous with those on the disconnected coverts during this period, but fail to show clearly the inverse relationship between recovery and breeding density.

As an average, the productivity on the Adirondack area was markedly lower, about thirty per cent, than on Connecticut Hill. Thus we have an indication that the productivity as well as the carrying capacity of connected coverts may be lower than that of disconnected coverts in the northeastern range.

CHARACTERISTICS INHERENT IN THE SPECIES THAT CONDITION PRODUCTIVITY

There are many innate characteristics of the ruffed grouse, as with all birds, that directly affect its productivity. For the most part these are consistent factors of the bird's physiological complex. The more important are discussed in the following paragraphs:

Sexual Relations. The ruffed grouse breeds at the age of about ten months. Practically all birds breed each year.[1] This matter has not been checked perfectly since it is impossible to locate all grouse nests on a sizable area, or to determine that every grouse has bred. However, all the evidence indicates that a failure in the breeding of grouse, at least in good grouse range, is rare.

The species is promiscuous in its sexual relations, which fact helps prevent unmated birds. Audubon (1856) recognized the species as being polygamous while Baird, Brewer, and Ridgeway (1905) suggested that both sexes were promiscuous. There is no doubt a fairly high proportion of grouse that mate with only a single bird in a breeding season but this is apparently more a matter of expediency than character.

A factor that tends to limit the breeding efficiency of the species is the sexual-readiness cycle which occurs in both male and female, and called "sexual rhythm" by Allen (1934) (see page 30). It apparently works out very satisfactorily in nature since infertility is very low, although it gives rise to serious problems with birds in captivity.

Size of Egg Clutches. The size of the egg clutch has been generally known for the ruffed grouse for well over a century. Wilson (1812) recorded the range as from nine to fifteen, while Audubon (1856) gave it as from five to twelve. Forbush (1929) gives the general range as from seven to fourteen eggs with occasionally up to sixteen or seventeen, and he notes one case of a grouse nest containing twenty-three eggs. Smith (1921) also records a nest of twenty-three eggs and notes that it was probably the product of two hens.

The average number of eggs per clutch for six hundred thirty-four first nests (that is, not including renests following a destroyed first clutch) in New York from 1935 to 1941 was eleven and four tenths. The commonest size was twelve eggs; the next commonest was eleven eggs, and these two sizes made up over half the total. Nests with nine, ten, thirteen or fourteen eggs made up most of the balance, although there were cases from three to twenty-four. Only in one year was any number of eggs other than eleven or twelve most prevalent; in that year there were more nests with thirteen

[1] King did not find this to be true in his Minnesota studies.

eggs than any other size. The yearly average varied from ten and nine-tenths per nest to eleven and nine-tenths, with no regular trends. There is probably no significance in these moderate variations.

It is likely that most egg complements below seven are the result of physiological deficiencies in the female, and those exceeding sixteen are probably the product of two separate females. A nest that contained nineteen eggs was definitely known to result from two birds, as was also one sixteen-egg nest.

The size of the clutch in renestings following the destruction of the first nest is much smaller than in the first attempt. The earlier in the season a nest is destroyed, the larger is likely to be any second nest clutch that is laid. In sixty second nests throughout New York the number of eggs ranged from three to twelve and averaged seven and nine-tenths. One case observed was apparently a third attempt at nesting, as judged by the time the eggs hatched (about July 25) (data taken from *N. Y. S. Cons. Dept. Ann. Reports*).

Fertility of the Eggs; Hatchability. The fertility records of several hundred first nests were obtained in New York State from 1931 to 1941. The average proportion of infertile eggs was about two per cent, the maximum in a single year three and five-tenths per cent and the lowest one and one-tenth per cent. There was no regularity in the variations and apparently no significance in them. The degree of infertility did not reach a high enough level any year to indicate any serious trouble. Records were obtained for a number of renests too. These averaged a little higher in the proportion of infertile eggs (for example, 5.4 per cent in 1937), thus confirming the well-established fact that fertility is lower with late breeding. This factor is of little significance, however.

These records may indicate higher rates of infertility than actually took place. Any egg not hatching that showed no embryonic development was considered to be infertile. A fertilized egg that dies within a few days of the start of incubation will present the same appearance; hence any cases of this nature that may have occurred were placed in the wrong category. This only further emphasizes the consistently low infertility rate.

When we consider the rather complex nature of the breeding of grouse, the near-perfect results are remarkable. Certainly we do not

see in this record any indication of a mishap likely to cause an abnormally low productivity. However, even a twelve-year record may not bring out such a relation, if it exists, particularly since no catastrophic declines occurred in the grouse populations in New York during that period.

Eggs that die during incubation are identified by the presence of the embryo when examined after hatching time. Most of these are birds that fail to hatch properly, or in time, and die at full development. However, as already noted, any cases of dead germs in the very early stages of incubation would be misidentified as infertile. Therefore, the figures given for losses by embryo death are possibly a little lower than actual. The average proportion of embryos that die during incubation, as determined from the New York records, is about two and one-half per cent and the annual figures varied from two-tenths per cent to five and nine-tenths per cent. Here, as in the case of the infertile egg record, there is no regular trend indicated, and the losses do not constitute a serious threat.

Dead embryos may result from either external influences, as low temperatures or too long exposure when the bird is off the nest, or an innate weakness of the germ. Since the latter cannot be identified as a cause of death, the tendency is to attribute the losses to exposure. The fact is we do not know the answer. Shifts in percentage of embryo losses do not correlate with recorded weather data, tending to indicate that some of these losses may well be due to inherently weak germs (data derived from *N. Y. S. Cons. Dept. Ann. Reports*).

Longevity and Breeding Years; Incubation Period. The full potential span of life for grouse is rarely, if ever, attained in the wild and never has been determined. In captivity, grouse have been known to live for many years, but here too they rarely live long enough to die from natural body degeneration. In the face of all the hazards facing a grouse in its life, the potential life span is unimportant. Judging from the character of the bird, it probably can live a decade or more.

The actual life span of grouse depends upon when its time is begun. If we count from the time of hatching, the average length of life is a very few months; if we begin counting only with birds that reach maturity, the span is about twelve months; if we count only

birds that reach a breeding season, the average lifetime extends to about eighteen months.

The number of breeding years for either sex is not known, but all indications are that it is the full life span. Surely, it is the full actual life of all wild birds.

The normal incubation period is twenty-four days. This may sometimes vary slightly, usually by being lengthened. This abnormality may result from excessive periods of time off the nest, which cumulatively result in a measurable extension of the full incubation period.

Ratio of Females Nesting. For the hen grouse, taken as an individual, it is normal to breed, nest, and lay a complement of eggs each year. When we consider all female grouse, however, we find that there are occasional exceptions. We might expect a few grouse to be unable to locate males in marginal grouse range or in poorly populated range; but this apparently does not constitute the full story of failure in breeding of wild grouse. Why some grouse do not breed when there is an adequate number and distribution of cock birds we do not know. We can only surmise that there are occasional individuals that are physiologically or socially out of balance, as among humans.

Determination of the nesting ratio is difficult, even as an approximation. Theoretically, the number of successfully nesting females (*i.e.* the number of broods), plus the number of broken-up nests, less the number of renest broods equals the total number of females when breeding and nesting are perfect. The nesting ratio can, therefore, be derived from the formula:

$$\text{Per cent nesting females} = \frac{(\text{no. broods} + \text{no. broken-up nests} - \text{renest broods}) \times 100}{\text{no. females}}$$

With a good census, the number of females and the brood data may be determined with accuracy. The difficulty arises in obtaining the number of destroyed nests. Even the most diligent search with trained observers will not bring complete success on a large area. With our figure for destroyed nests too low, it is clear that the nesting ratio will be lower than is actually the case. We can estimate this discrepancy if we may assume that the broken-up nests not found are in the same ratio to those found as are the un-

found hatched nests to the hatched nests actually located. Knowing these items we calculate the fourth. However, this assumption is not always valid.

Applying the above formula, and applying the corrective factor for unfound destroyed nests, the nesting ratio ranged from well below one hundred per cent to well over one hundred per cent. Without the corrective factor, the nesting ratio was somewhat below one hundred per cent. These latter figures are, of course, conservative. At least some of the first set are excessive.

From this wide variation we may conclude: (1) There was a marked variation in nest-location success year by year; (2) the proportion of hatched nests located exceeds that for broken-up nests; (3) some grouse fail to nest, and this proportion seems to vary in different years; (4) the nesting ratio is high, approaches perfection (if not actually reaching it) in some, and probably in most, years.

Number of Broods. The ruffed grouse raises one brood of young a year. There are no exceptions to this rule in nature despite occasional written statements to the contrary. For example, Davie (1898) concluded that grouse not infrequently rear two broods between the first of April and the middle of October. He was probably mistaking a late brood coming from a renest as a second brood. When one considers that the mother bird cares for her young ones for three months or more, and consumes more than another month in egg-laying and incubating, it is obviously impossible to produce more than one family in a season.

Sex Ratio. The proportions of the sexes is most accurately obtained in the spring during the breeding season when many types of data that bear on it are available. It is at this season that the sex ratio assumes its greatest importance too, affecting as it does the breeding and productivity of the species.

All our evidence indicates that an approximate balance of the sexes is normal,[1] all seasons considered, but that there tends to be a slight preponderance of males in the fall, and a small but consistent excess of females in the spring. This adjustment of the ratio from fall to spring results from the greater mortality of the male

[1] King advises (letter of October 5, 1943): "My work in Minnesota leads me to believe that at some phases of the cycle there is far from a balanced sex ratio."

birds in the early spring because of their courtship behavior.

The spring records from 1931 through 1941 on the Connecticut Hill area showed an extreme variation in percentage of males, ranging from forty-two per cent to fifty per cent in different years, with the corresponding proportion of females being from fifty-eight per cent to fifty per cent. Sex ratio records on the Adirondack, Pharsalia and Catskill areas of the New York investigation varied from forty-five to fifty per cent of males in different years.

The sex ratio has been watched with great care as it has been suspected of being an indicator of abnormal mortality, possibly having a correlation with cyclic losses. Forbush (1912) recognized a differential mortality among the sexes of grouse during population declines as early as 1906. Leopold (1933) attributes this differential mortality, which results in an abnormally high loss of females and correspondingly unbalanced sex ratio, to disease.

The evidence I have observed has not shown this phenomenon. However, the populations have not dropped precipitously in this period either, and hence have not produced the conditions where the unbalanced sex ratio is alleged to occur (New York data derived from *N. Y. S. Cons. Dept. Ann. Reports*).

POPULATIONS IN RELATION TO PRODUCTIVITY

We have discussed the fluctuations in the population of grouse over periods of several years. These changes took place in specific sets of conditions, but do not correlate the grouse populations to the cover, or enable us to compare the populations with those on other areas. To reduce population figures to a common basis, we may obtain the ratio of birds and cover, either on a units-per-acre or an acres-per-unit basis. Since grouse densities are relatively low (compared with many rodents and small birds for example), the figures will be most easily handled if derived as an acres-per-grouse unit.

Grouse Nest Densities. If all females nest, and the sex ratio is fifty-fifty, the density of nests would be half that of the adult birds in the spring season. Due to the difficulties in locating the nests, the entire number on a sizable area is never found, hence the actual density of nests is never determined with full accuracy. Evidence

does indicate, however, that the nest density is very close to a one-to-two correlation with breeding bird density.

Individual distances between nests has varied greatly. In one instance, two nests were only twenty-five feet apart, but only one nest was in use when observed, and hence both may have been made by the one bird. In another instance, two females nested seventy-five feet apart. In still another instance, two females were incubating concurrently in nests just fifty feet apart. In other years the closest nests were from one hundred feet to over three hundred feet apart. As an average, of course, nests are much farther apart, even though they are relatively concentrated in the outer fringe of the woodlands and brush areas. Most nests are more than six hundred feet from the next nearest grouse nest even when the density is high.

Densities of Grouse Broods. The density of grouse broods is lower than the nest density by the proportion of nest failure that is not adjusted by successful renesting. In comparison with the rather incomplete determination of nest density, the brood statistics can be very accurate, based as they are on observations taken over a whole summer period.

In most years, the density will range between forty and seventy acres of cover per brood in good range.

The number of broods seems to vary less by a notable degree than either the density of grown grouse or the survival of the young birds in these broods. There appears to be somewhat of a correlation between nesting success, *i.e.*, number of broods, and breeding density: the greater the breeding density, the lower the nesting success ratio; and the lower the breeding density (within optimum bounds) the higher is likely to be the success ratio. Thus an equalizing effect tends to stabilize the number of broods on an area.

Somewhat correlated with brood densities is the area needed by broods. Since grouse brood territories overlap, in contrast to breeding territories, the territorial requirement does not in itself limit the brood density. The area actually used by broods, as indicated by location of a series of observations, varies greatly. Of considerable significance is the minimum area of cover that may support a grouse brood. Evidence indicates this to be in the neighborhood of nine acres, or slightly less. I know one isolated covert of nine acres that

raised a single brood year after year, and another of nineteen acres raised two broods in some years. No smaller isolated coverts I have known have maintained a grouse brood throughout the summer.

The average brood travels over a much more extensive area than this. An average territory diameter of one-quarter mile is about normal, while extremes of travel range from possibly a very few acres (a brood flushed every time from June through August in a single briar patch), to several hundreds of acres over a diameter of at least one and five-tenths miles.

Densities of Adult Populations. Densities of game bird populations are usually taken during the spring breeding season and at the peak population period in late summer or early autumn just as the young birds have matured. For the grouse these times are April and September. Because the grouse uses only a part of the total range in partly farmed areas like Connecticut Hill, all figures are based on the ratio of area of coverts, exclusive of open land, to numbers of grouse.

For this area as a whole, the greatest breeding season density was about a grouse per nine acres. The lowest was thirty-six acres per grouse, although lower densities had occurred before 1930. Most years, the density was nearer the maximum.

There is less variability in the population density during the peak period than in the breeding season. The greatest density was five and two-tenths acres per grouse and the least nineteen acres per grouse. Whatever the breeding density of grouse may be, within the limit of a grouse per eighteen acres, the summer's productivity will normally bring the population up to a fairly high and fairly constant level in September. Stating this another way, a satisfactory fall population normally results from any breeding population that has not fallen below a density of a bird per eighteen acres. The effect of high breeding populations in reducing the recovery rate tends to prevent irruptive peaks, thus somewhat stabilizing the population.

The October hunting season densities are from about five to twenty-five per cent below the early September figures, the average drop being about twelve to fifteen per cent.

When we consider individual coverts (units of cover that are more or less isolated from other cover by open fields, and ranging

usually from one hundred to three hundred acres each), we do find greater variation in grouse densities from year to year. Some units increase their group populations from one year to the next while others decline. Summation of these records for the whole area tends to average out these irregularities. These records for individual coverts are of interest primarily in showing the potentialities of the different coverts for producing and holding grouse. Some show a particular ability to produce grouse, *i.e.*, high summer productivity, others to hold them over fall and winter until the breeding season.

Extremes of breeding season densities of single cover units range from less than four to almost fifty acres per grouse. Areas that reach the greatest densities in their highest years, have relatively high densities in their lowest years; those with low densities in poor years also have a low density even in the best years. The primary key to the spring density of levels of cover units lies in the winter shelter (primarily evergreen cover) conditions.

The cover units that provide the extremes of peak population densities are not usually the same as give the corresponding extremes in breeding population densities. The greatest density of grouse at about September 1 in a single cover unit was a grouse for every one and eight-tenths acres (*N. Y. S. Cons. Dept. Ann. Report, 1935*), while the lowest peak density was less than one to thirty acres.

These extremes, together with all the other year-to-year records of individual coverts, show clearly that animal populations are very dynamic, ever changing, and, barring occasional losses that prevail rather uniformly over large areas as a result of some climatic factor, are normally little related to other populations even a short distance away. General increases and decreases in population, such as we have discussed for a whole area, are merely the summation of these individual unit trends. When the majority of units are increasing in population, the whole area will probably show an increase; when the majority are declining, the net total is likely to decline too. And, as already noted, the population fluctuations for a whole area are less violent than those of the individual component coverts, for, as we make the summations, the individual gains and losses will cancel each other to some extent.

Population densities on other areas have shown as much variation from Connecticut Hill as have the individual cover units among

themselves in each of the areas. This is as would be expected, and may indicate a different productivity or carrying capacity; or it may simply mean the records were obtained at a different phase of the population trend.

An area of eight hundred sixteen acres of continuous forest in the eastern Adirondacks that was censused from 1932 to 1936 showed consistently lower densities than Connecticut Hill. The breeding season densities ranged from a grouse per twenty acres at the high (although there was evidence of a somewhat higher population the previous year) to forty-three acres per grouse. Productivity was also consistently lower here than on Connecticut Hill. The peak densities ranged from thirteen and six-tenths acres per grouse to forty-one acres per grouse. (*N. Y. S. Cons. Dept. Ann. Reports, 1932–36;* Edminster, 1938). This record supports the general principle that areas of continuous forest are not as productive and do not have as high a carrying capacity as broken-up cover.

Records were obtained on an area in the Catskill Mountain region of New York of one thousand one hundred twenty-eight acres of almost continuous woods in the western part of the mountains. It was censused in March, 1936 and 1937 by biologists of the Resettlement Administration. Here the densities were considerably lower than on the broken-up covert Connecticut Hill area, being thirty-seven acres per grouse in 1936 and thirty-one acres per grouse in 1937.

From all these records we may conclude that in the better Northeast grouse range we may anticipate a breeding season density of eight to ten acres per grouse and a peak-season density of a bird per five acres in the good years. In poorer cover and poorer years the density falls to half these densities or even poorer, even on an ordinarily good range. Shooting season populations are usually around fifteen per cent below those of the peak season.

Numerous other censuses of ruffed grouse have been made in recent years, notably in Pennsylvania, Michigan, and Minnesota. While comparisons of these data with New York records are difficult to interpret, they do indicate the adaptabilities of the species in various regions and the great variations that occur in grouse abundance.

Fisher (1939) gives data on grouse densities on five areas in Michigan censused for two or more years each between 1932 and

1936. All were continuous forest. They are consistent in showing the highest spring densities in 1933 with a marked decline in 1934. In only one of three of the areas observed in 1936 had the population regained its 1933 level. Maximum spring densities recorded by Fisher for various areas were six and five-tenths, nine and two-tenths, fifteen and two-tenths and fifty-three and three-tenths acres per grouse; minimum spring densities on these same areas, in order, were thirty-three and six-tenths, twenty-two and one-tenth, two hundred thirteen, and one hundred twenty-eight. Here it appears that grouse densities were higher than those of the Adirondack New York area, but lower than those of Connecticut Hill. The September peak season densities for these areas indicates a greater maximum summer productivity than for any New York areas. These maxima were: two and seven-tenths, three and five-tenths, four and seven-tenths, four and eight-tenths and seven and three-tenths acres per grouse; minimum peak season densities on these same areas, in order, were nine and seven-tenths, eight and nine-tenths, twenty-one and three-tenths, fifty-eight and two-tenths, and eight and seven-tenths acres per grouse. These high densities were never repeated two years in succession; in fact, on all but one of Fisher's areas, a very high density level was reached only once in the period involved. This indicates greater variability in peak populations than observed in New York.

King (1937) reported on April and October populations of grouse on an area of forest in Minnesota for the years 1927–36. The maximum spring breeding densities, four acres per grouse, were notably higher than any New York areas achieved, although comparable with many individual cover unit records. The high density period extended three years from 1932 to 1934, increasing gradually from a spring density of forty-two and eight-tenths acres per grouse in 1927 to the maximum and dropping back to twenty-six and one-tenth acres per grouse in 1936.

The October grouse densities in King's area show much greater range of variation than I have experienced. The maximum density reached two and six-tenths acres per grouse in 1933. A decline to a low of thirty-three and six-tenths acres per grouse took place by 1936. These records support the conclusion that grouse populations fluctuate more widely in continuous cover regions than in disconnected cover.

In the scrub oak-pitch pine forest type of Pennsylvania, Studholme (1941) studied the grouse populations on a 1,440-acre area from October, 1939, to April, 1941. The breeding season densities were very uniform, about sixteen acres per bird, while the fall shooting season densities were from nine to ten acres per bird.

Population Densities of All Game Birds in Grouse Range. There are several other species of game birds that occupy the same range as ruffed grouse in the Northeast. The one of greatest importance, and which occupies substantially the same range as the grouse, is the woodcock (*Scolopax rusticola*). An occasional ring-necked pheasant (*Phasianus colchicus*), or bobwhite quail (*Colinus virginianus*) utilizes the margins of some ruffed grouse coverts. In broken-up grouse range the mourning dove (*Zenaidura macroura*) is quite common, while an occasional black duck (*Anas obscura*) will be found in territories of partridges. All of these species are found on the Connecticut Hill area, the woodcock and mourning dove [1] being most prevalent.

Woodcock ordinarily are from one-seventh to one-fourth as abundant as grouse, the latter usually occur in years of rather low grouse abundance.

Ring-necked pheasants occurred in small numbers except in winter. The numbers of quail and black duck were not significant. Mourning doves were about as abundant as woodcock.

The density of the mixed stands of game birds is only an approximation. The average spring density was about six acres per bird. This was composed roughly of seven-tenths ruffed grouse, one-eighth woodcock, one-twentieth ring-necked pheasant, and one-eighth mourning dove. September populations averaged about four and one-half acres per game bird. Here the proportions of species were approximately three-quarters grouse, one-sixth woodcock, one-thirtieth pheasant and one-twelfth doves.

CARRYING CAPACITY AND SATURATION POINT

Carrying capacity plays a key part in the determination of population density, hence in productivity. Leopold (1933) states that

[1] The mourning dove is not legal game in New York.

"carrying capacity is a property of a unit of range" rather than a property of a species. Errington and Hamerstrom (1936) define carrying capacity for bobwhite quail as "the upper limit of survival possible in a given covey territory as it exists under the most favorable conditions." They then restate it "as the level beyond which simple predation upon adult birds, their own territorial intolerances, and their tendencies to depart from coverts overcrowded with their own or some other species do not permit continued maintenance of population." In a later paper, Errington (1941) again summarizes it thus: ". . . carrying capacity functions as a threshold of security below which the numbers of wintering birds can rarely be forced very far through attacks of wild predators alone." While we repeatedly refer to the carrying capacity of the environment or range, these definitions clearly imply that it may not be a property of the range alone but also partly a species property. This is commonly the case with the ruffed grouse.

Any unit of grouse range unquestionably has a fixed upper limit of winter survival, but this limit is conditioned primarily by environmental attributes, such as the strategic location of cover components, predation, and weather plus innate species characteristics, rather than by limitations of food and shelter. Just as carrying capacity for bobwhite quail is more a function of species properties than is the case of the hoofed mammals, so carrying capacity for ruffed grouse is even less dependent upon the food and shelter conditions of the range than in the case of the quail.

The food and shelter conditions in normal grouse range have a potential carrying capacity far in excess of the actual. Predation, either direct or conditioned, usually reduces the winter population well below the ability of the range to sustain and shelter. Even more important, the species itself will not tolerate crowding beyond a definite point. This brings in the concept of "saturation point," a purely species characteristic. When the potential carrying capacity of the range is a density that exceeds the saturation point, then saturation point becomes a component in determining the actual carrying capacity. This seems to be the case on good grouse range. On poorer or marginal range, the potential carrying capacity of the environment is more likely to be lower than the saturation point, thus not allowing the latter to be a factor. In this case, the carrying capacity may actually be an environmental attribute exclusively. But even

here, intraspecific intolerance sometimes plays an important role in determining the number of birds accommodated.

Using saturation point as the maximum density that the species itself will tolerate (a somewhat broader conception than that given by Leopold), evidence shows this to be a bird to four acres. In every case where this density was surpassed in the early fall, immediate reaction set in in the form of dispersion and accelerated decimation. On these well-populated coverts, carrying capacity was conditioned by the action of this species characteristic. The maximum actual carrying capacity exhibited by any covert observed (as measured by winter survival) was four acres per bird of coverts exclusive of open land. Areas like Connecticut Hill, taken as a whole, have a carrying capacity of about eight to ten acres per bird. On a continuous forest range like the Adirondack Mountains, it is about twenty acres per bird.

ENVIRONMENT AFFECTS PRODUCTIVITY

We have observed that the actual productivity of a wild animal like the ruffed grouse is far below the potential productivity. It was noted that some of the inherent characteristics of the species are important in holding back the attainment of this potential; that its own populations provide a check to its continued increase. We now consider the other major limitation on productivity—the environment. The environment is the physical world, organic and inorganic, in which the grouse lives. It includes shelter, food, climate, and other animals, including man—all the plants, animals, soils, and physiography that make up its home and associates.

It takes no imagination to appreciate the profound effects that the environment exerts in reducing the numbers of any animal species. They succumb from exposure and starvation, are eaten by predaceous enemies, and waste away as a result of the actions of parasites or disease organisms. But just how important are these various factors? How are they interrelated?

Decimating Agencies. Most obvious factors are those agencies that actually cause the death of grouse, either in the egg, immature, or adult stages. The following discussion of grouse mortality is based primarily upon the studies of the New York State Conservation De-

partment on the Connecticut Hill area in New York, supplemented by reports of other workers where available.

Mortality of Grouse Nests. My first year or two of experience in observing the fate of numbers of grouse nests left me feeling quite concerned over the future of the species. It was quite a shock to learn that such a large proportion of the nests were destroyed. Gradually it became apparent that what had seemed to be a high rate of loss was actually normal and the birds increased in number at a rapid rate in spite of these losses. Further analysis clearly reveals that this loss is a natural part of the ecology of this species, as are similar losses with many other birds.

Nest losses are generally high, ranging roughly from one-quarter to three-quarters of all, which indicates a wide variation. The variation occurs on any area in different years, and also appears to be consistently higher in some areas than in others. On Connecticut Hill, nest losses ranged from thirty-two per cent to seventy-seven per cent over eleven years while nests observed over the state at large showed annual losses ranging from twenty-seven and five-tenths per cent to fifty-six and one-tenth per cent.[1] The general average annual loss on Connecticut Hill was slightly under fifty per cent, compared with an average of only about forty per cent over the whole state. This indicates that the Connecticut Hill nest mortality has been somewhat higher than the general average (*N. Y. S. Cons. Dept. Ann. Reports*).

The nests examined from the Adirondack Mountains had a notably lower mortality rate than for the rest of New York, ranging from seven and one-tenth per cent loss to twenty-four per cent. This is quite logical since the predator pressure in these continuous cover areas is generally lower than elsewhere in the state (data derived from *N. Y. S. Cons. Dept. Ann. Reports*).

In west-central Pennsylvania, Studholme (1941) found the mortality of eggs he observed to be twenty-two and five-tenths per cent.

Almost all nest loss is due to predation. Over the state as a whole, over three-quarters of the nest loss was ascribed to predators, with some cases being unidentified as to cause of destruction. No doubt some of these were the result of predation too. On Connecticut Hill,

[1] This figure is unduly affected by the 77 per cent loss on Connecticut Hill and a high loss on the Pharsalia area. Excluding the data from these two areas, the figure drops to 31.9 per cent.

practically all of the nests that failed were destroyed by predators.

Most of the other nest losses are due to man (farmers, lumbermen, etc., in their various work operations), with some losses resulting from fire (which may assume great importance locally), desertion, flooding, etc.

The time of destruction is of considerable importance since it has a direct bearing on the probability of renesting, hence on the ultimate success in nesting. Very few nests are destroyed during the egg-laying period—the last half of April and first week or ten days of May in southern New York—probably not over five per cent of the total nest losses occurring at this time in normal years. As soon as incubation begins the rate of destruction increases, slowly at first, then quite rapidly after the first week. Most of the nests are broken up during the last ten days of incubation.

Now there is an inverse relationship between the length of time that incubation has progressed and the likelihood of the bird's renesting. The longer the incubation has proceeded, that is, the nearer the nest is to hatching, the smaller is the probability of renesting. If a nest is destroyed before incubation has begun, the hen will probably make another nest. It is even possible that some of these second nests may occasionally be mistaken for a late first nest. Up until about two weeks after setting there is some chance, though a constantly reduced one, of the bird renesting if broken up. Hens whose nests are taken during the last ten days of incubation rarely make another nest that year. And since most of the nest losses occur during this last ten days, most broken-up birds do not make another attempt.

Ratio of Females Unsuccessful in Nesting and in Rearing Broods. We have seen that the mortality of grouse nests averages about forty per cent. This means that about sixty birds out of every hundred succeed in hatching their first clutch. We also noted that a rather small but significant proportion of birds that lose their first nest will try again, and some of these will succeed in hatching. Thus the ratio of unsuccessful nesting is somewhat lower than forty per cent.

The exact ratio of renesting is difficult to gauge on the relatively sparse data available. It is likely below twenty-five per cent. Using this figure, about ten of each forty birds that fail in their first nesting attempt (out of an average hundred birds), will nest again. The

mortality among these second nests will be about half. Hence, we may anticipate that five of them may hatch. This brings average success in nesting to sixty-five per cent, and the failure ratio to thirty-five per cent. Fluctuations will, of course, follow the same course as occurs in rate of first nest mortality.

Another way of stating this fact is that on an average sixty-five per cent of female grouse will hatch a brood. However, not all of these hens will succeed in bringing their brood, even a single chick, to maturity. Some will lose their entire family before the summer is over. The facts on this matter may be derived by obtaining the number of female grouse with and without a brood at summer's end (*i.e.*, when the chicks are mature). Generally only about half the hen grouse succeed in bringing at least one youngster to adulthood. About one female in six that hatches a brood fails to raise any of the chicks, in an average year. The ratio of hens succeeding in rearing broods varies widely in different years from about three-quarters to only one-quarter of the females.

Losses Among the Young Birds. Most baffling of all grouse mortality problems is that of the young in the first two or three weeks after hatching. Our experience indicates that a loss of from one-quarter to one-half of the chicks may be expected in the first month of life, and that most of this loss usually occurs in the first three weeks. This large initial loss was estimated by Sandys (1902) as likely being at least one-third of the young before they attained the size of quail; Forbush (1913) gave one half as the normal loss of young before reaching maturity, while Roberts (1932) stated that young grouse have so many enemies that even under normal conditions only a small remnant of a brood escapes. The mean of twelve years' records on Connecticut Hill for brood mortality up to September is sixty per cent. Extremes have been fifty per cent and seventy-seven per cent. Excluding two years of unusually high losses, 1933 and 1935, the annual loss has ranged from fifty to sixty-three per cent. On the Adirondack area the mean loss over a ten-year period was about sixty-three per cent with extremes of forty-three per cent and eighty-eight per cent (*N. Y. S. Cons. Dept. Ann. Reports*). Studholme (1941) gave the brood loss in Pennsylvania as sixty-two and six-tenths per cent. Thus the losses of young grouse are fairly constant, with an occasional bad year when the results are apt to be

disastrous. While the immediate causes of death of these chicks remain obscure, the relationship of high population density to poor recovery, and vice versa, is probably the guiding consideration.

The normal curve of infant loss is steep during the first month of life, levels off considerably during the second month, and then drops a little more abruptly for a time in the third month (see Fig. 15). The causes of the early season losses are somewhat obscure. Certain facts are quite clear, and these help to delimit the prob-

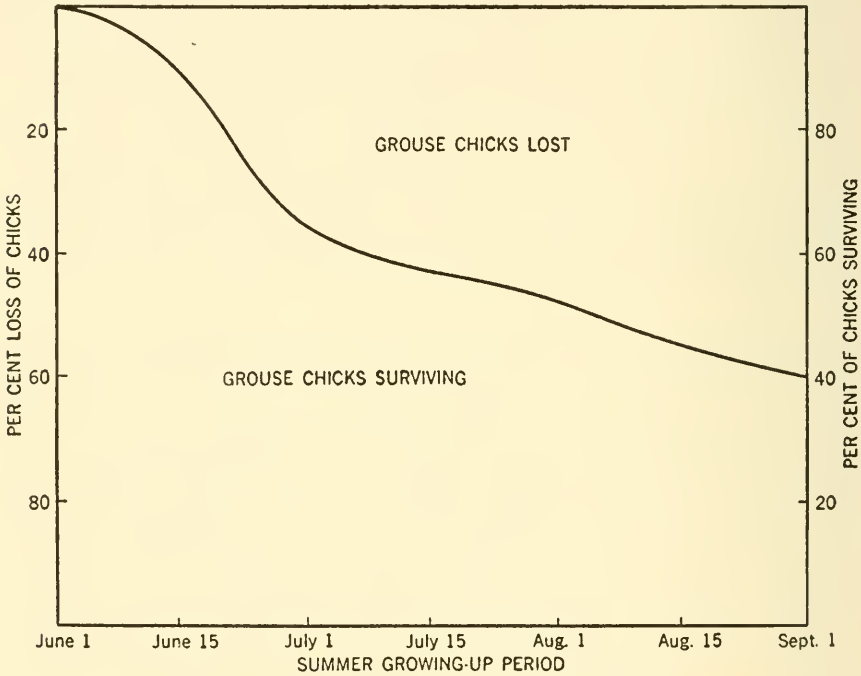

Fig. 15. Normal Grouse Infant Mortality Curve June to September

lem. Predation is of little significance at this season. Diseases and parasitic infestations apparently are not of great significance in normal years. And man has little direct effect on brood survival.

When a mother grouse brings off an average brood of about ten chicks she has a big problem of family control on her hands. Ten active little birds are no simple group to keep well fed, brooded, and husbanded together. In the first place, there will be considerable variability in the vitality of the individual youngsters. Even as with us mortals, some grouse will be born weaker than others. These

weaknesses may arise from unequal incubation, excessive chilling during embryonic development, through some accident of development in the egg, or they may be carried through the egg from some weakness in the mother. We have no proof for any of these hypotheses other than the inference that may be drawn by the elimination of other factors and by parallels with the known facts of domestic animals. There is little question but that a considerable portion of the early deaths of grouse chicks arises from these weeklings' dropping by the wayside when they fail to keep up with the travels of the family.

An interesting sidelight on grouse psychology is the reaction of mother grouse to the size of their broods. Evidence gathered time and again indicates that they have little cognizance of numbers. Following a disturbance when the brood is flushed and dispersed, the chicks reassemble at the call of the mother when the coast is clear. If some of the birds fail to arrive with the majority, the brood will go its way with no apparent concern on the part of the parent. She seems to be quite satisfied as long as she still has some chicks with her. It is apparent that this characteristic will result in the abandonment and consequent loss of quite a few chicks. Accidents of other types will occasionally result in losses: chicks that stray and become lost, little ones that tumble into some cavity from which they cannot escape, and other similar chances sometimes cause the death of young grouse.

Probably the most vital immediate cause of early brood losses is the weather. Young grouse are not always able to withstand the drenchings of a cold June thunderstorm or the chilling of an abnormally cold night. If well brooded during these emergencies little trouble is likely to occur. But with many chicks to care for, the likelihood of some of them getting chilled or soaked is considerable. As the size of the brood decreases the mother's ability adequately to brood them in adverse weather improves and the chicks themselves are more hardy as they grow older. Thus the losses from exposure are usually over in the first few weeks.

It must be recognized that these heavy losses to baby grouse soon after hatching are a normal expectancy if they do not exceed about thirty-five per cent in the first three weeks. But occasionally an abnormal combination of adverse weather in June or early July will result in far greater losses. In 1935 a period of excessive rains in early

July, covering a three-day period, clearly caused a large loss of young grouse, and led to the highest brood mortality (77 per cent) observed in the eleven-year study. Since these excessive losses occurred following high breeding populations, it is likely that they were preconditioned by population density relations, whatever may have been the immediate decimating agencies.

As the young grouse grow older, predation gradually becomes a more important cause of losses. Along about the time the birds reach eight weeks of age, the loss from predation notably rises. This August increase in deaths from predators is largely attributable to the accipitrine hawks, mostly sharp-shinned hawks, as they are more common. The susceptibility of the young grouse to these attacks increases at this time for a short period. The chicks assume more independence of their mother and take more excursions on their own as they begin to feel their oats. Those that escape are soon educated to cope with this danger and the rate of loss drops off again. After the moult in August and September, the young birds assume adult plumage and are hardly distinguishable from their elders. Their losses then are considered to be a part of the adult mortality.

Adult Mortality. As a matter of convenience, we calculate the annual losses of adults from September to September rather than on a calendar year basis, since the young grouse become adults in September. The yearly losses of adult birds on New York's Connecticut Hill study area over a twelve-year period have a mean of forty-eight per cent. This mean was exceeded in eight years and in four years the losses were below this figure. The extremes were twenty-three per cent and sixty-four per cent. In five of these years the loss was between fifty-one per cent and fifty-eight per cent, and only once did it exceed the top of this range. On the Adirondack area the extremes were similar, twenty-two per cent minimum and seventy-three per cent maximum with a mean of about forty-six per cent over a ten-year period (*N. Y. S. Cons. Dept. Ann. Reports*).

The spacing of losses of grouse through the year is fairly consistent. The high mortality period is from January through April, with the hunting season period added in heavily hunted regions. Summer losses are ordinarily negligible, but rise considerably in September as the young of the year join the ranks of the grown-ups. There is a generally steady increase in rate of loss through fall and winter,

culminating in a peak in the breeding season in March and April. From then on to summer, the losses drop off rapidly.

The increased mortality rate in winter is due in a large measure to the greater vulnerability of the birds to predation resulting from winter weather and poor cover conditions, and from the increased intensity of hunting by predators. The continuance of the high mortality into the breeding season is to a considerable extent the result of increased losses of male birds resulting from exposure during the courtship period. This differential mortality among the sexes seems to be balanced at other times of the year by greater losses among females than males. This is particularly true in the summer and fall.

In most years the greatest immediate source of adult loss is predation. However, it is highly probable, in fact quite certain, that predation takes more than its fair share of the blame. When there is evidence of predator work on the remains of a grouse, the cause of death is usually credited to the predator. Many times the predator plays a secondary, and often unimportant part in causing the death of the grouse. Grouse that are weakened by wounds from hunting or from physical accidents are often taken by predators before succumbing from their injuries. I recall an occasion when a man winged a bird and was unable to retrieve it. Over a month later my setter dog pointed a grouse within a hundred yards of this same location and, finally breaking point, caught the bird. It proved to be the one winged some time before—still in good health but unable to fly. Ordinarily this bird would have been caught by a wild predator—and its loss erroneously attributed to that animal. Likewise, some grouse that die from disease or accident are eaten as carrion. These cases too would have evidence of predator work, although many times they can be identified as carrion from other evidence.

Notwithstanding these facts, most adult grouse in the Northeast wind up their lives as food for some other wild creature, as the Lord intended they should. The exact proportion that die primarily at the "hands" of claws or talons cannot be determined because of the obscuring evidence already noted. And even among those that actually die directly and essentially from predation are many whose fate was influenced by weather conditions, overpopulation, scarcity of other prey species, etc. After an evaluation is made of all of the complicating factors, we conclude that predators cause about fifty per cent of the killing of grown birds in normally hunted coverts and

eighty per cent in coverts protected from hunting by man. The difference, thirty per cent of the mortality, is the normal hunting-season loss from gunning. In coverts not well hunted this figure may be lower, in overhunted areas sometimes higher. The other one-fifth of the mortality accrues from disease, accidents, and other causes.

Disease as a decimating agency is difficult to evaluate. Often its effects are obscured by predator action. It is inconsistent in that its importance varies greatly year to year and from one area to another. Generally it apparently is not a high or widespread cause of death in grouse. In ordinary years of good grouse abundance, that is years when grouse populations are not rapidly and sharply declining, we estimate that the various diseases and parasite infestations cause from five to ten per cent of the mortality. It is probably greater in unshot range than elsewhere.

There is evidence that diseases sometimes play a much bigger part in grouse mortality, these usually being years of great decline from peak populations. Allen found that unusually large numbers of grouse died from attack of the gizzard worm on an area near Ithaca, N. Y., in 1926–27 and apparently contributed largely to the cyclic decline that took place.

In spite of the many organisms that afflict the grouse, many of which can be lethal, we are hesitant in gauging the importance of disease as a factor in grouse mortality. During the period of my observations, no epidemics in grouse were observed. True, there were great variations in the incidence of infestations, the incidence generally rising with the increase of grouse populations. There was also variation in the observed losses from disease in different years. But in no year did we find evidence to show that disease was a mortality factor of prime importance.

Death resulting from mechanical injuries sustained in physical accidents is not uncommon with grouse. Here too, as with disease, the primary cause of death may be obscured by the handling of the bird by predators. Accidents are more common with young adults than with older birds, many occurring during the first autumn after reaching maturity. These early autumn losses are often associated with the "crazy flight" phenomenon (see page 43), and are a function of the fall shuffle of grouse that takes place with the break-up of the family groups.

As a general rule, accidents usually cause about five per cent of

the losses of adults, but this figure will vary widely in different localities and years.

I have already indicated that hunting by man in normally well-hunted areas results in losses approximating fifteen per cent of the birds. This is the equivalent of about thirty per cent of the yearly mortality. It is self-evident that this figure will vary widely in different times and places. Adding up the losses from predation, hunting, disease, and physical accidents, we practically account for the whole mortality. An occasional bird may be killed by fire; very rarely it is possible that one succumbs from starvation or over-exposure to bad weather. These factors are negligible, however, as direct decimating agencies.

Limiting Effects of Environment. There are many environmental influences that condition the decimating agencies in one way or another. We have just noted that starvation is of no importance as a killer of adult grouse. But when a grouse wanders out into an apple orchard to get at a desired food, it may thereby expose itself to an easy attack by some predator, or a hunter. Thus the food problem is interrelated with predation and hunting losses. The pursuit of food may likewise be a factor in bringing about disease. Concentration of a food source may mean concentration of grouse, and thereby facilitate the spread of disease organisms. Some items of food carry disease organisms, as for example the sow bug that is the alternate host for the parasite, *Dispharynx spiralis*. If the parasitic infection weakens the bird so that it is killed the more easily by a predator, then the food relation, the sow bug, is two steps removed from the actual cause of death.

Climatic factors are of immense importance in conditioning the decimating agencies. When conditions of snow, temperature, and wind cause grouse to roost in the snow, the birds become more vulnerable to predator attack. Likewise the quality and distribution of food and shelter play a part in the complex of weather-cover-predation. Then man further complicates these relationships by affecting the area in various ways—by cutting, burning, cultivating, draining, or by adding still another in the chain of factors, livestock, that graze and browse the vegetation. Insects and the other lower forms of animals play many parts in the interrelationships of the grouse environment. Physical factors, as slope and light, add to these complexi-

ties. And finally the grouse themselves affect each other's survival by their fighting, courting, and other relations.

We cannot unravel all of these many involved relations of grouse ecology. Even if we could, we would surely find that all must be considered in evaluating the needs of the species, and in translating them into management. No one aspect of the maze can get far out of balance without seriously affecting the whole.

Pervading all grouse environmental needs as of first importance is habitat: food, and shelter. The cover definitely delimits the possibility of grouse inhabiting any portion of the range. Within the framework of acceptable cover, all of the other factors and influences combine to determine the level of the grouse population.

Cycles of Abundance. A cycle, according to the dictionary, is a round of operations or events—a series which returns upon itself. A recent adaptation of this usage in connection with animal populations refers to changes in numbers of a species that take place regularly according to uniform time intervals, and usually include a precipitous decline phase. During this decline, the species may lose up to ninety per cent or more of its members in a relatively short time. Species that are thus regular and violent in their population changes are said to be cyclic species. The ruffed grouse has been among the group so classed.

The general concept of an animal population cycle is that an abrupt drop in numbers occurs some time after the species has built its population up to carrying capacity—*i.e.*, all that the environment can support. In some cases this carrying capacity level is temporarily exceeded, thus assuring a quick and large drop in numbers. The size of the population itself may bring about its downfall through the medium of some mass-decimating agency; in this case the regularity of the cycle would be due to the constancy of the time required to bring the population to the critical level. It may be that the periodicity is involved in a factor that is independent of the animal population in question. Such might be the case if years of sunspot maxima, which themselves occur in cycles, brought about some environmental influence which caused catastrophic decimation regardless of the position of the population level at the time.

That these two types of cycles exist in nature, no careful student of the subject can deny. Whether or not ruffed grouse populations adhere to any such biological or physical laws is another matter.

Before we examine the evidence relating to grouse and cyclic behavior, let us pause a moment to cite clear-cut examples of the two types of cyclic effects on living things.

The case of the apple tent caterpillar (*Clisiocampa americana*) is a good example of the cyclic effect brought about by a population increase to an untenable density. The caterpillars find an abundance of food on wild and cultivated apples, cherries, and other food plants and, with their inherently high reproductive ability, increase their numbers rapidly over a period of years. The parasites that live on these larvae have a progressively easier task of locating their hosts as the population of the host grows. The curve of parasitic infestation heightens even faster than the curve of tent caterpillar abundance and finally, in one opportune year, catches up and causes the abrupt loss of most of the worms. The next year the population of the caterpillars is at the low of the cycle. Likewise the parasitic infestation is lowest, since the parasites have nearly ruined their own food supply. The upward trend of the cycle begins, slowly at first, but gathering momentum each year. And once more the curve of infestation sets out to catch the curve of host abundance. Thus we have a simple cause-and-effect cycle of abundance in two animal species brought about by the specific relationship of parasite and host. True, other factors such as the weather conditions will affect this picture so that it never appears in actuality quite as smooth in action as we have pictured it. Nevertheless, these populations do follow this basic cyclic pattern.

Cycles in some forms of plant and animal life caused by physical phenomena that themselves occur in cycles are fairly well established. Best known are the cycles in "sunspots" that repeat at about ten- to eleven-year intervals (see writings of R. E. DeLury, Harlan Stetson, and others). These solar changes apparently are related to the well-established weather cycles [1] that occur in periods bearing multiples of about eleven years (Abbot, 1935). It has been shown

[1] Authorities do not yet agree as to the effects of sunspots on our weather. In *Science* (Vol. 95, No. 2473, May 22, 1942) it was reported: "Sunspots have their own effect on the earth's weather. They give off vast streams of electrically charged particles that shoot through space. Some of them, entering the earth's atmosphere, serve as nuclei for the condensation of water vapor in the upper atmosphere and thus lead to the increase of cloudiness and of rainfall." Nine months later, in *Science News Letter* (February 27, 1943, p. 137), Dr. Seth B. Nicholson of the Mt. Wilson Observatory was reported to have concluded that "Vague correlations between sunspots and the weather probably exist, but the weather is affected so much by other factors that the influence of sunspots is insignificant."

that these long-term variations in temperatures, precipitation, and other weather factors affect tree growth (Douglass, 1941), as they logically would. There is considerable evidence that sunspot cycles are related to changes in population of some rodents, of migratory salmon, and other animals. The relationship may be indirect, through the effects on environment or climate; or it is conceivable that it may bear some direct relationship, as yet not understood. It is now well-known that sunspot activity affects our radio waves. Who are we to say that these changes in solar radiation may not directly affect forms of life on the earth, with animals dependent on vitamins, hormones, and what not? One author has even gone so far as to correlate wars and business cycles with sunspots (Stetson, 1937).

Now what is the evidence supporting and refuting the existence of grouse cycles, and what conclusions may we draw?

That there are fluctuations—and wide too—in grouse numbers is well-known. Clear and fairly complete records of years of abundance and scarcity go back to 1904 for some areas, notably the northeastern states. Scattered records indicate certain years of scarcity or abundance for some areas back as far as the late 1860's, and inferences may be drawn from a few writings prior to that time. But until the studies of the last two decades, little reliable information was available on the population mechanics of the bird.

Mere fluctuations in population of a species does not in itself indicate any tendency to a cyclic behavior. All species are constantly changing their numbers, not only in detail but often in general sweeping surges. On the mathematical law of probability, when a species has a high population level (for its kind), it is most likely to decline in numbers; and conversely, when it is scarce (but not below the threshold of satisfactory mating), it is most likely to increase. This is one more case of the natural law of biological equilibrium commonly referred to as "the balance of nature."

In order to evaluate the evidence on grouse cycles, let us now consider the many causes, features, and characteristics of cycles and see how they fit into our knowledge of *Bonasa umbellus.*

1. Peaks and Troughs of the Cycle are Regularly Spaced in Years in any One Portion of the Continent.

Years of scarcity of grouse in the Northeast are well documented for 1927–29, 1924, 1915–17 (Stoddart, 1918), 1907 (Forbush, 1912), 1904 (Forbush, 1912), 1896–97 (Dillin, 1920). There is some evi-

dence that grouse were also relatively scarce about 1877, and shortly after the end of the Civil War. Years of abundance have been recorded as preceding these years in each case since 1895. There is enough regularity to these dates, especially when the declines of 1904 and 1924 are segregated as being markedly less violent than the others, to lead one to the conclusion that cyclic spacing is involved. However, no such declines have occurred in the Northeast from 1927 to 1944, although many relatively local scarcities have occurred. A fairly general reduction of grouse in 1937 might be classed in the category of the 1904 and 1924 declines but hardly with the others. A general decline in grouse numbers has taken place from 1944 to 1946, how serious we are not certain owing to war-time cessation of grouse studies. It was bad enough to cause the Pennsylvania Game Commission to close the season in 1946. It may be particularly significant that the failure of the expected major cyclic decline of the 1930's to materialize occurred when, for the first time, scientists were waiting ready to delve into its every manifestation. Had no such critical group attended the grouse situation during these years, a cyclic decline might have seemed more apparent in many places. In fairness to the evidence supporting the concept of a quick, immense decline, it should be pointed out that such a loss of grouse did occur in the Minnesota-Michigan region in 1933–34 with grouse studies in progress there at the time.

2. Years of Decline in a Single Cycle will Vary with the Portion of the Continent, the Progress being from Northwest to South and East.

This progressive, temporal sweep of progress of the cyclic die-off, apparently a marked feature of rodent cycles, is not at all consistent in ruffed grouse. In comparing the western and northern cyclic years with those of the east, some are ahead in phase, some behind, and some in harmony. Thus Criddle (1930), records low population years in Manitoba as 1898, 1907, 1918 and 1928. Here the 1907 record coincides with the eastern records, while the others are one to two years behind. This is just the opposite of the general cycle characteristic. Michigan cycles (Tubbs, 1940) have produced low ebbs in grouse in 1901–02, 1915–16, 1923–25 and 1933–35. With the exception of 1915–16, which is synonymous with the northeastern low, these troughs occurred ahead of the more eastern area. This is the opposite of the Manitoba case. Wisconsin and Minnesota grouse declined to a low ebb in the 1933–34 period, along with

Michigan, but a corresponding die-off did not occur in the Northeast. Leopold and Ball (1931) generalized the cycle curve for the whole continent but noted several exceptions, among them: the Wisconsin low in 1919 is later than average; in 1905–06 a little ahead of most areas; in 1899 again it is late, this time about two years. Clarke (1936) gives cyclic low periods for Ontario as: 1933–35; 1924–25; 1914–16; 1904–06; 1894–95; 1883–85; 1874. These are consistently a few years ahead of the dates for the northeastern states. From all the information at hand we may conclude that the geographic lag from Northwest to South and East that is a characteristic of true cyclic species does not hold consistently for ruffed grouse.

3. The Occurrence of Cyclic Trends in Different Animal Species is Synchronized.

There is apparently a correlation in cyclic declines of many, if not all, of cyclic vertebrate species. When one species of rodent declines in an area, others may disappear at the same time. Carnivorous species may decline a year or two after the herbivores decline, after the loss of their food supply takes full effect. Synchronism in the latter case is the result of simple cause and effect: loss of food, loss of life (see Elton and Nicholson, 1942; Chitty and Chitty, 1941). Elton (1942), in discussing wild-life cycles in Labrador and Ungava, summarized it thus: "The lemming crashes; the predators crash and migrate; the lemming begins to recover before the slower-breeding predators can catch it up. This is a rough description of a part of a phenomenon that is now known to be generally found in nature . . ." In the case of uniform die-off, it must occur as a result of a common cause acting on more than one species.

This correlation in population trend between species was well exhibited on the Connecticut Hill study area in 1935–36. Red squirrels, gray squirrels, cottontail rabbits and mice (mainly *Microtus*) were from seventy-five to over ninety per cent lower in numbers the second winter compared to the first. Predation was not primarily responsible, nor could significant disease conditions be correlated (although our ability to diagnose pathological troubles is admittedly very limited). No answer was apparent in connection with food, cover, weather, man, or any other matter that could be discerned. The cause, or causes, of this mass decimation remained unsolved. It did, however, show up the simultaneous occurrence of a precipitous decline in several species. The general thought

has been that grouse follow the rodents by about two years in their own die-off. This did not occur on this area in anything like a cyclic decline although the grouse population did show a marked decline in 1937.

The cause and effect synchronism in one group of animals is set up by the loss of lemmings, white hares, and ptarmigan in the far north. This dislocates the food supply of such predators as the snowy owl, lynx, Arctic fox, and goshawk. A shortage in their food supply causes them to migrate southward in search of better hunting, or die where they are. Those that migrate come into the grouse range and exert abnormal pressure on that species, which results in their marked decline. There is no doubt that this chain of events occurs to some degree. Southward winter incursions of snowy owls and goshawks have often been recorded. A few of each species were seen on Connecticut Hill in some years. And there is no doubt that the goshawk is a very efficient grouse predator (see page 206). Criddle (1930) suggests that a single goshawk may take as many as fifty grouse in a winter. An "invasion" of these birds into a grouse range already adequately populated with indigenous predators may therefore have a significant effect on grouse numbers. Criddle records that such an invasion occurred in Manitoba in the winter of 1907–08. This period was immediately following the drop in grouse and could not have caused it, although, as Criddle says, "we . . . need to know more of the influence of goshawks on a grouse population already depleted by other agencies."

The evidence seems clear that the recorded declines in grouse are not consistently synchronous with die-off periods in other species. This adds weight to the evidence against the grouse being typically cyclic in this respect.

4. Uniformity of the Die-off.

When a cyclic decline occurs it strikes all coverts within the broad area of effect, possibly continent-wide for some species some times. King (1937), referring to grouse says: "Cyclic declines are not the result of overpopulation . . . when the crash comes it includes all areas, those on which there are peak populations and those on which there are very sparse populations." There is considerable evidence to the contrary.

When grouse disappeared in Wisconsin in September 1933, it was noted as "spotty" (Wisconsin Conservation Department, News Re-

lease, October 18, 1933), and "up to the present time it has affected ruffed grouse principally, and on areas where the birds were most plentiful . . . In many instances (it) is affecting only townships . . . In other counties practically the whole grouse population seems to be affected . . ." Out of thirty-four counties submitting reports, grouse were seriously affected in eleven, but were normally plentiful or better in twenty-three.

Experience in New York indicates great local variation in population trends. One portion of Connecticut Hill had a high population in 1927 when most coverts in the region were at a low ebb. Throughout the years of the detailed studies in several areas in New York, some cover units would be at a peak while others were low. Broad effects result from the cumulative effects of local conditions. When the majority of coverts are up, there is a pronounced peak; when the greater proportion are down, there is a trough in the general curve of population. But at any time there will be some coverts, and some areas or regions, that are contrary to the general condition.

Clarke (1936) concluded: "Periodically, ruffed grouse populations in Canada suffer serious diminutions in numbers. They do not occur simultaneously throughout the whole country. Even in Ontario there are local differences of at least three years in the time at which diminution begins." Fisher (1939) says: "The fluctuation in abundance of ruffed grouse is not uniform throughout its range in Michigan. The birds may be increasing in some localities while decreasing in others."

This evidence is supported by recent writings on the irregular nature of mammalian cycles too. MacLulich (1937) found cycles in varying hares to be regional phenomena arising from changing local conditions. Cross (1940) concluded that ". . . periods of maximum abundance in the numbers of (red) foxes in Ontario are regional phenomena and not province-wide . . ."

5. Severity Varies with Location and Species.

The typical cyclic surges are most severe in the North and West, less severe to the South and East, with any given species. Likewise, the severity, that is the degree of loss in the die-off periods, is consistently greater with some species than others, as for example with the voles and lemmings in the north. It is most severe on range extended from its indigenous range.

Testing these hypotheses with ruffed grouse is difficult owing to the lack of adequate quantitative data. There is some indication that grouse decimations may be more severe in the North and West than in the East. Both King (1937) and Fisher (1939) have recorded losses exceeding ninety per cent for early fall populations in Minnesota and Michigan respectively. The New York State hunting statistics between 1923 and 1935 indicate a decline of about seventy-five per cent although this may be lower than the actual drop, since no hunting was permitted in 1928 and 1929, years of lowest abundance. No such severe declines have occurred in the Northeast in the 1930's to correspond with the records from the North-central states.

How the ruffed grouse die-offs compare with those of other species as to severity is not wholly clear. There is little doubt but that they are less violent than the decimations of some of the rodents, such as the lemmings, the red and gray squirrels, and the snowshoe hare. There is some evidence (Criddle, 1930) that sharp-tailed grouse fluctuations are more violent than those of the ruffed grouse. Other species, as the bobwhite quail (in its northern range), the red fox, and some other predatory species exhibit fluctuations alleged to be cyclic in nature that are less severely marked than those of ruffed grouse.

The contention that a cyclic species exhibits its most violent changes in population at the periphery of its range, a doubtful attribute at best, does not hold with grouse. The species is notably stable in its southern Appalachian range. Chapman (1939) says: "There is no evidence of a grouse cycle in Southern Ohio."

6. Cyclic Mortality Primarily Affects Young Birds.

It is believed that all, or practically all, the losses of grouse in a cyclic decline are birds of the year. King indicates this to be true of ruffed grouse and Green and Evans (1940) come to essentially the same conclusion for snowshoe hares. This is likely to be true whether the losses are cyclic or not. There are normally more young birds than old, and the resistance to all decimating agencies is lower with the young ones. This is truer when the birds are mere chicks in the brood period. Abnormally high losses on the Connecticut Hill area in 1933 and 1935 were both the result of losses in young birds. This may not always be the case, however. The 1937 spring population fell to the lowest level since 1931 as the result of winter

losses. There was no evidence of an undue preponderance of birds of the year in these losses. Since these cases appear to deal with noncyclic losses, they do not disprove the point. Since the evidence that has been recorded supports this characteristic, we may accept it. Certainly it checks with the breeding density-recovery inverse ratio principle.

7. Weather Conditions have no Correlation with Cyclic Grouse Declines.

Criddle (1930) says "that rainfall seems to be a far less influence in accounting for grouse fluctuation than is generally supposed." Braestrip (1940) concludes that "there is probably general agreement today that it is impossible to explain the phenomenon by direct climatic influence on the animals, as was at first supposed." Clarke (1936), Middleton (1934) for British grouse cycles, and King likewise come to the conclusion that climatic factors do not affect the cyclic die-off.

Certain it is that some climatic factors, notably temperature and precipitation, profoundly affect grouse survival. As we note in the chapter devoted to weather in its effect on grouse, abnormalities of weather conditions can bring about abnormally high losses of grouse. These have been observed on Connecticut Hill both during early summer (on young grouse) and in late winter.

It has been suggested that adverse weather just after hatching time may cause starvation of the young chicks by killing off their insect food supply. Counts made on Connecticut Hill showed a normal average insect density in the zone available to grouse chicks of around 300,000 per acre in typical grouse brood cover types. Since a large share of these insects live in the duff on the ground and are types (such as ants) that are not greatly affected by weather changes, this suggestion does not seem to offer much likelihood of importance.

8. Parasitic Infections and Diseases are not Correlated with the Cycle.

Following an early enthusiasm for disease as an answer to the cycle problem resulting from the work of Allen and Gross (Allen, 1928; Gross, 1925) in the mid-twenties, most workers have discounted the importance of epidemic sickness in grouse. However, Clarke (1936) attributes to a particular blood parasite, *Leucocytozoon bonasae*, primary association with grouse cyclic losses in

Ontario. Green (1935 et ante) has long held that disease plays a dominant part in wild-life cycles, particularly documenting evidence in the cases of snowshoe hares and ruffed grouse. Elton (1942) pointed out the occurrence of disease in foxes and sledge dogs in the North associated with cycles. He stated that ". . . the cycle rests on mice or lemmings, . . . and is also marked by outbreaks of epidemic nervous disease that devastate fox populations and appear also among sledge dog teams . . ."

If cycles are a function of population density, then disease is likely to play a large part. There is no question but that the incidence of infestations increases with increasing grouse abundance. This was clearly observed in the specimens taken annually on a portion of the Connecticut Hill area. Not only does the incidence of infestations of all sorts increase with growing populations but the severity of the average case increases. For four years, from 1929 to 1933, the density of grouse increased on Connecticut Hill, paralleled by increasing incidence of infestation, before a case of death from disease was found. That year several were noted. This is significant considering the difficulty of finding grouse bodies before the scavengers get them. Likewise, there is no doubt but that disease (lesions caused by *Dispharynx spiralis*) was an important cause, if not the most important cause, of an abrupt loss of grouse observed by Allen near Ithaca, N. Y., in the fall of 1927. The evidence surely does not permit us to discard the disease factor in major grouse declines.

9. Predator-Buffer Species Relations are not Primarily Correlated with Grouse Die-offs.

Practically all authors of recent years have supported this conclusion.[1] Nevertheless, when an agency normally accounts for a large proportion of a population, as predators do with grouse, a delicate balance exists that may be seriously upset if conditions temporarily favor an increase in predation. This occurs most commonly in winter and spring and is usually induced by climatic conditions. The possibilities of increased predation on grouse resulting from losses in rodent prey species may be of considerable im-

[1] It may be inferred from Elton (1942) that grouse may well fall victim to buffer-predator population changes. He notes: "After the lemming crash, the foxes were seen to have turned in the emergency to other supplies." Then: "The vole cycle profoundly influences some predatory birds. . . . These changes are reflected in the southward migrations of several species. . . ."

portance. Predators may not cause major grouse declines but in most areas they play a part in implementing them.

10. Sunspot Cycles are Correlated with the Die-off in Grouse.

Among the first to suggest that sunspots might be correlated with wild life population fluctuations was DeLury (1930). The concept of some direct action from the sun affecting animal life so fitted the need for an all-pervading, mysterious something to explain the newly recognized animal population cycles that it was grasped quickly by many workers in the field. To make the solution complete it was even felt (or possibly hoped) that in some unexplained manner the recurring intensities of sunspots, with their effect upon the ultraviolet and possibly other vitally important rays from the sun, directly resulted in the decimation of vast multitudes of susceptible animals. Such a theory is generally discounted today.

As the meteorological and biological specialists working in this field progressed with their studies, it was evident that sunspot cycles actually do affect life on the earth but little agreement was reached as to their relation to animal cycles. Effects upon the weather, which in turn greatly affects animal survival, seem to be clearly demonstrated. It is conceivable that the changes in the sun's rays accompanying the sunspot phenomenon may alter the quality in vegetable foods developed through photosynthesis. Braestrup (1940) gives evidence that mineral deficiencies may thus be caused, deficiencies that may be vital to life. Wing (1935), in studying wild-life cycles, came to the conclusion that "the sun is the dominating factor in wild life," logical enough but not unveiling the *modus operandi* of cyclic behavior. Clarke (1936) is among those who discount any connection between the sunspot and wild-life numbers cycles, as are also MacLulich (1936) and Cross (1940), Canadian associates all. MacLulich, with convincing evidence, thoroughly lays the ghost and concludes: ". . . the fluctuation in numbers of neither lynx (*Lynx canadensis*) nor varying hare (*Lepus americanus*) are correlated with sunspots. . . ." Elton (1942) likewise discounts this theory, concluding ". . . There can be little doubt that it is wrong. . . ."

The shortcomings of the sunspot theory are many. In the first place, the cycles do not always check by any means. The grouse fluctuations are too erratic geographically to be guided by such an all-pervading force. The geographical lag does not fit into the

character of sunspot action. The fact that some grouse populations are high when the general trend in an area is low does not fit the pattern. And, except for its effect on animals through weather conditions, the mechanics of sunspot effect on animal numbers leaves a lot of explaining to be done. Nevertheless, there is enough meat to the theory so that it cannot be entirely disregarded. Affecting weather as they do, they must exert some effect on animal life. The possibility that the retarding effect of ultraviolet rays on plant growth may affect the food supply of certain herbivores, thus in effect causing a type of starvation, has yet to be proved or disproved. It may have merit.

11. Numerous Other Suggested Causes of Cycles Warrant Less Consideration.

The possibility that inbreeding may result in degeneration of the stock is adequately taken care of by the fall shuffle of populations which prevent inbreeding. Man's hunting is easily ruled out since the cycle is effective in wilderness areas where no hunting takes place. In fact, there is some indication that the periodic decimations are more pronounced in extensive wilderness range than in broken-up range in man-inhabited country.

Lack of food can hardly be considered seriously,[1] except as already noted: (1) quality of food may conceivably be affected by sunspot action; (2) adverse weather may affect insect food supply of young chicks. Criddle (1930) indicates a correlation between cycles in grasshoppers and cycles in sharp-tail grouse, and suggests there may be a correlation also with ruffed grouse cycles. However, this seems remote when we consider the minor importance of grasshoppers in the ruffed grouse diet. Shelter likewise cannot be correlated with abnormal die-off since these decimations seem to take place in all types of cover and range. There is no evidence from the

[1] Elton (1942) makes a good case for food scarcity being connected with the precipitation of cyclic decline of lemmings and voles in the north. "Lemmings must make very great inroads upon the vegetation, which sets definite limits to the amount of their increase and to their local distribution on the tundra. . . . As the cycle in population mounts steadily for several years, it reaches a breaking point and crashes. The danger signals are not long delayed in a community dependent upon the exiguous supplies of a northern land. Vegetation is denuded of the reserves built up in the previous time of lemming scarcity." Kenneth Doutt of the Carnegie Museum says lemmings were abundant in Labrador when he arrived there in Winter 1945. By June most had died. Their remains were everywhere, and many were found dying. There was plenty of food available. He believes lack of food could not have caused the losses.

eastern states that the bird's ability to reproduce is periodically lessened. King advises (letter, October 5, 1943) that he did find evidence of this condition in Minnesota.

SUMMARY OF ANALYSIS OF PERIODIC FLUCTUATIONS

From all of the information available and from the field studies I made, the following conclusions seem to be warranted:

The ruffed grouse undergoes marked periodic changes in population over its optimum range. These fluctuations are not sufficiently regular to be caused directly by some all-pervading common cause. They are inconsistent geographically, both in time of occurrence and severity of action. The supposed Northwest to Southeast lag is not consistent. The decimations that annually occur, whether normal or abnormal, are the product of the interaction of environmental factors, primarily weather conditions, parasite and disease infestations, and predation. These factors are conditioned by the habitat, by variations in climate (including sunspot cycles) and, in some areas, to a minor extent by man. These factors may individually or collectively go berserk on occasion with resulting catastrophic losses of grouse. The effect on grouse is sometimes felt only after a chain of connected events is set up with other animals, such as the rodent loss = predator's food scarcity = shifted predator pressure chain. The rodent declines may be set up by food scarcity, may be connected with climatic factors, and are probably not directly correlated with sunspots.

Grouse naturally have a high potential productivity which results in high populations in favored years. High breeding densities then lead to poor recoveries through high losses in young birds. This mechanism, whatever may be the immediate decimating agencies, seems basic to the periodic losses in this species. Further, this phenomenon is not assumed from individual year's records, but is shown to follow in series of years. It seems to have three phases, one of high recoveries from moderate breeding populations, a second of poor recovery from a high breeding population, and third, in occasional periods, a continued poor recovery from low breeding populations. Irregularity is a normal characteristic of grouse population changes.

Cause of grouse die-offs cannot be traced to a single source. There is no simple answer. It is the result of a complicated interplay between a multitude of natural factors and many kinds of organ-

isms. It is probably not the result of any unknown agents but it is brought about by little understood biological mechanics of well-recognized factors. To say that there is much still to learn about this subject is to state the obvious.

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11

Management of the Ruffed Grouse

The grouse is essentially a bird of the woods. Hence its management, so far as it concerns its habitat, must be woodland management. To be intelligent this management should be derived from a broader base of interest than the production of wood products alone. It must be based as well on the whole ecology of the grouse; on its cover preferences, food requirements, principles of interspersion; the need for drumming logs, dusting sites, and escape shelter; and the relations of the bird to other animals and to man. Merely the considerations of timber growing will not suffice. The assurance of a stand of the most valuable lumber species, well-formed trees properly spaced, handled by "sustained yield" methods will not automatically care for the development or maintenance of good grouse habitat. It can operate to depreciate the grouse cover value.

We have heard much in recent years of the conflict between game and forestry interests. Some have held them to be irreconcilable. This feeling was well summarized by Davenport (1941): "By now, I presume it is quite generally understood and taken for granted . . . that stands of timber trees such as are in condition to produce the most high-quality timber per acre per year are automatically low in their game carrying capacity. In general, therefore, the practice of intensive forestry on any sizable area is due to eliminate game management as a major consideration on that area."

I believe that this clashing is unnecessary and that we cannot afford to continue it. Fundamentally it has resulted from a conflict of personalities, one which will gradually disappear with greater understanding. When we can have the wisdom to look at our forests and woodlands for all that they are—sources of a great variety of vegetable products from ferns to ship masts; sources of many valuable animal products; modifiers of local climate, watershed pro-

tectors, and soil savers; and finally, and sometimes most important of all, a medium for escape and recreation where we humans may build our health, our character, and keep from going insane—then we may see the natural and logical integration of other interests, including the management of grouse, with forestry.

Since we must begin woodland management with forestry as a nucleus, we may say that grouse are a by-product of woodland management attained by modifying forestry practices in manners favoring grouse to the fullest extent practicable without interference with the major use. There will be some circumstances under which grouse, or more likely game in general, will be the primary crop, with wood products secondary, but these will not be general.

EXTENSIVE *VS.* INTENSIVE MANAGEMENT

There has been a great advance in recent years in our knowledge of practices that can bring about a greater game supply. The game-management methods advocated have been derived through "research"—I put this word in quotation marks owing to the widespread abuse it has received in the wild-life field—experiments directed toward learning the needs of a particular animal or group of animals. Having a restricted point of view, it is to be expected that recommendations founded upon this type of investigations would conflict with other interests. However, where game is the primary crop, the major interest, the game management recommendations should generally prevail. This is intensive game management, where the objective is to produce the greatest possible number of the desired game species almost regardless of other values, as on game preserves.

Extensive game management may be practiced where one or more game species are desired in reasonable numbers along with other products and values that are of primary interest. This type of operation implies merely the modification in favor of game of the practices used to produce the paramount crops, and possibly the addition of some simple practices especially for the benefit of game. By far the most of grouse management will be in this category.

It must be recognized that the distinction between intensive and extensive management is not always great. There is a complete series of intermediate degrees, meeting at the point where game and one or more other products are of equal value as primary crops.

Ruffed grouse management, like most practical game management, must be largely of the extensive type for economic reasons. Intensive management for grouse will largely be demonstrational on public lands (as Connecticut Hill is) or on estates where the value attached to each grouse is very high.

To emphasize this point let us consider for a moment the economics of grouse production. To paint the best possible picture, let us assume optimum conditions. The highest shooting season population possible is about a grouse to each two acres of cover (we will assume that only woodland and brush areas are considered). The maximum possible safe kill is fifty per cent (and this only on the assumption that winter losses are negligible), or the bagging of one grouse for every four acres. If we assign a value of $2 for a grouse brought to bag, we have a return of 50¢ an acre. The investment value of these lands may average around $10 per acre (from $4 or less per acre for "skinned" and worn-out areas to very high values for mature timber stands). The gross return from grouse would, therefore, be about five per cent. This just about covers the interest on the investment, but with no margin for development, maintenance, taxes, or management costs. And no profit.

Moreover, such a return never would be attained. Even in the best range the birds do not attain the production quoted, year after year. There will always be considerable winter loss, hence the kill in fall should be kept below fifty per cent. The desired kill will not be returned from some coverts as it is not possible to hunt an area uniformly. Counterbalancing some of these factors, it may be contended that $2 is too low for the value of a grouse. Well then, how much is a bird worth? If one values a bagged grouse much over $2 he is placing a high money value on the recreation enjoyed in pursuing it. This is the condition I have already referred to as justifying intensive management. But this will hardly be of interest to the run-of-the-mill, "one-gallus" hunter, or to the average landowner.

Thus, most grouse management must of necessity be of the extensive type. This will be true on public lands if for no other reason than limitations of funds. It will also be true of private lands with the exception of some estates. The economics of grouse production on private lands is further complicated through most lands in grouse range being open to free public hunting, so that the landowner does not get the full return that our discussion of economics assumed.

DEVELOPMENT OF HABITAT

The foundation of grouse production is the habitat. Hence manipulation of the habitat is the core of management. In discussing the various methods of developing and handling grouse habitat, the recommendations will be directed specifically at producing grouse, but correlations with other interests will be indicated. The degree of application will be suggested with all land management objectives in mind so that it may be thoroughly practical.

In considering measures that may be used for the improvement of grouse range let us assume that we are talking about a certain type of range. The principles that are found to be good for this set of conditions may be modified for other situations as needed.

Let us assume the land to be privately owned, in a hilly farming area where the woodlands are on the back of the farms, overlying property lines in masses of several hundred acres. The owner accepts the concept of "multiple use," as to game and forest crops and he desires to handle his woodlands so as to give the fullest measure of economic returns and social benefits. Being interested in birds as well as trees, he is perfectly willing to concede the use of certain small areas for brush cover, to keep his woods roads brushed out a bit more than is ordinarily done, or to plant some shrubs—whatever reasonable things the job requires.

WOODLAND PROTECTION

The first essential of woodland management is the protection of existing values. Four types of protection are most commonly needed; two of these being cared for by proper silviculture. Most important and most commonly lacking in many parts of the range are the exclusion of domestic livestock and prevention of uncontrolled fire (see Plate 41). The other destructive elements are insects and disease organisms. The control of these infestations is a part of the silvicultural handling of improvement and harvest cuttings.

We have already noted that livestock are incompatible with woodland preservation. The obvious remedy is to confine the animals to their pastures by adequate fencing. To some farmers this seems to be economically unfeasible, especially if the stock are sheep, which

require a rather expensive woven-wire type of fence to hold them. Surely, most farmers would not consider this fencing justifiable only for improvement of the woodland for grouse. Fortunately, under almost all conditions in the northeastern country, many other values combine to make fencing between woods and pasture feasible. The continued production of wood products of all kinds definitely requires that grazing be kept out in order that ground cover and reproduction of trees remain normal and healthy. Watershed protection is greatly enhanced by ungrazed woodlands in which the forest floor is much more absorptive than in those trampled by stock. Lastly, and most telling from the point of view of the farmer, it is usually true that domestic livestock lose more than they gain from woodland grazing. Poor forage and excessive exercise, combined with increased difficulties of control, make woodland pasturing a losing proposition.

Occasionally wild herbivores, usually white-tailed deer in the Northeast, may overbrowse the range with essentially the same results as with domestic stock. The solution, however, is vastly different. Adequate seasons, bag limits, and hunters to reduce the herd below the carrying capacity level can solve the problem in a single shooting season, provided the public is not so oversold on the buck-law principle as to refuse to allow the killing of does. After all, correlating the kill to the production is merely a form of sustained yield management.

The status of fire in woodlands in the Northeast is clear. All precautions should be taken to prevent the occurrence of accidentally man-set fires, and adequate provision should be provided for the efficient control of fires set by lightning, or made by man for legitimate purposes. This principle does not in any way invalidate the proper use of fire.

In extensive forest areas, often containing a high proportion of public land, the setting of fires is most often by recreationists. Control is nowadays well organized in these areas and large areas are seldom burned. Adequate trails for transportation, lookouts, telephone and radio equipment, and other fire-spotting and fighting facilities are generally well organized. In the noncontinuous range the problem is different. Fires are most commonly the result of field and hedge-row burning in connection with farm or road-maintenance work. Control facilities are few and not so well organized. But the

human population is denser and transportation facilities are good, so that in these instances, too, fires do not ordinarily damage very large areas. Farmers should be particularly careful with fires to prevent such escapes. Burning of fields and hedge-rows is misdirected effort and should be discouraged. And, of course, any use of fire in the woods itself should be attended by the greatest care.

In some parts of the country where fires are most prevalent in farming lands, especially in the Appalachian oak and oak-pine areas, the use of cleared lanes for fire control is justified. The greatest need in that section is for a change of habit on the part of the residents with respect to burning the land. They should be taught and shown that it does not pay.

IMPROVEMENT OF WOODLAND COVER

In forestry, the systematic tending of woodland is known as silviculture. If the objective, or one of the objectives, is a crop of grouse, and improvement work is directed partially toward that end, it is still essentially silviculture, although some wild-life men, fearing a confusion with timber culture, prefer to use other terms, such as fericulture, game management, etc. The attempt to substitute other terms implies separation from woods culture for wood products, and such separation is not only undesirable but impossible.

"The ideal woodland for wild life . . . will be an uneven aged stand, predominately second growth and immature . . . a mixed woods of both hardwood and conifers. . . . It is well to maintain a scattering of all species native of the type. . . . All shelter and food types needed . . . must exist within the area covered by an individual of the species" (Edminster, 1941). This is in general consistent with sound timber management, in that we need stands of all ages to insure a continuing harvest and the inclusion of many species for diversity of products. The degree to which the needs of trees for wood products agree with those of grouse will, however, depend considerably upon local markets, for markets are vital in deciding what the crop plants should be. But market and other problems merely modify the general forestry principle that a good woodland is well-balanced with respect to both age classes and species composition.

Determination of silvicultural practices to be followed in any

given woodland first requires an analysis of the existing situation. From the standpoint of grouse needs, the two primary considerations are shelter and food. Other requirements must be fitted into the framework of these basic facilities. These must be evaluated with respect to quantity (*i.e.*, extent), quality, and arrangement (*i.e.*, interspersion). Varying needs of the different seasons must all be cared for. To illustrate, let us plan the development of a unit of grouse cover; a hypothetical cover entity which provides all the needs for a single grouse population group—a breeding pair in spring and its subsequent production through the summer, fall, and winter seasons, or any multiple of such a group occurring on the unit. Of course this hypothetical area is useful only as a standard; it never actually exists, nor is it feasible to attempt to reproduce it in existing cover. It merely serves as a pattern by which we may evaluate deficiencies in actual habitat and plan for improvement measures.

A unit of grouse cover is shown diagrammatically in Figure 16. Two basic variations are shown: the square unit, here measured as twenty-five acres, which is most useful in analyzing cover that has many and irregularly-shaped cover type subdivisions; and the parallel strip unit of indefinite length, for application to extensive coverts.

These cover unit diagrams indicate several basic needs: (1) All seasonal cover requirements are included (conifers for shelter needs; hardwoods for nesting and winter food; brushy areas of cut-over or overgrown land for summer and fall food; open areas to make edges); (2) proportions of basic seasonal cover needs are indicated; (3) interspersion of types is idealized. Cover composition, controlling quality of shelter and food conditions, is not included; quantity and arrangement are.

In analyzing an actual area of grouse range we may consider the quantity and arrangement elements first, the quality problem later. First we must determine what cover types exist, and where. This can well be done by making a map.[1] If aerial photographs are available (as they are for most of the Northeast today—inquire of the nearest office of the Agricultural Adjustment Administration or Soil Conservation Service), these are very useful for this purpose. Other-

[1] For a detailed method of mapping forest areas for wild-life management, see Webb (1942).

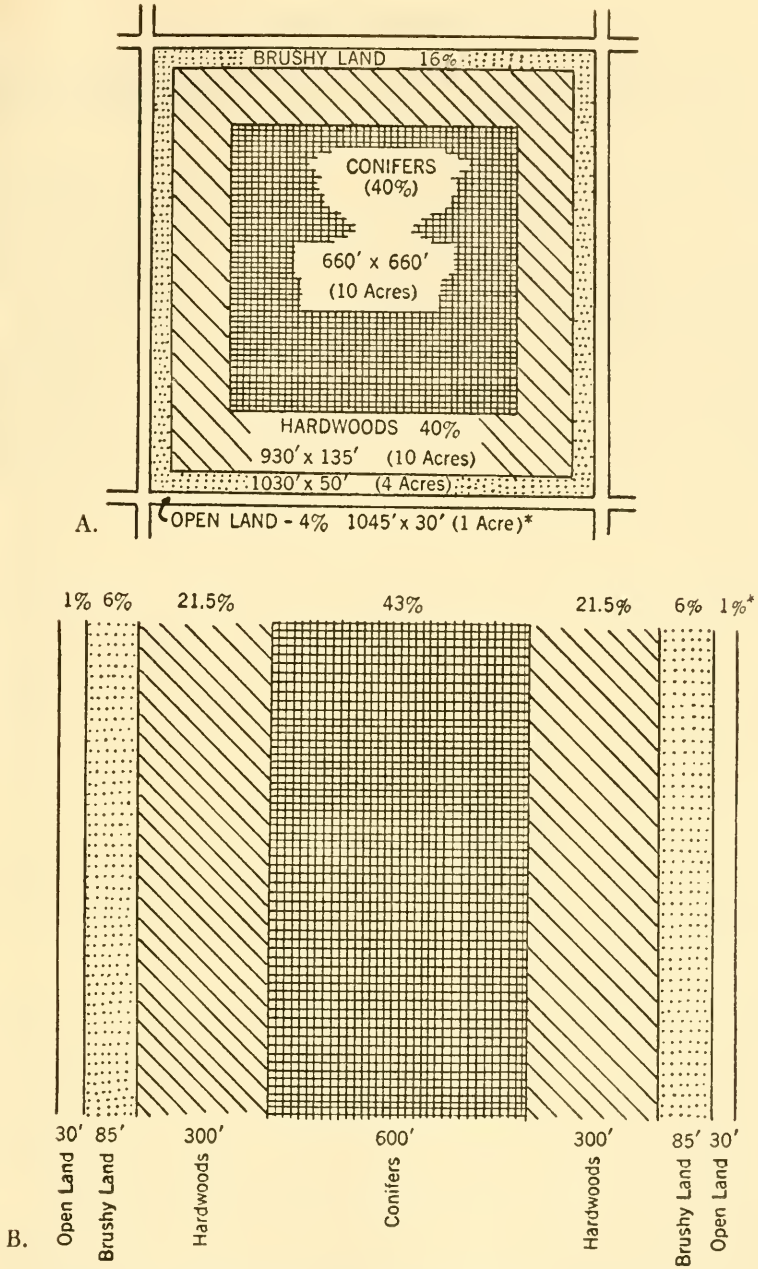

FIG. 16. Hypothetical Unit of Grouse Cover. A. Square Unit of 25 Acres. B. Linear Unit of Parallel Strips, 1400 Feet Wide.

* Only half the open land indicated is counted in a single "unit," since each serves two adjacent units. This "open land" may sometimes be part of a slashing which is often recut.

wise a sketch map may be made by compass and pace measurement, or by plane-table, according to the facilities and abilities of the individual.

Upon measuring the amounts of the five basic cover types (see page 63):—predominantly conifers; mixed woods; predominantly hardwoods; brushy areas; and open fields or lanes—the excesses and deficiencies may be gauged. A balance between conifers and hardwood woods with from thirty to fifty per cent of each element is very desirable. A good distribution of brushy edges and openings covering about ten to twenty per cent of the area is very important. Open land is not so important in quantity but is most valuable when available in great length of edge in proportion to cover area. Sometimes cuttings, woods roads, streams, and lakes must substitute for open fields in providing these edges.

In Fig. 17 we have taken an actual area of woodland and have cover mapped it to evaluate the material with which we must work (A), and have applied the principles of Fig. 16 to indicate the changes in cover type arrangement that may expediently be carried out to improve the area for grouse (B). Our area in this case consists of one hundred and ninety-six acres of cover with eleven thousand feet of open field edge, and continues on the south with more woodland cover across the property line. It is twenty-nine per cent overgrown land, located in three large fields; fifty-seven per cent even-aged hardwood stands that are deficient in shelter; and fourteen per cent conifers, mostly in one large piece. There is no slashing since the hardwoods were mostly lumbered thirty to fifty years ago, and there are no mixed woods.

Our plan for adjustment of the cover arrangement and proportions requires several changes. The objectives are an increase in the coniferous element, and a better distribution of shelter and brushy cover. The ratio of open edge to area (feet to acres) of fifty-six is already good. The quantity of overgrown land is too large to maintain, hence a portion will be planned for maturing woodland.

It is not our purpose now to go into the details of the silviculture involved in this particular job, except it may be said that it served both wood production and game. Interplanting of conifers was made in the overgrown fields. A portion of the interior of the big hardwood stand was spot-lumbered for selected wood products and the openings planted to white pine and spruce. Improvement in distribution

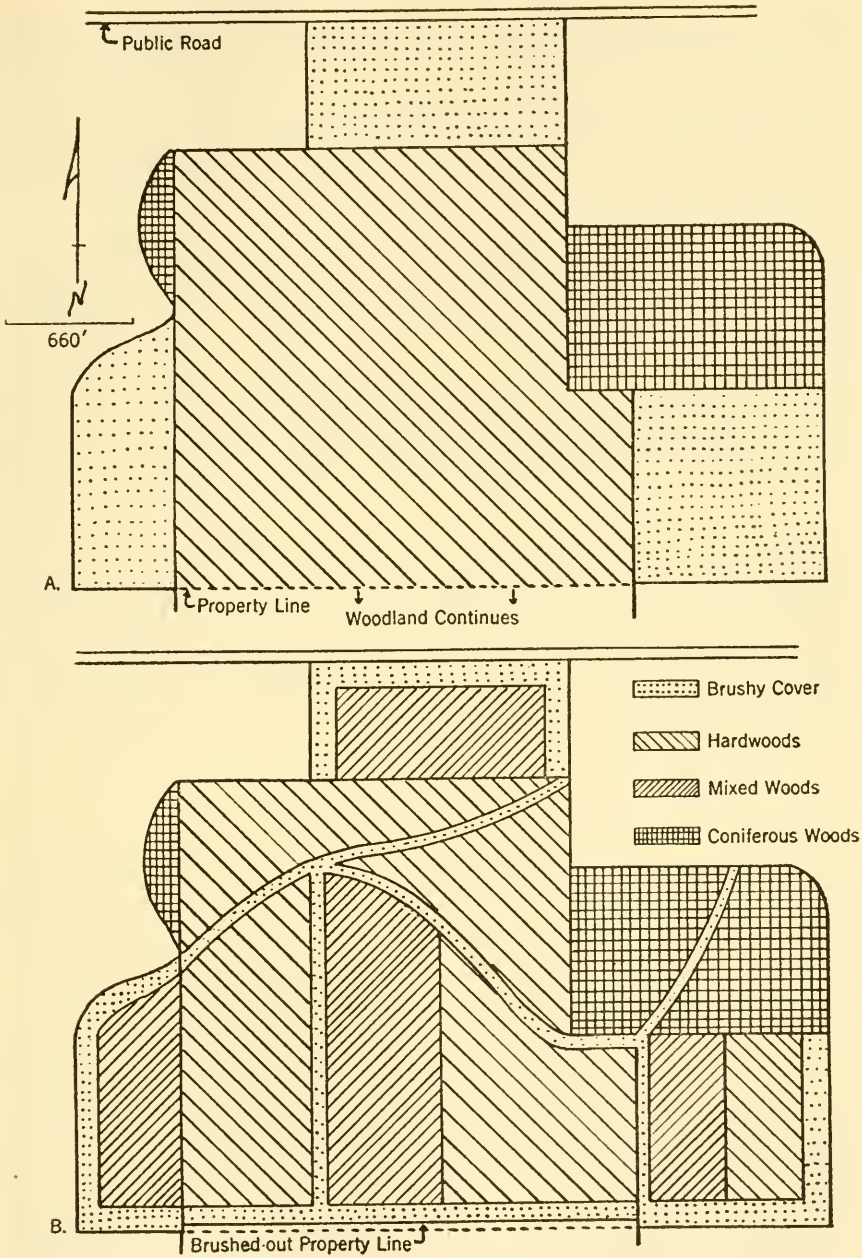

Fig. 17. Plan for Cover Type Changes in a Woodland. A. The Woods before Treatment. B. After Changes are Complete.

of openings and brushy cover was accomplished mainly by maintaining favorably located portions of the overgrown fields, opening up a woods road system, and devoting a narrow strip along each to the production of wood products requiring frequent cutting. Along the south boundary the property line was cleared as a part of the road system.

As a result of these changes we find that the proportions as well as the arrangement of the cover types have changed materially. Brushy cover has dropped to nineteen per cent but is much better scattered; hardwood stands have decreased to forty-two per cent, while conifers are finally only thirteen per cent. The great improvement in shelter came by the change to the mixed woods type, now composing twenty-six per cent of the area. This, with the stands of evergreens, makes a total of thirty-nine per cent of adequate shelter.

One of the best indexes of improved conditions for grouse is the increase in interior edge between cover types (only one side of woods road openings are counted). In this case we had fifty-eight thousand feet of interior type edge at the start, and at the completion of the change two hundred and one thousand feet, an increase of three hundred and forty-six per cent.

INTERPLANTING OF CONIFERS

Changes in the woodland are ordinarily brought about by removing trees and planting trees. The former is generally the more important. Planting within a woodland is often unsatisfactory, and is definitely limited in application. When extensive hardwood areas exist that are seriously deficient in shelter, the underplanting or interplanting of tolerant conifers may be advisable. Areas of open land abandoned and overgrown with natural reproduction of hardwoods may often be interplanted to advantage with conifers (see Plate 42). The need for that type of improvement must be judged in the light of the probability of natural regeneration of these species. If seed trees of desirable species are lacking, there is little likelihood of natural establishment in the predictable future. In such areas planting is necessary if coniferous shelter is to be had.

So far as practicable, plantings should be confined to open areas, *i.e.*, fields in herbaceous cover, or sparse, young, woody reproduc-

tion. But cases are common where there is little opportunity for open land plantings, or even if there is such opportunity the range is still largely deficient in shelter. In these cases interplanting is the only solution. Both game shelter and the diversity of wood products are thereby improved.

Full advantage should be taken of existing crown openings in which to plant. Here the young seedlings will have the most sunlight. Additional planting areas should be prepared by making openings in the crown through removal of large-crowned "wolf" trees, group selection cutting, or small clear cuttings. So far as possible this should be accomplished by making cuttings of marketable materials in places that suit the needs of the wood harvest plan. Planting should be made in the spring immediately following the cutting. Plantings are not recommended under a full-canopied woods.

Species of conifers for this use should be quite shade-tolerant. Best in the Northeast for this purpose are the spruces (Norway, white, or red), white cedar, and white pine. If the openings are fairly large and the anticipated competition from hardwoods not severe, balsam fir, red pine, Banks pine or other adaptable species may be used. Spacing of plants should be the standard plantation spacing, five to eight feet apart. The stock should be the best quality available, with an even balance of roots and top. This is generally a four-year-old transplant (known to foresters as a 2-2 plant, indicating two years in a seedling bed, followed by two years in a transplant line) if white pine, white cedar or spruce are used, or a three-year seedling of the other species. Most state, federal, and commercial nurseries handle these grades.

IMPROVEMENT OF SHELTER BY CUTTINGS

The improvement of shelter in pure hardwood stands as suggested above requires considerable time. Even when the best of planting stock is used and the soil is adapted to conifers it will be five to ten years before their shelter will be of much value. In the interim, temporary improvement may be gained through cuttings of the type which foresters call "cleanings." Two methods may be used. One is to half-cut small trees that are not needed for wood products. By cutting each tree enough to cause it to fall to the ground, yet leaving

some continuous bark and sapwood between top and stump, the top will remain alive and produce a leaf crop. Being close to the ground, these tops improve shelter for birds. Certain species are better than others—as oaks (particularly pin oaks) and beech—since they hold a part of their dead leaves on the tree through the winter. The second method is simply clear-cutting units big enough to open the crown. Species that coppice abundantly are best. Beech, oaks, and the maples are all good. In about two years the sprouts will have created considerable thick cover. Brambles, pin cherry or aspen may come in quickly to add to the cover. The waste tops and branches may be thrown over a few high-cut stumps in large loose piles (see Plate 43). The result is a thicket of the slashing type which has considerably more shelter value than the open hardwoods. By the time these temporary values are lost, the conifer plantings are beginning to be effective.

In stands that possess a scattering of conifers, improvement in shelter value may often be brought about by careful cutting. If the few conifers are old trees, a heavy seed crop may often be induced by girdling a few of them in the spring. Hemlocks seem to be particularly adept at producing a swan-song crop of seed, the final contribution of a dying matriarch. When the conifers are very small their growth may be speeded by a light release cutting—just enough of the surrounding plants removed to give the seedlings a little direct sunlight. This practice is most effective with the native pines and spruces. Caution should be exercised in this type of release cutting for shelter, as it must be remembered that we wish the evergreen branches to remain alive close to the ground. We do not wish them to grow high and less useful as shelter too quickly. Hemlock and spruce in particular should not be released once they are big enough to furnish cover above the winter snows. They should be allowed to remain under a canopy in order to retain their shelter values as long as possible.

We must continually remember that for grouse the best winter shelter is furnished by the evergreen woody plants, primarily the conifers in the Northeast. From Pennsylvania and southeastern New York southward the mountain laurel and rhododendron often make a fair substitute when the pines and hemlock are absent. Even among the conifers some are better than others. By species, the hemlock is clearly best, the spruces and white pine next, then balsam fir,

red pine, arborvitae, red cedar, and the hard pines follow in about that order. In respect to age and size, the best winter cover is made by an all-age stand in which young trees with low-hanging branches are protected by other trees with sturdy boles. When the younger trees are absent, the shelter is entirely up in the air and much less useful. This condition often results from an overstocked stand in which the lower branches soon die. Some of the pines, in particular, are apt to develop this way. The solution is to thin the stand as it ages in order to allow some light to reach through to the ground. This may be accomplished by the orderly development of the crop trees and the marketing of the small material for Christmas trees, pulpwood, etc. The trees along the edges of the conifer clumps or stands often are limby and of poor form for timber use because of the extra light on the open side. They may well be allowed to remain until mature for their game shelter value.

IMPROVEMENT OF FOOD BY CUTTINGS

While it is generally true that any grouse range meeting the shelter needs of grouse will probably have an adequate food supply for a fairly good population, the food problem must not be overlooked. Most woods possess considerable grouse food at certain seasons, but many are seriously deficient in the food requirements for all the seasons.

Protection from domestic livestock is fundamental to a good food supply. Without it the succulent herbaceous vegetation in the ground cover will be destroyed. The second need in providing for this vitally important phase of the woodland association is a moderate crown density over much of the area—sixty to eighty per cent of the ground shaded at midday. This condition is easily maintained by selective cutting of crop trees and by needed thinnings or weedings. Thirdly, a well-balanced association as to species aids in producing variety in the ground cover. Contrarily, single species stands often have a poor understory.

The importance of the ground cover plants to the grouse is often overlooked in considering woodland management, particularly since direct control of these plants often seems impossible. Actually, they may be controlled by adjustments in the tree cover. In our discussion of the grouse foods it was noted that eight of the first twenty-

five year-round important foods belong to the woodland ground cover association, namely: sedges (*Carex*); bunchberry (*Cornus canadensis*); strawberry (*Fragaria*); wintergreen (*Gaultheria*); Canada mayflower (*Maianthemum*); partridgeberry (*Mitchella*); ferns (*Polypodiaciae*); and sheep sorrel (*Rumex*). Among the forty-one genera of secondary food plants, twenty-one are in the ground cover association, mostly in the woodland understory. Protection from fire and grazing plus a controlled crown density are the management measures needed to maintain a supply of these important foods.

A considerable part of the grouse's food comes from shrubs. Like the ground floor herbaceous plants, shrubs in the understory of a woodland must be managed by controlling the light conditions at the canopy. Protection from grazing is quite essential for a satisfactory shrub stand, since many of these plants are eaten by cattle. The same sixty to eighty per cent crown canopy recommended for stimulating the ground cover is suggested for shrub development. But, while shrubs are an important element in the whole woodland plant association, they serve best as food when along the woodland edges and in openings in the woods (see Plate 43B). It is here that their fruiting is best and the production of buds most abundant.

Among the twenty-five primary food-producing genera, eleven are predominantly shrubs or vines. The shrubs include most of the dogwoods (*Cornus*), the hazelnuts (*Corylus*), hawthorns (*Crataegus*), laurels (*Kalmia*), sumacs (*Rhus*), roses (*Rosa*), brambles (*Rubus*), blueberries (*Vaccinium*), and the viburnums (*Viburnum*). The vines include poison ivy (*Rhus toxicodendron*), greenbrier (*Smilax*), and grape (*Vitis*). Of the forty-one genera of plants of secondary value, thirteen are shrubs or vines.

The mountain laurel, flowering dogwood, and some of the blueberries and viburnums are prevalent in the woodland understory. The others are predominantly found along the edges and in openings. All fruit best where they receive plenty of sunlight. It is advisable then to develop shrubs mainly along the woodland borders and in woodland clearings or lanes.

ESTABLISHING WOODLAND SHRUB BORDERS

A shrub border between the woodland proper and an open field is a logical conservation development on farms. In addition to its wild-

life value the border of shrubs affords protection to the woods from drying and damaging winds. It benefits the field crops by keeping the trees far enough away to avoid root competition for moisture and plant food, and the shading of tall trees. The width of such a shrub border must necessarily depend upon the desires and needs of the individual owner. A minimum of about twenty-five feet is needed to maintain the association and to provide a gradual increase in height growth from the low outside shrubs next to the open field to the trees of the woodland proper. On large units of land managed for timber and game these shrub borders may well be fifty or more feet in width.

Two methods may be used to develop such a border: planting the desired species in the open field edges; or cutting out the trees from the forest border (see Plate 44). The planting problem will be taken up later when we discuss development of open lands.

Ordinarily there are enough shrub seeds and seedlings available in a woodland edge to take over the strip when the trees are removed. If this is not true, they may be established by planting. It is suggested that no planting be done for at least two years after cutting in order to give full opportunity for germination of dormant seeds.

Elimination of the trees is accomplished by cutting. All classes should be removed or girdled. Many will sprout abundantly and these will have to be cut back each summer until their vitality is lost. This may take several cuttings, but in the interim the shrubs are assuming dominance of the stand.

USE OF POISON IN ESTABLISHING SHRUB BORDERS

Those who may wish to avoid the repeated cutting necessary to eliminate the hardwood trees from the borders where shrubs are wanted may wish to kill them completely the first year by use of poison. Sodium arsenite or white arsenite has proved satisfactory for this purpose. The solution is made by mixing the chemical powder with water. From one and a half pounds to three pounds of poison, or even more, for each gallon of water may be used. The stronger the solution the more quick and sure will be its killing effect. Since some species are more resistant than others, and larger trees more resistant than smaller ones, it is best to begin with a weak solution and strengthen it as the results indicate the need. It is also advisable

to add caustic soda (lye) to the solution in the ratio of one pound to each four pounds of the poison. The solution may be kept in a corked container until used up. Full respect should be paid to its properties as a poison to animals as well as plants.

The poison solution is applied to cuts made around the base of the tree at six-inch intervals. The cut should go well into the sapwood, and about a thimbleful or teaspoonful of poison solution applied in each. The best season for this work is late summer.

An ordinary ax and oil can may be used for applying the poison solution, but special tools are available for those who plan to do very much of it. The "Cornell tree killing tool" is made by the Ireland Machine & Foundry Co., Norwich, N. Y. This instrument makes the cut and applies the poison in one motion. However, it operates with a valve that must be kept clean and pliable. The Council Tool Co., Wananish, N. C., makes a special ax for tree poisoning which is used in conjunction with an oil can applicator.

It is recommended that the poisoned trees not be removed until completely dead. And again it should be warned that containers of this poison should not be accessible to animals or left where children might find them.

SHRUBS ALONG THE WOODS ROAD

The association of shrubs in the woodland interior that is analogous to the shrub border is found only in openings of one sort or another. The simplest way to develop a well-distributed brushy cover is in connection with the woodland road system (see Plate 43B), (page 335). Every woodland needs roads to facilitate the harvest. By keeping them well brushed out, a narrow crown opening is maintained through the woods. If more effort can be afforded here for the improvement of game cover, these road openings may be widened to thirty feet or even more. This is the easiest way of making a little work go a long way in creating openings in the woods. Experience indicates that an open lane, thirty feet wide, makes a good set of edges and admits plenty of light for the development of shrub cover. It is desirable to keep the road in the center of the lane, or on the shady side.

Small openings in the woods may be made in connection with various types of wood product cuttings. Improvement cuttings made

by the removal of large-crowned "wolf" trees leave scattered small clearings which quickly develop into thickets of brambles, shrubs, and sprouts. Where two or three such trees are removed close together, an opening results that will be particularly valuable to grouse as a feeding area. When removing large, badly formed trees, caution should be used not to take good den trees, *i.e.*, those with well-developed hollows in the trunk or major branches. The squirrels, owls, and raccoons that a good den tree may support are worth far more than its wood value. At least two per acre should be left if they are available.

The group selection system of woodland harvest is conducive to the improvement of food conditions in the woodland. Instead of choosing crop trees singly, they are taken in small groups of three to eight or ten (see Plate 45). When the group of trees removed is small—up to about a quarter of an acre—the result is a woods with many small glades. When the groups are larger—up to an acre or more in size—the woodland is broken up with numerous small clear-cuttings or slashings. These provide good grouse food conditions.

The two conditions most to be avoided are extensive clear-cuttings and the opposite extreme of no cutting at all.

So far emphasis has been placed on the use of woodland-management methods for wood product harvest that will provide the best distribution of openings and brushy cover. This is the most economical and practical method of improving and maintaining grouse cover, and little or nothing need be charged to grouse management. If more idealized grouse cover is desired, a deliberate system of cuttings for game management may be undertaken. Such cuttings will seldom return their cost, for the added increment of grouse and other game to the woodland income will not suffice. In circumstances where the economics of cuttings for game management do warrant it, a system of game clearings may be made.

CLEARINGS FOR FOOD AND COVER IMPROVEMENT

Studies have shown that grouse seldom penetrate a uniform woodland cover more than three hundred feet from an edge having some brushy or open cover (Edminster, 1935). A plan for proper distribution of edges and clear-cuttings should thus provide that such units be within six hundred feet apart to provide for full use by grouse of

the intervening cover (Edminster, 1934). Slashings (used here to mean small clear-cut units) cut specifically to improve the grouse habitat provide better food conditions by permitting sunlight to reach the ground and develop a suitable herbaceous and shrubby cover (see Plate 46). As has already been noted, such cuttings may also improve shelter conditions in areas deficient in conifers or other evergreens. They may be handled in a system of units cut in rotation.

In planning the location for a system of game slashings, the determining factors to be observed are: (1) Space the units about six hundred feet apart, or from natural openings, for ideal distribution. (2) Cuttings are best when next to two or more other types of cover. (3) Sites with good fertility will grow a good bushy vegetation cover quickly, while the poorer soils will return to woodland slowly. Therefore the units in the poorer soils will require less upkeep cost. (4) Where possible they should be located conveniently to the woods road system in such manner that the wood products may be removed on skid trails running along the contour, thereby reducing erosion. (5) Steep slopes should be avoided.

The units should be no larger than necessary to accomplish the objective. One-quarter acre to one acre is usually adequate. The cutting of the unit should be done so as to take advantage of the natural features of the area. Avoid clumps of conifers but cut the margin close to them. Leave seed trees of good food and shelter species. Make the shape irregular, thereby providing more edge.

The maintenance of such a system of openings may be accomplished by the repeated cutting back of the area. This eliminates a useful wood crop after the first cutting. An alternative is to allow each unit to grow into cordwood before cutting, and rotate in a series with other contiguous units. The latter method requires more area to be devoted to this use, but it is better forestry practice. Each unit is cut at the pole stage, usually twenty to thirty years old. The cutting time of the several units is staggered five to ten years apart so that the series consumes the entire rotation period. The length of usefulness of a game clearing depends upon the fertility of the site and upon the species that prevailed before cutting. Generally a fertile site will lose its opening value in about eight to ten years; poor soil sites last longer. The best gauge is the vegetation itself. When the brambles, pin cherry, and similar pioneer plants are eliminated, the site is no longer of much value as a summer-fall food area.

In making game clearings it is well to follow the general rules of forest cover improvement, and remove the trees of least value and retain the best. Since we wish to keep a few mature trees in any clear-cutting, these should be selected from the best shelter and food species. As a general thing, if the cutting is in a stand predominantly hardwood, favor the conifers, and vice versa.

When the usable wood products are removed from the cut-over area, most of the slash may be disposed of by piling and then burning, preferably on snow. Some of the slash piles may be permitted to remain as shelter for rabbits and grouse, say three or four piles per acre. The burning will serve to stimulate the germination of certain plants, thus adding variety to the cover. Among those commonly taking over burns are the blueberries, scrub oak, and pin cherry. Where burning is too hazardous, the surplus tops may be lopped and scattered over the ground.

SELECTIVE CUTTING TO IMPROVE FOOD CONDITIONS IN THE WHOLE WOODS

If a woodland is being managed on a selective cutting basis, the crop trees in an uneven-aged stand being removed when mature, it is desirable to give some attention to the species that are important in furnishing grouse food. These are mainly certain of the hardwood trees and they are primarily important as food sources in the winter and early spring.

Unfortunately, many of the important trees that furnish these foods are considered weeds by many foresters because they are unimportant in the present-day lumber market. Seven tree species are among the twenty-five primary food producers, and seven more are in the group of forty-two secondary food sources. Among these more important ones, beech, oak, apple, and cherry furnish nuts and fruit; the birches, poplars, apple, hophornbeam, and cherries supply buds. Only the oaks are consistently regarded as "crop" trees for a woodland harvest. In some areas black cherry is made into lumber and the poplars are used for pulp. The rest are merely tolerated or are often "persecuted" by those who have visions of forests of pure lumber. Apple, of course, is an exception since it is not a woodland tree.

However, the concept of forests composed exclusively of the bet-

ter hardwood lumber species is impractical. There is a need for variety in the woodland, if for no other reason than as insurance against excessive insect or disease loss. A woodland composed of trees of all ages will contain many "filler" trees, those that are not intended for ultimate timber harvest but are needed to maintain the stand density as the crop trees mature. Much of this filler stand will be used only for cordwood, and may as well as not be good grouse food species.

I recall a recent visit to a forest being managed by a young professional forester who was anxious to develop a game crop as well as wood products. In some of his improvement cuttings he had removed hophornbeam and beech in favor of elm and white birch. In fact, he had planned to eliminate the hophornbeam as completely as possible, seeing no use for it. It was pointed out that the beech and hophornbeam were as good as the others for fillers and were much more useful as winter food for grouse. He immediately adjusted his cutting plan in this detail.

It should be particularly noted that those woodland tree species that produce fruit or nuts, as the oaks, beech, and black cherry, require much sunlight to seed properly. If they are crowded their crops will be small or wholly lacking. Releasing them from the competition of adjacent trees helps by allowing their tops to develop in the open crown. If the trees to be cut in the release are of no value they can merely be girdled with satisfactory results.

When one is concerned with a typical woodland of the Northeast, say of the beech-birch-maple-hemlock association, where there is plenty of opportunity for species selection in improvement cuttings or thinnings, the question arises as to how many good bud-producing trees are needed to support a satisfactory population of grouse through the winter. Theoretically this could be computed mathematically if we knew the average number of buds per tree in a balanced woodland, the daily consumption of buds per grouse, and the proportion of buds a tree may lose without serious damage. The result would actually be conservative, for the birds do not feed evenly over the whole woods. In portions in, or next to, good conifer shelter the consumption would, no doubt, exceed the average rate, and in areas remote from coniferous or brush cover, use would be low. The application of the principle is obviously most important in hardwood stands close to other cover, particularly coniferous

types. On the basis of an average daily requirement of four hundred buds over a fourth-month intensive budding season, a stand of a grouse per four acres would consume twelve thousand buds per acre per season. If we assume a fifty per cent safe removal of buds from the trees, and add another twenty-five per cent safety factor to cover the additional birds that survive for only a part of the winter, an annual requirement of thirty thousand buds per acre results. This need can be met with a minimum of three trees per acre of average submature size. They should be of the better buds species, particularly the following: apple, birches (except gray), cherries, hophornbeam, and popples.

So far we have developed the silvicultural practices for game management on the basis of furnishing shelter and food. While these are the primary facilities of the environment, and provide a handy objective for the discussion of management measures, they are by no means the birds' entire needs. In discussing silvicultural practices it has been rather essential to consider the details of cover. It is also necessary to fit these practices into the creation of suitable range in a broader sense. The characteristics of the land cover must exist in a well-interspersed arrangement of all the major cover types: hardwoods, conifers, brushland, and open edges. We must not lose sight of the cover type pattern while dealing with individual trees.

PROVISION OF DRUMMING AND DUSTING PLACES

Among the needs of grouse are suitable drumming and dusting places. In most good grouse range these needs are well met without particular attention by man. But many woodland areas definitely lack one or the other, and here it is well to give attention to these requirements. If the woodland floor does not have a scattering of old, large-diameter logs lying around, or moss-covered boulders, it is advisable to leave lying a few butt logs from "wolf" trees, logs that are of little or no value as a wood product.

Dusting spots are furnished either by exposed dry mineral soil or by dry rotted wood at old logs or stumps. If these are lacking, the turning up of mineral soil every few hundred feet along the woods roads or burning brush piles will aid in providing dust bathing facilities.

PLANTINGS AND SEEDINGS

The pioneers who cleared the land for farming in the Northeast opened up some lands that were physically unable to sustain cultivation or grazing, with the result that many thousands of acres had to be abandoned when they no longer could be economically farmed. Exploitive use and changing economic conditions caused other farms to become submarginal to profitable agriculture. Many of these lands are coming into government ownership, either through purchase or tax delinquency. The proper use for most of these areas

TABLE 11. IMPORTANT SITE REQUIREMENTS OF TREES AND SHRUBS FOR PLANTATIONS

Species	*Moisture tolerance* [1]	*Fertility requirement* [2]	*Geographical range* [3]
Conifers:			
Norway spruce	Well-drained	Low	All except coastal plains—Pa., N. J., and north
Red spruce	Well-drained	Low	Except coastal plain
Red pine	Dry or well-drained	Low	All except coastal plain and low altitudes south of Pa.
White pine	Dry to moist	Low	All except coastal plain
Arborvitae	Well-drained to moist	Moderate	All except coastal plain
Hardwoods:			
Red maple	Well-drained to moist	Moderate	Entire region
Sugar maple	Dry to well-drained	Moderate	Entire region
Black cherry	Dry to well-drained	Low	All except northern Maine
White oak	Well-drained	Moderate	All except northern New England
Red oak	Well-drained	Moderate	All except northern New England

[1] Moisture tolerance is rated as: *dry*, if adapted to a soil that normally becomes crumbly moistureless in dry season; *well-drained* if the soil holds enough moisture in dry seasons to maintain adherence of particles when squeezed; *moist* if the soil drips when squeezed even in dry season.

[2] Fertility requirement is rated as: *low* if species will tolerate almost complete loss of topsoil; *moderate* if considerable good topsoil is required for satisfactory growth.

[3] The range covered here is from Virginia and West Virginia northward to New York and Maine, including adjacent portions of Canada.

Shrubs & Vines:			
Bittersweet	Well-drained	Moderate	Entire region
Silky dogwood	Well-drained to moist	Low	All except northern New England
Flowering dogwood	Dry to well-drained	Moderate	Mass. to central New York and southward
Graystem dogwood	Dry to well-drained	Low	All except Maine and coastal plain
Hazelnut	Dry to well-drained	Moderate	All except northern New England
Hawthorn	Dry to well-drained	Low	All except coastal plain
Apple and crabapple	Dry to well-drained	Moderate	Entire region
Bayberry	Dry to well-drained	Low	Entire region
Virginia creeper	Well-drained	Moderate	Mass. to central N. Y. and southward
Bear oak	Well-drained	Low	Mass. to central N. Y. and southward
Dwarf sumac	Dry to well-drained	Low	All except northern New England
Staghorn sumac	Dry to well-drained	Low	Entire region
Swamp rose	Dry to well-drained	Low	All except northern Maine
Mountain ash	Dry to well-drained	Moderate	All except coastal plain
Nannyberry	Dry to well-drained	Moderate	All except coastal plain
Blackhaw	Dry to well-drained	Moderate	Mass. to central N. Y. and southward
Highbush cranberry	Well-drained to moist	Moderate	All except coastal plain
Fox grape	Dry to well-drained	Moderate	All except coastal plain
Riverbank grape	Well-drained to moist	Moderate	All except coastal plain

seems to be to keep them in woodland, hence the former croplands and pastures present a problem in revegetation.

The same condition of unproductiveness from overuse is found on parts of many farms that are, in their entirety, sound economic units. Whole fields or portions of fields that were inherently unsuited to farming or that have been worn out by farming should be retired to woody vegetation.

In both these cases the problems and principles of revegetation are essentially similar. We will assume for the purposes of this discussion that the area is in grouse range and that grouse produc-

tion is an important objective to be accomplished in connection with planting the land. However, it should be noted that by far the greater opportunity for grouse cover improvement lies with existing woods rather than in plantations.

There are certain basic principles that must be followed in all plantation work. First, the species used should be well adapted to the climatic and site conditions. Most important of site conditions are the level of fertility and degree of dryness of the soil. These requirements for all species recommended for use are summarized in Table 11. When the correlations of range and site are cared for, the next requirement is good planting stock: large and sturdy enough to withstand competition, but not too large to handle easily; well balanced as to root-top ratio; and properly cared for after removal from the nursery. Finally, it should be set in the ground with the roots well spread, and with the root-collar at the ground line. In most planting work a large "scalp" of the sod should be removed (at least twelve inches in diameter) and the plant set in the middle of this area. Still better is a plow furrow every six feet (closer for shrubs), made on the contour. These enable the seedling to make good growth before the competition of herbaceous plants can retard it.

Pattern of Plantations. Plantations may be divided into types according to the nature of the resulting cover. Three types of plantings are needed for grouse: conifers, hardwood trees, and shrubs. These correspond to similar natural stands in furnishing cover and food. The first need in planting for new cover is to correct the deficiencies in existing stands. In the Northeast the most prevalent shortcoming is in coniferous cover. The greater part of the planting area is likely to be conifers for this reason, as well as because several of the conifers are among the most profitable for planting from the forestry standpoint. In many areas there may also be a lack of adequate brushy cover, or overgrown land. Shrub plantings may be made to fill this need.

The positional relationship between the several types in the plantation is of great importance. The outside of the planting area, that is, where it bounds on open field, road, or other opening, should receive the shrubs, thus creating a border. Behind the shrub borders a band of hardwood trees provides good nesting and winter-

feeding cover, while the interior of the unit should be dominantly conifers. This principle may be followed either in a square unit or a parallel band system (see Plate 50). When the planting unit exceeds twenty acres and is quite evenly proportioned in shape, it may be desirable to consider the need of more shrub bands than merely along the outside borders. Areas of forty acres or more may well be planted in two or more units of bands and blocks of shrubs, hardwoods, and conifers.

Integrally related to the pattern of large plantations is the need for open land. So far as possible interior openings may be supplied by roads maintained for transportation of products, administration and patrol, and fire control. These roads through plantations and woodland also serve somewhat as firebreaks and provide an opportunity to improve grouse food conditions. The need for roads of this type depends upon the lack of open-field edges, pond borders, and wide stream margins. When points in the plantation (or woods) are three hundred feet or more from the outside, there is need for open edges in the interior. Six hundred feet apart is as close as these openings are recommended for grouse habitat.

The Coniferous Plantings. Reforestation has been practically synonymous with conifer plantings until very recent years (see Plates 51, 52). The problem of reforesting public land had been attacked almost entirely from the forestry and watershed protection points of view. So habitual had the practice become that it was generally advocated by sportsmen and others interested in wild life. Within the last decade wild-life studies have indicated the limitations of coniferous plantings as desirable cover for game (Edminster, 1935). The principle of edges, so well enunciated by Leopold and other pioneer wild-life ecologists, was gradually clarified as it applied to reforestation work. It was shown that when a uniform type plantation exceeds a certain size, its center becomes a biological desert as far as game is concerned. The distance that a bird or animal will habitually penetrate this cover varies with the different species. Grouse are more tolerant than many. They utilize the outer two hundred-foot band of conifer stand fully, and make considerable use of the next hundred feet. Beyond this it is practically worthless to them. We may then proceed on the basis that a coniferous planting, not exceeding six hundred feet in the narrow dimension, will

be well used by grouse. Fortunately, most plantings will not exceed this size, the exceptions being mainly on public lands.

In planning the coniferous plantings, as well as others, it must be remembered that a mixture of species is desirable. Single-species plantings of any great size are an immense hazard. Just one bad insect infestation and the whole thing may be lost. It's a good example of the old adage of not putting all one's eggs in a single basket. Don't base the future of your plantation on a single species.

The selection of species will be based mainly on the wood products desired. Not only is it a good idea to mix several kinds of conifers in the planting, but it is also good for grouse to have some clumps of hardwoods in the conifer cover. This may be achieved by not planting spots already seeded to hardwoods, by leaving the fail spots that are likely to occur on poor land (seventy per cent survival may be considered a satisfactory establishment if quite evenly distributed), by planting them in scattered clumps of ten to one hundred each, or by leaving such spots unplanted and trusting to natural seeding in places where desirable seed trees are nearby.

Species of conifers best for grouse shelter are hemlock, white pine, red, white, and Norway spruce, red pine, and arborvitae. All are practicable to grow for this use or are purchasable at reasonable prices. Other species may be used to give variety. Where enough of those recommended are not adapted to the conditions, scotch, pitch, jack, and Virginia pine, any of the other spruces, and firs, are suitable.

The Hardwood Plantings. We have suggested that the best arrangement for the planting of hardwoods is in a band between the conifers and the shrub border. This is ideal from the point of view of cover type arrangement, but is, of course, not essential. In large plantings it may be more expedient to plant hardwoods in alternating bands with conifers (see Plate 50). The width of the band, whatever its arrangement with respect to the conifers, should be a hundred feet or more in extensive reforestation work. In that arrangement it will act as a break for crown fires. In small farm plantings of only a few acres, it may be necessary to reduce this dimension to fifty feet or even less, or handle the whole tree arrangement in clumps. In a small planting there may be set out three or more rows

of hardwoods, then a few rows of conifers, and so on, in order to develop a mixed stand. The total proportion of the planting to be given over to hardwoods will depend largely on the need for balancing the existing woods and upon the type of wood products wanted. The end result should be a fair balance between hardwoods and conifers, the two taking eighty to ninety per cent of the area, with the remainder in shrub borders and openings.

Establishment of the hardwoods stand will be guided by existing seed trees and by site conditions. Many of the hardwoods are notoriously difficult to establish on poor sites by planting. As far as possible the better, that is, the more fertile and well-drained soils should be given over to hardwoods. While many hardwood trees are slow and difficult to establish by hand planting, many establish themselves readily by natural seeding or by sprouting. Popples, cherries, ash, maples, and sometimes many others, are often found to be taking over old fields in the Northeast a few years after abandonment. If seed trees of satisfactory species are located within a few hundred feet (or one hundred feet for the more heavily-seeded species), we may count on nature taking care of the hardwood planting for us. Under those conditions, merely refrain from planting conifers where hardwoods are wanted (see Plate 53A). On the other hand, if seed trees of desired species are not close by, the probability of getting a stand of good hardwoods where you want them is remote. Then it is best to plant.

A good mixture of several species is particularly important in the hardwoods planting, both from the standpoint of ecology and from the grouse food needs. Among the more important grouse foods that come from trees, the most practical to establish by planting are: the oaks (particularly white and northern red) (see Plate 54), black cherry, and the maples, both sugar and red. Others may be aided in establishment by planting seeds. A light spot-burning will prepare the ground for the popples and pin cherry, and usually no seeding will be required. The owner of the land will probably be interested in other hardwoods too for their wood products or for their value to other forms of wild life. Black walnut, hickory, butternut, Asiatic chestnut, and oaks may be planted by using the nuts—setting them twice the depth of their own long diameter in the soil. (Here one should be cautious about rodent damage; plant in years of low rodent abundance, or keep away from edges of

existing woods.) Black locust, basswood, ash, tulip and others may well be included in the planting although of little food value to grouse. These should be handled as nursery-grown seedlings, usually one year of age. Occasional clumps of conifers may also well be planted among the hardwoods.

The Shrub Border. The advantages of a border of shrubs along a woodland margin have already been noted. The best way of insuring a good shrub border on new woodlands is to provide for it in the planting (see Plate 53B). This should be arranged on the edges that are to remain next to an open field, road, or other open area.

The width of the border will depend upon the desire of the owner to provide this type of cover. At least twenty-five feet of the border is needed as a matter of good land use between fields and woods. Beyond this minimum any extra width of shrubs is largely a matter of planning for more game food cover. On public lands it may be desirable to plant borders up to a hundred feet in width, using as much as ten or fifteen per cent of the area. Planting of the taller shrubs and small fruit-bearing trees should be at standard five to six foot spacing. These species are most useful in the part of the border next to the forest tree species. Here they will get plenty of light for good fruiting, yet will not be in the way of the lower-growing shrubs. The smaller shrubs may be placed next to the open field and can be planted three to four feet apart. The rows may be the same spacing.

By using lower shrubs on the outside, and slightly higher species in each successive row, we may develop a graduated border that will serve to protect the woods from drying winds, and the crop field or pasture from the shading effects of the high trees and the food and moisture competition of the tree roots.

Since a major purpose of the shrub border is to furnish summer and fall food, we should select shrubs that best serve this use. Those that are among the better grouse foods and are also practical to propagate and plant are listed on the next page. As a general rule it is well to use at least four species in each border. Most successful of these species for planting are bittersweet, swamp rose, silky dogwood, graystem dogwood, hazelnut, bayberry, nannyberry, blackhaw, and highbush cranberry.

Low shrubs and vines	*Medium shrubs*	*Tall shrubs and small trees*
Bittersweet	Silky dogwood	Flowering dogwood
Virginia creeper	Graystem dogwood	Hawthorn
Dwarf sumac	Hazelnut	Apple and crabapple
Swamp rose [1]	Bayberry	Staghorn sumac
Fox grape	Bear oak	Mountain ash
Riverbank grape		Nannyberry
		Blackhaw
		Highbush cranberry

[1] Multiflora rose is even better suited for plantations but no information is available as to its value in furnishing grouse food.

The thicker the shrubs develop the easier will be the maintenance. But since this association of plants is not ordinarily a climax in the plant succession, some tree species will encroach eventually even if not at the start. These should be periodically cut out or poisoned. This is preferably done when the adjacent woodland or tree planting is being thinned, improved, or market products removed. Little extra effort will then be required to keep the shrub border in good condition.

Open Edges. Any open area of herbaceous cover, water, or bare ground next to woody cover furnishes an open edge. In grouse cover these edges serve several important functions: food production, notably through herbaceous plants and insects; keeping adjacent cover exposed to the sun to the end that it produces more food; and providing dusting and sunning spots.

Most of these edges will be supplied where farm fields meet woodlands and where roads traverse them. To the degree that fields continue to be farmed will most of these edges be maintained. We have already stressed the importance of woods roads in the woodland proper for the opening and cover change that they furnish. These woodland roads offer an opportunity for improving grouse food conditions by the simple expedient of disking the road center and seeding with wild white clover (*Trifolium repens*). The soil must be fairly high in lime content, or at least neutral, or lime will have to be added to make this treatment successful. The seeding may be made at a rate of about four pounds per acre, or one pound for each thirteen hundred feet of seeding eight feet wide.

In extensive forest areas where open field edges are lacking, roadway openings are particularly important. A good system of logging

roads kept well brushed out will serve this need. Clover will often come into these roadways naturally as a result of the horse manure dropped during wood harvest operations. It then needs only continued sunlight to thrive and provide grouse with a source of succulent green food.

PROPAGATION OF WOODY PLANTS FOR PLANTATIONS [1]

Seedlings grown in a nursery are generally most suitable for woody plantings. The problems of growing the trees and shrubs for field use are many and can be discussed only briefly here. In the following subheadings the essential steps in growing seedlings for field use are summarized. Propagation information for trees and shrubs recommended for plantings for grouse cover in the Northeast are given in Table 12. It will be noted that with a single exception (Norway spruce), all the species listed are natives. It is generally best to use indigenous plants, although there are a few instances where exotics may better serve the purpose.

Procuring the Seed. The first problem is obtaining good quality seed. It is generally wise to gather the seed as near as possible to the nursery or, if it is to be planted elsewhere, in the same climatic zone where it will be used. Both altitude and latitude of the seed source should be as close as possible to that where the plants must live. Only thrifty specimens should be utilized as sources of seed as the character of the mother plant often has a marked influence on the development of the transplants.

If the collection of seed from wild plants is not feasible, it may be possible to purchase it through commercial seed dealers. In this transaction it is well to state carefully the desired specifications as to seed source and germination percentage.

The most difficult seed collection problems arise with the larger trees, especially the pines, spruces, and maples. The seed should be picked from the tree, often requiring a difficult climb. The operation should begin as soon as the seed is ripe in order to avoid losses from shattering, or from animal feeding. Periodic inspection of the

[1] This section was written by Robert Thornton, formerly Regional Nurseryman, U. S. Soil Conservation Service.

Table 12

Propagation Information for Trees and Shrubs Recommended for Plantations

Species	Time to collect seed	Type[2] of cleaning required	Quantity cleaned seed	Average no. clean seed per lb.	Average cutting test or germ.%	No. usable plants per lb. clean seed	Type of seed storage	Preplanting treatment: No. days	Preplanting treatment: Temperature	Preplanting treatment: Medium for stratification	Time to sow	Rate of seeding 100 sq. ft.	Seed bed covering	Optimum plant density per sq. ft.	Age of usable planting stock	Size for field planting[4]
			Per Bu.													
Conifers:																
White pine	Early Sept.	1	.8	25000	70	8000	Dry sealed		36–38° F.		Fall	10–12 oz.	Sand	35–40	2–2 or 3–0	6 × 3/16
Red pine	Sept.-Oct.	1	.7	52000	70	10000	Dry sealed		36–38° F.		Fall	5–6 oz.	Sand	35–40	2–2 or 3–0	6 × 3/16
Norway spruce	Oct.-Nov.	1	.4	55000	75	15000	Dry sealed		36–38° F.		Spring	5–6 oz.	Sand	40–45	2–2	6 × 3/16
Red spruce	Oct.-Nov.	1	.4	130000	60	5000	Dry sealed		36–38° F.		Spr or fall	1½–2 oz.	Sand	40–45	2–2	6 × 3/16
Arborvitae	Sept.-Oct.	1	1.5	325000	40	10000	Dry sealed		36–38° F.		Spring	2–4 oz.	Sand	40–45	2–2 or 3–0	6 × 3/16
			Per 100 Lbs. Fruit													
Hardwoods:																
Bear oak	Sept.-Oct.	3	75	700	95c[2]	100	Sow as collected				Fall	12 lb.	Soil	10	1–0	6 × 3/16
Red oak	Sept.-Oct.	3	75–80	90	80	35	Sow as collected				Fall	18 lb.	Soil and mulch	10	1–0	6 × 3/16
White oak	Sept.-Oct.	3	80–90	150	80	50	Sow as collected				Fall	10 lb.	Soil and mulch	10	1–0	4 × ⅛
Black cherry	[1] Sept.	2	20–25	4000	80	1700	Dry	120	41° F.	Peat	Fall	2.5 lb.	Soil and mulch	20	1–0	9 × ⅛
Red maple	May-June	none	100	18000	45	2000	Sow as collected				Spring	1 lb.	Soil	20	2–0 or 1–0	6 × ⅛
Sugar maple	Sept.-Oct.	none	47–50	7000	40	500	Sow as collected				Fall	4 lb.	Soil and mulch	20	2–0 or 1–0	6 × ⅛
Flowering dogwood	Sept.-Oct.	2	18	4000	70	200	Dry	100–130	41	Sand and peat	Fall	5 lb.	Soil and mulch	15	2–0 or 1–0	6 × ⅛
Gray dogwood	Sept.-Oct.	2	12–15	12000	90c	1000	Dry	140	41	Sand and peat	Fall	1.66 lb.	Soil and mulch	20	2–0	6 × ⅛
Silky dogwood	Aug.-Sept.	2	17–20	12000	90c	1000	Dry	120	41	Sand and peat	Fall	1.5 lb.	Soil and mulch	20	2–0 or 1–0	9 × ⅛
Hazelnut	Sept.-Oct.	1	25–30	500	95c	120	Sow as collected				Fall	5–10 lb.		10	1–0	6 × ⅛
Hawthorn	Sept.	2	6–9	10–15000		400	Dry	H_2SO_4 20 min. +120 days	41	Peat	Spring	5 lb.	Soil	20	2–0	6 × 3/16
Staghorn sumac	Oct.-Nov.	5	10–15	28000		1800	Dry	+120 days	41		Fall	1 lb.		10	1–0	6 × ⅛
Dwarf sumac	Oct.-Nov.	5	10–15	32000		1500	Dry	+120 days	41		Fall	1 lb.		10	1–0	6 × ⅛
Swamp rose[5]	Late Oct.	2	6–8	45000	75c	10000	Dry	90–100	41	Peat	Fall	6 oz.	Soil and mulch	25	1–0	6 × ⅛
Highbush cranberry	Oct.-Dec.	2	6–10	10000		2000	Dry				Late Jun	1 lb.	Soil and mulch	20	2–0	6 × ⅛
Blackhaw	Oct.-Nov.	2	25–30	5500		1000	Dry				Late May	2 lb.	Soil and mulch	20	2–0	6 × ⅛
Nannyberry	Sept.-Oct.	2	18–20	4000		2000	Dry				Early Jul	1 lb.	Soil and mulch	20	2–0	6 × ⅛
Fox grape	Sept.-Oct.	2	10–12	7500	90c	4000	Dry				Fall	½ lb.	Soil and mulch	15	1–0	6 × ⅛
Riverbank grape	Sept.-Oct.	2	8–10	15000	90c	18000	Dry				Fall	¼ lb.	Soil and mulch	15	1–0	6 × ⅛
Bayberry	Oct.	4	40–50	55000		2000	Dry	90	41	Peat	Spring	1 lb.	Soil and mulch	20	2–0	6 × ⅛
Crabapple	Oct.	2	2–3	75000	90c	2000	Dry				Fall	1 lb.	Soil and mulch	10	1–0	6 × 3/16
Mountainash	Sept.-Nov.	2	1–1.5	150000	85c	5000	Dry	90	32–34	Peat	Fall	2 oz.	Soil	20	2–0 or 1–0	6 × 3/16
Bittersweet	Sept.-Nov.	2	15–18	25000	80	4000	Dry	90–100	41	Sand and peat	Fall	4–6 oz.	Soil	20	1–0	6 × ⅛
Virginia creeper	Sept.-Nov.	2	16–20	15000	80	3500	Dry	100	50		Fall	8 oz.	Soil and mulch	10	2–0 or 1–0	6 × 3/16

[1] Removal of fruit unnecessary if sown immediately following collection.

[2] c — by cutting test.

[2] Type of cleaning: 1. Extract seed from cones or husks (e.g., Corylus); 2. Remove fleshy pulp by maceration and fermentation; 3. Remove acorns from cups — fumigate if very wormy; 4. Remove waxy outer surface by rubbing; 5. Crush fruit heads and winnow out refuse.

[4] Figures are given in inches for top height and caliper (½ inch above root collar), respectively.

[5] Multiflora rose is also recommended for plantations.

seed trees every few days during the ripening season will assure accurate determination of the best collecting time.

Cones of the pines and spruces should be taken just before they open. When squirrels begin cutting off the cones and dropping a few to the ground, maturity of seed is indicated. Red pine cones turn a deep purple, with brown on the scale tips at ripening, while those of white pine turn yellowish-green with brown scale tips. Maturity of these pine cones may also be ascertained by their specific gravity. When the majority of red pine cones float in kerosene, they are ready for picking. White pine cones may be picked when they float in linseed oil. The best method of verifying the maturity of spruce cones is by the general browning of the cone scales. Pine cones can be removed most easily by using either hand or pole pruners. The spruces and arborvitae are best gathered by hand picking or raking onto a tarpaulin.

Since maple seeds are winged and disperse quite widely upon falling it is generally advisable to collect from the tree. In towns it may be more efficient to collect from places of concentration such as gutters. Tree collection is done by hand stripping from ladders from the outside of the tree canopy.

Oak acorns can easily be raked up from the ground after they have fallen. Since the acorns of white oak start germinating immediately after falling, they should be gathered promptly.

Fruits, nuts, or seeds of most shrubs and vines may be collected with little trouble either from the ground or from the plants by the aid of stepladders. Of the shrubs listed in Table 12 the hazelnut and dogwoods require the most careful watching. The dogwoods drop much of their fruit quickly upon maturing while the hazelnuts are gathered quickly by squirrels. Fruits of the other species remain on the plant long enough so that speed of collection is not urgent. Rose, bayberry, bittersweet, and the sumacs generally remain for some months while the others hang at least one or two months during which collections may be made.

A word of caution in respect to handling quantities of freshly collected fruit. Keep them well aerated, especially when in containers, in order to prevent decomposition through heating.

The times for collection of seeds given in Table 12 are general and will vary some according to location and weather conditions.

By keeping notes on dates of maturity for a few years, these local variations may be learned.

Cleaning and Extraction of Seed. Seeds should be removed from their coverings before storing or planting.[1] With the fleshy fruits this may be done by maceration and fermentation. Some kinds, however, must be treated carefully. Mountain ash and crabapple deteriorate rapidly if they remain in the fermentation bath more than forty-eight hours. Hence they should be very thoroughly macerated before being subjected to fermentation. The fermentation bath may be prepared by adding a small quantity of yeast to the water and leaving it standing in a warm room.

The dry nuts are prepared by removing the husks (hazel) or cups (oak). Sumac "bobs" or heads should be broken apart before removing the thin outer coat of the seeds. After separating the trash from the seeds, the outer coat may be taken off by abrasion.

Extraction of seeds from cones should be done soon after collection is completed. This is most true of the pines and spruces which become very pitchy if allowed to lie about. Arborvitae cones are very dry and do not form pitch. The cones are placed in thin layers on trays having screen bottoms for air circulation. They should be kept in a hot dry room (with the temperature not exceeding 120° F.) and stirred occasionally. When the cones have opened, the seed may be shaken from them. After the wings are removed they are ready for either storage or planting. Sometimes the scales will stick together through the first drying attempt. These cones should be sprinkled with water and then redried, repeating the process as many times as necessary.

Care of Seed Prior to Sowing. After the seed has been cleaned and dried or extracted it is advisable to make a simple cutting or germination test at once. Germination tests immediately after seed collection are not satisfactory for certain species having a period of seed dormancy. In the cutting test, viable seed is recognized by the clear white meat. If the interior is discolored, deep yellowish or brown, the seed is considered nonviable. The percentage of seeds that are viable as shown by cutting or by a trial germination is an indication of production that may be anticipated. The actual num-

[1] This is not essential for black cherry if it is sown immediately after collection.

ber of seedlings produced, however, will be much lower than the number of viable seeds as shown in these tests. Table 12 gives average figures for viability tests and for the corresponding numbers of resultant usable plants per pound of seed. By comparing the actual viability test with the average, one may easily compute the probable seedling production per pound of the seed on hand. The rate of seeding may then be adjusted from that recommended in order to compensate for the variation in viability.

Some seeds, such as those of the pines, spruces, arborvitae, and the maples, are capable of immediate germination after maturing. All the shrubs and vines under consideration have a period of dormancy during which certain physiological changes take place prior to the time when germination can take place. Also, some seeds have hard coats that prevent absorption of moisture and thus delay germination. For those species that can be collected early enough for fall planting, the over-wintering in the seed bed provides the necessary conditions to carry them through the dormancy period. Those that are to be spring-planted must be stratified over winter to prepare them.

Seeds to be stratified should first be soaked for two hours in a saturated chloride of lime solution to prevent molding. The medium for stratification may be acid peat or an equal mixture of sand and peat. The best medium for each species and the number of days of stratification needed are listed in Table 12. The desirable temperature for stratification is about 41° F.[1] and the seeds should be placed in thin layers in the slightly moist medium. In handling large kinds, the seeds may be mixed generally through the medium. For very small seeds, as bittersweet and mountain ash, it is advisable to keep a layer of cheesecloth above and below to facilitate recovery at the end of the stratification period.

The hard-coated seeds of hawthorn and sumac must be scarified before planting if quick germination is desired. The seed should be thoroughly dried and then immersed in a solution of concentrated sulphuric acid (H_2SO_4). The liquid should cover the seed to twice its depth and should be stirred occasionally for the twenty-minute treatment. After this the acid is poured off and large quantities of water are quickly added. The operator should be very careful when adding the water because of the violent boiling that would

[1] Mountain ash seed should be kept at about 32°—34° F.

ensue if any acid remains, possibly causing acid burns. After the seeds are thoroughly washed, add one tablespoonful of washing soda for each quart of water to neutralize the acid. Then rinse again thoroughly in clean water after which the seeds are ready for planting.

Bayberry seed should have the outer wax coating removed just before stratification. This may be done by abrasion. Sand paper is useful for this purpose. Separation of the cleaned seed from the granular bits of wax may be done through a screen.

The seeds of the northern viburnums also require special consideration. They go through two stages of germination instead of one. The root develops after a period of warm weather and the leaves are not released until after a period of cold. The seeds should not be stratified but rather held in dry storage until midsummer of the year following collection when they should be sown.

Preparation of the Nursery Seed Beds. Selection of suitable soils for the nursery beds is of the utmost importance. For all species the soil should be deep and well drained but not drouthy. A light sandy soil is the best for growing the conifers and small-seeded hardwoods. Heavier loam soils are better for the large-seeded hardwoods, although tight clay soils should be avoided.

Location of the seed beds should be made with great care. Sites that can be worked early in the spring and soon after rains are best. Friable soils free of stones make operations easier. Fields in sod should be put through a cultivated crop before they are used for seedling beds in order to reduce the weeds and white grubs, and to eliminate clods.

The area should be deep-plowed and thoroughly harrowed a month in advance of seeding time so as to eliminate as many weeds as possible. Do not use manure in the preparation of the beds. After thorough disc-harrowing it is convenient to lay out the area in standard beds four feet wide and a hundred feet long. Bounding all sides a pathway two feet wide should be left. Soil from the paths is thrown up on the beds so as to make them four to six inches higher. This insures good drainage and helps to prevent washing. When the bed has been built up, it should be raked thoroughly, filling in the low spots, and making a level surface. Beds should be raked out a little wider than the four-foot dimension so that a full four-

foot width can be planted without breaking the shoulders. After it is thoroughly raked and leveled, the bed should be rolled to form a firm soil.

Beds to be used for conifers should have all nutrients added prior to seeding. Never apply lime to conifer beds at any time. Those devoted to hardwoods may be top-dressed after seeding and at intervals through the summer. Fertilization practices will vary with the needs of the soil in each location and the rapidity of growth, and should be about the same as for ordinary farm crops. Likewise, the need for lime will depend on the present acidity of the soil and upon the species to be grown. The conifers need an acid soil while the hardwoods mostly prefer a neutral one. Bayberry is an exception.

Seeding and Seedling Culture. The time of seeding and rate of seeding are given in Table 12 for each species. It is recommended that the seed be sown by hand broadcast, mixed with sand to get an even distribution where necessary, except with bear oak and mountain ash. These two species should be seeded in rows about ten inches apart.

The method of covering the seed of the conifers is to spread on top of the seed a layer of sand ¼–⅜ inch thick. For the hardwoods the covering is either soil alone, or soil covered by a mulch. Clean grain straw is suitable for the mulch. Soil covering depth is three times diameter of clean seed or at least a quarter inch. The mulch is removed when the seeds start to germinate.

Conifer beds should be covered with slat frames about a foot off the ground during the early growth period to give about half shade from the sun. The screens should be removed occasionally during cloudy damp days to prevent the "damping off" of the young plants. The frame covering is gradually abandoned after about midsummer.

One of the great problems in most nurseries is providing adequate water during the dry season. Where operations are large enough to warrant, an overhead irrigation system should be installed. For small nurseries hand watering or a portable irrigation system must suffice when rainfall is inadequate.

Competition of weeds with the young seedlings is a big problem, especially during the first half of the summer. Continual vigilance and lots of handwork are necessary to prevent them from stifling the

crop. Careful and frequent weeding during the early season will reduce the problem to minor proportions in late summer.

As the seedlings develop, it is very important to reduce their density to a desirable level so that each plant will have adequate space and food. The optimum densities for each species are given in Table 12. The thinnings should be started as soon as the plants are large enough to begin crowding. For conifers this is three to four weeks after germination; for hardwoods, after they form their second true leaves. It is required to insure an evenly spaced stand.

Weeding (or cultivation if row-seeded) and irrigation should be gradually tapered off beginning at midsummer and should be stopped completely about six weeks before frost is expected. This gives the plants an opportunity to harden before cold weather.

Various species of trees and shrubs require different periods of time for the attainment of size suitable for field planting. A number of the hardwoods grow to sufficient size in a single summer. These are known as one-year seedlings and are designated "1–0," meaning one year in the seedling bed and no transplanting. All the northern conifers require more than one year and those recommended in Table 12 require three or four years, depending upon the growing conditions in the individual nursery and upon the weather. These pines, spruces, and arborvitae are usually kept in the seedling bed for two years and then transplanted in field rows. Two more years as a transplant give the young tree its final designation "2–2." When they are to be grown to usable size in three years, it is generally best not to transplant.

Some of the hardwoods require two years and are designated in Table 12 as "2–0." Others may sometimes, in good years, reach usable size in one year and then in other seasons grow so slowly as to require a second year. Those hardwoods requiring a second year in the nursery may be transplanted to become 1–1 plants if desired. This is usually done only with beds of uneven growth where some plants are ready for field use after one season while others are too small. The small ones may be saved, after the bed is dug, by transplanting.

The final column of Table 12 gives the smallest size recommended for field-planting stock. The first figure is the height in inches above ground, the second is the diameter of the stem one-half inch above ground. In all cases it is assumed that the plants

have a good root-top ratio, that is, roots about equal to top in development. Stock may be larger than the dimensions given as long as the plant is small enough to be easily handled in planting.

CONTROL OF THE HARVEST

Proper and Flexible Laws. Any sound system of game management requires a framework of good, workable laws in which to function. Since the grouse is a very dynamic resource, the laws pertaining to it should be flexible enough to provide for quick adjustments when needed. Fundamental is the centering of discretionary authority for harvest limitations in the executive of the conservation agency of the state. This requires the delegation of this authority by the state legislative body. And to be successful it requires an intelligent, responsible, and independent executive branch backed by an able staff of technical men.

Most state legislative bodies up to the present have been unwilling to release this authority. But it is manifestly impossible for a large political body to gather the necessary facts that bear upon hunting restrictions, seasons, bag limits, and the like, or to take timely action. When changes are needed they may be required quickly and often at times when legislative action is out of the question. The only sensible system is to place the responsibility where it can be used with speed and be guided by impartial attention to the biological facts.

The history of grouse laws, as with all game laws, is one of gradually increasing restrictions on the freedom of the individual to hunt. Changing conditions of habitat and human populations made these laws a necessity if the sport and species were to be preserved.

However, it should be borne in mind that the purpose of game laws is fundamentally to protect a living resource and to provide for an equitable harvest of the annual crop. Both objectives are of the utmost importance, but it is also true that they tend in opposite directions. The greater the protection the smaller is likely to be the harvest; and the bigger the harvest the more likelihood of endangering the safety of the species. Game laws are therefore a compromise. They should be designed to permit the greatest possible sustained harvest without endangering the status of the breeding stock.

In states having adequate grouse range, there should be an open

season in most years. Only in years of catastrophic losses will it be necessary to close the season—but then it should be closed quickly. Ordinarily one or two years' protection are then needed to effect sufficient recovery to warrant renewal of open seasons. With grouse we should be able to anticipate an average of eight years or more of open seasons out of ten.

The limitations on the individual in an open season must be determined by existing conditions. In states like New York, New Jersey, Connecticut and Pennsylvania where the hunting pressure is generally intense, bag limits must be low. The present New York law of three a day and fifteen a season is probably safe and yet satisfactory to the fair-minded sportsman. Length of season is the subject of divergent opinions in various states. Most experience has shown that a season of moderate length produces little, if any, more hunting than a short, intense season. In most places with good range a season of at least a month is warranted. In years of good abundance it is actually better to lengthen the season and harvest a bigger crop. Two months of continuous hunting might be warranted in some years, provided such a liberalization did not add unduly to problems of conservation of other species.

I think we can fairly say that under modern conditions of hunting the sale of grouse and taking of the birds by means other than gun or bow and arrow are definitely not warranted.

Refuges. In our discussion of man as a conservationist in his relation to grouse, we pointed out that the refuge principle is not as applicable in grouse management as it is to that of some other species. Protection of this type during the breeding season is of little value in most grouse range; if any protection is needed then it is from cattle, fire, or lumbermen, not from the hunter. The establishment of grouse (or game) refuges to protect breeding birds will rarely be justified. Protection from hunting through the means of escape, or "seed stock," refuges will only occasionally be warranted, and then in areas of high hunting pressure, or where there is a combination of hunting intensity with inadequate natural escape cover. In many areas of grouse range it may be desirable to establish refuges primarily for other game species. This discussion does not refer to that problem.

Because of the rather short daily cruising radius of grouse, any

refuges that are to benefit this bird should be small—say from ten to one hundred acres. Within these limitations the exact size is not of much importance. Of more import is the location of the refuge with respect to cover. It should contain the best available shelter and some good feeding area of the available fall foods. This usually means that the refuge will be in the outer part of a woodland.

The distribution of refuges need be no more than one to three per square mile under most circumstances. In range with rough topography and variable cover, the pattern may be quite irregular. The refuges should be placed where grouse are most sure to use them regardless of whether this provides an even distribution.

Most of the intensive hunting in the Northeast is in the disconnected cover range, hence refuges will most often be needed on small units of land ownership—the predominant condition in this partly farmed country. A man who owns only a hundred or so acres will not be able to give much consideration to the needs of a refuge pattern. The most he is likely to require on his own land will be a single unit. It is therefore quite largely a problem for the organized sportsmen of the locality or for the state game agency to plan and organize for the grouse refuge needs in any particular range.

The mechanism of making a refuge is simply the posting around the boundaries of a unit of signs that will legally prohibit the use of firearms therein. The type of sign, and the distance apart that they must be posted, is generally specified in the state conservation laws. When making a refuge, many states bound it with a single strand of smooth wire, hung about breast height. This is not essential, but it is important that the boundary be apparent to one approaching it if it is to serve its purpose. This means that expediency will often alter the selection of its location and size from what might otherwise be the more ideal. Roads, trails, woods edges, fence-rows, and similar natural boundaries should be used so far as possible. When it is necessary to have the line traverse woody cover it must be kept brushed out if people are to see and respect it.

Use of Censuses. A census is essentially an enumeration of a population. In field studies of animal populations it is of fundamental importance to know the number, type (sex, age, etc.), and location of the individuals comprising the population. The greatest possible accuracy is needed, therefore time and cost are not the most im-

portant considerations. The use of the census in practical wild-life management is quite a different matter. It must be simple, quick, and inexpensive. Its basic purpose is the same—to determine the size and distribution of a population—but the accuracy required is not so great and no supplementary data are needed. The use of a management census is to determine the harvestable crop. This may be the crop on a single area of cover, such as a private holding or a public hunting ground, or the crop over a whole state. In the latter case, the estimate would be based on sample censuses from representative areas and would furnish the basis for seasons and bag limits.

Accurate determination of a grouse population in most of the northeastern range requires detailed coverage of the entire census area by trained observers. In most circumstances this expenditure is not warranted. The most expedient method is one of using indexes and samples.

The period of census-taking for the estimation of shooting season populations is from mid-August to mid-October. The middle of this period falls in the height of the moult when the birds are difficult to flush. It is generally best to avoid the month of September and confine the counts to late August and early October.

One of the best indexes of grouse populations is the productivity of the year. A count of brood size in late August is a quickly available method for gauging the productivity. If the brood size, female included, averages four, the probability is for a population the same size as the year before (if other factors are equal). If the brood size averages five or more, the probability is for an increasing population; if three or less, the likelihood is for a decline.

The second figure needed in addition to brood size is brood density. To obtain a fair index of this figure the census should be made in good weather: moderate in temperature for the season, at least partly sunny, and with little or only moderate wind. The best hours are from an hour after daylight to an hour before sunset. The coverage should be confined primarily to summer cover: brushy cover, and hardwood edges. Covering fifty acres per man-day of eight hours, an average of two broods per man-day would constitute an average good year record. This, with an average unit size of five, would give a full brood count of ten birds per man-day on fifty acres. If the brood density is one per man-day on a fifty acres per

man-day coverage, or less, the population may be gauged as quite low, the degree by which it falls below the 1.0 average indicating how low.

It is apparent that population estimates made in late August may not truthfully portray the condition of October or November. Of course there is a normal loss during September and October that is regularly anticipated, but there may be extra losses that would make the August prediction for fall conditions invalid. However, this is not commonly the case, as most of the serious losses occur in late winter or in summer. Few serious late-summer, early-fall declines have been observed in the East. But there apparently was a serious autumn decline in at least some parts of New York in 1926, and a similar one was observed in Wisconsin in September, 1933.

In view of the chance of error in depending upon an August brood count for predicting grouse shooting season populations, it is a good thing to check conditions again in October. At this season we cannot use a brood count but must depend upon a time-index of adult flushes. Again the work should be confined to balmy, calm days, and to the best early fall coverts. These are nearly the same as those used in the August count, but with more attention to the overgrown shrub cover, including adjacent orchard and hedge-rows, and a little less to the slashings.

The cover should be traversed systematically, as in August, but whereas a close coverage of lines twenty-five to forty feet apart is best for checking broods, lines of fifty to seventy-five feet are more suitable for the autumn work.

The cover with a normally good brood count in August (two broods per man-day with a ten-bird total) would ordinarily result in an average rate of grouse flushes in October of fourteen per man-day, excluding reflushes where determinable. Thus this figure may then be used as a criterion for checking the population at this season. The degree to which the average daily flush total varies from this number may be taken to indicate whether a high population or a lower-than-good population prevails. If the average flush is seven or lower, the population is low and consideration may be given to curtailment of the harvest.

It should be emphasized that the validity of the indexes used will depend in good measure upon the conditions under which they are derived, the equality used in covering the area involved, and the

number of times it is covered. It is never safe to draw conclusions from a single day's census. Of course the more times the area is covered the more accurate will be the average. As a general thing, four surveys should suffice.

If the area for which information on grouse populations is desired is large, it may be well to census portions as samples and then apply the data to the whole. Again, the accuracy will be greatest when we cover most of the area; that is, get the best sample. We well know that coverts only a mile or so apart will sometimes vary widely. In using samples of cover, we must also be careful to select units that are fairly representative of cover conditions on the whole area. When we attempt to gauge conditions in counties or states, the distribution as well as the adequacy of the samples used for censusing is very important. Representative units of all types of range and of all geographical areas must be surveyed, each with sufficient thoroughness to yield a reliable result. What is considered "reliable" will depend upon circumstances. If a close knowledge of the population of the coverts is needed, a sample of a hundred acres or more out of each ten thousand is about the minimum. On a state-wide basis, a group of four or five samples in each range type should suffice, if well distributed.

The application of the census information to local areas is in safeguarding the grouse population during the hunting season. This means hunting control.

Hunting Control. Control of hunting implies the limitation of the harvest to a predetermined number of birds—within the framework of applicable state laws, of course. Such control should be based upon a knowledge of the hunting season population based on censuses. The need for hunting control implies a very high hunting pressure. Otherwise there would be no need for this particular attention. And it should be remembered that under normal circumstances in good grouse range, no special local control is needed. The grouse is an adaptable creature and has a faculty for becoming more wary as hunting pressure increases.

If the hunting take is to be held to a stated limit, the trespass problem must be thoroughly under control. In most instances this requires posting of the land under the legal requirements of the state. It often means patrol in order to prevent illegal poaching.

It means that some system of checking in the hunters must be maintained and records kept of their bag. It may be that the hunting time or the take of each eligible hunter will have to be apportioned. In any case, the take will have to be kept to the desired limit by stopping the hunting entirely when the full number of birds has been taken.

If, with the approval of all these administrative problems and the expenses they entail, we still find it worth while to insure a limited grouse kill on an area, what take should be allowed? For a normally good hunting season population of about a grouse per eight acres or thereabouts, a take of twenty-five per cent is warranted. In years of high populations when densities of a bird per four acres or better are attained, the kill may safely be allowed to reach forty or even fifty per cent. In seasons of low populations the kill should be kept well below the twenty-five per cent figure, and if the density is lower than a grouse per thirty acres, no hunting at all is warranted.

Predator Control. In our analysis of experimental work aimed at an appraisal of the possibilities of increasing grouse by controlling predators, the conclusion was that it not only doesn't pay; it doesn't even work. This is true of various methods that have actually been applied, especially bounty payments. When we add to this the very serious questions concerning the unfavorable effects of predator destruction on the rodent balance, the prospects for improving grouse conditions through this medium are thoroughly discouraging. And this in the face of the very important part that predators play in decimating grouse. Even stripping our minds of all sentiment for the persecuted predators, we cannot honestly recommend any systematic destruction of predators in the interest of the grouse. This is especially true as regards the predatory birds, accurate control of which by species is itself impossible and indiscriminate killing very unwise.

The mammalian predators that have valuable furs not only can, but should be, controlled (*i.e.*, harvested) without regard to their relations to grouse. Foxes, skunks, weasels, and raccoons are among those grouse predators whose taking by trapping should be considered as a part of the wild-life harvest. Here, as with game, the take should be confined to the annual increment in order that the stock may not be endangered.

Restocking of Grouse. The liberation of game birds is usually done in order to build up a population that has, presumably, been overshot, or has for some other reason been reduced below a safe survival level; or at least what the sportsmen think is a safe level. There are many questions concerning the efficacy of this restocking which we may not take time to discuss now, but it is clear that it can be carried out successfully only with species that are easily produced on game farms at a low cost per head. This is not true of the ruffed grouse. It may conceivably be the case some day, but it is far from true in the present state of our knowledge of grouse propagation, and the prospects do not seem much brighter for the near future. Thus we must dispense with any notion of building up the native stock of grouse by liberations of more birds. Fortunately this is seldom needed with this species for it has a great ability to recover its numbers even when reduced to a remnant.

There is one place where the stocking of grouse is warranted; namely, on areas of formerly good grouse range where the species has been extirpated, where the cause of its extirpation has been removed or corrected, and where there is no reasonable probability of infiltration of grouse from surrounding range. Under these circumstances the reintroduction of grouse may prove well worth while.

As an example we can cite the occasional area of hilly or mountainous land that has been subjected to repeated, complete burning of the forest with consequent elimination of the grouse. If, in subsequent years, people have left the region or have changed their habit of burning the land so that this destructive influence no longer prevails, it may be feasible to attempt the re-establishment of the ruffed grouse.

In restocking such lands, either wild-trapped or hand-raised grouse may be used. They will be expensive in either case. As far as we know, either type is able to establish itself provided the specimens are in good health. This is absolutely essential. If the birds are even slightly droopy or lazy when liberated they are almost surely doomed.

The best time to stock grouse is at the very first break of spring. At least four pairs should be stocked together in order to give fair assurance of mating and nesting in the approaching spring season. Since the birds will inevitably move away some distance, a few hundred yards to several miles from the point of release, several pairs

of birds in a vicinity will be needed to give assurance of establishing a colony.

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