The Ecology of BOBWHITES in south-central Kansas

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Introduction

What is the effect on bobwhites of changes in climate, land use, density of cover, and other parts of their enviroment? Answers to these questions are of great interest to the growing number of Kansas hunters. Although much already is known about increasing the numbers of bobwhites too little information is available concerning the bobwhite in Kansas. Management procedures that are successful in Georgia, Texas, Missouri, and elsewhere often are impracticable in Kansas, and probably *vice versa,* owing to differences in vegetation, topography, and climate in the different areas. It seemed advisable, therefore, to learn more about the life history and ecology of bobwhites in Kansas in order the better to manage the species in our State. The research upon which this dissertation is based was planned and conducted with this in mind.

The bobwhite quail, *Colinus virginianus* (Linnaeus), is a member of the cosmopolitan Family Phasianidae, and of the Subfamily Odontophorinae. The latter is limited in distribution to the New World, and members of this subfamily collectively are termed quail. The geographic range of the bobwhite includes the eastern United States from the southern edge of the northern coniferous forests, south through the Atlantic and Gulf coastal states and eastern Mexico to western Guatemala in Central America, and west to southeastern Wyoming, east-central Colorado, and southeastern New Mexico (Aldrich, 1945:495, and Peters, 1934:48-49). The masked bobwhite, *C. v. ridgwayi*, has a range discontinuous with that of the remainder of the species, occurring in southern Arizona and northwestern Mexico. Bobwhites occur in all counties in Kansas, as shown by results from quail-wing surveys of 1951 through 1955 (Robinson and Baker, 1952, 1953, 1954, and 1955, and Robinson, 1956), and information obtained from Mr. Jim Coats, Game Biologist, Kansas Forestry, Fish and Game Commission. Distribution of bobwhites in the western counties of Kansas is more local than in the central and eastern counties, presumably owing to the scarcity of woody vegetation in the arid high plains of the western third of the State.

The relationships among the geographic races, or subspecies, of the species are said to have been confused by the introduction, into the United States, of thousands of bobwhites (*C. v. texanus*) from Texas and northern Mexico, the widespread release of hatchery-reared bobwhites, and the movement and release of bobwhites trapped within the United States. Seemingly two races of bobwhites occur in Kansas, according to the most recent systematic treatment of the species (Aldrich, 1945). *C. v. mexicanus* (equivalent to, in Kansas, *C. v. virginianus* of the A. O. U. Checklist, 1931: 88), is found in northeastern Kansas to approximately as far southwest as Lawrence, Douglas County. The remainder of the State is occupied by *C. v. taylori*; the latter is somewhat paler than *mexicanus*.

Field studies were made on one square mile, in south-central Kansas, approximately 270 miles (by road) from the University of Kansas. Field work was begun on September 6, 1951, and terminated on November 9, 1953. For approximately half of this time (June 8, 1952, to September 10, 1953) I resided one mile south of the study area. Field work in the other months was done on weekends, or during University holidays.

Although the distance of the study area from the University imposed certain limitations on my research, the location of the area near the western limits of the geographic range of the bobwhite is fortunate in some respects. Environmental factors that are limiting to an organism may operate throughout all, or a part, of the geographic range of that species, but the effects of these factors upon the organism often are most apparent and thus most easily studied near the limits of the organism's range. It was hoped, therefore, that some of the enviromental factors that limit populations of bobwhites might be determined in an ecological study of the species in south-central Kansas.

Illustrations in this paper, unless otherwise noted, are by the author.

Acknowledgments

The research here reported on was supported, in part, by a fellowship from the University of Kansas Endowment Association, made possible by the generous gifts of Messrs. Floyd and Henry Amsden of Wichita, Kansas. A research assistantship on the State Biological Survey of Kansas, University of Kansas, provided for many of the expenses incurred in travel and while in the field. Permission to use as a study area Plum Thicket Farm, a managed game area in northeastern Barber County, Kansas, owned by the Amsden Lumber Company of Wichita, was kindly granted by the Amsdens. They also provided for my use a residence conveniently situated near the study area.

I am particularly indebted to Mr. Floyd T. Amsden for the many courtesies shown me, and for his sincere interest in this project. His astute observations and inquiries opened new pathways of investigation that proved fruitful, and my conversations with him have helped me to clarify many of the results of this research.

I am grateful to Mr. Jess M. Crocker, caretaker at Plum Thicket Farm, for many hours of assistance rendered me in the field. His expert handling of bird dogs and his knowledge of the wildlife of the area greatly expedited my research.

Information regarding meteorological instrumentation was furnished by Mr. Richard Garrett of the U. S. Weather Bureau, Topeka, and by employees of the Weather Bureau installation at Dodge City, Kansas. Dr. J. W. Twente, Jr., gave helpful suggestions regarding exposure of meteorological instruments, and frequently assisted me in the field. I am grateful also to the employees of the County Clerk's office, and the office of the U. S. Production and Marketing Administration, both in Medicine Lodge, Kansas, for their many courtesies. Mr. Dave Leahy, Director, Kansas Forestry, Fish and Game Commission, granted permission to live-trap and band bobwhites on the study area; Mr. Jim Coats, formerly Game Biologist for that organization, has been helpful in many respects.

For helpful criticism and guidance in the course of the investigation I am especially indebted to Professor Rollin H. Baker. Professors Harrison B. Tordoff, Henry S. Fitch, E. Raymond Hall, and Worthie H. Horr also offered suggestions on methods and other assistance especially in later stages of the work. Professor A. Byron Leonard gave valuable suggestions in the preparation of illustrations, as did Mr. Victor Hogg, Staff Artist. Professor John A. Weir made helpful suggestions regarding the statistical treatment of some of the data. Acknowledgments of aid by other individuals will be made in subsequent sections of this paper.

THE STUDY AREA

The study area, Sec. 34, T. 31 S, R. 10 W, Barber County, Kansas, comprises 640 acres and is situated approximately three miles north and one mile east of Sharon (see Pl. 1, fig. a). Lowest elevation, in the bed of the creek at the south edge of the area, is approximately 1510 feet; highest elevation, at the eastern and western edges of the northern part of the area is approximately 1640 feet. Sandy Creek, an intermittent, sand-bottomed stream that arises from several tributaries approximately six miles to the north, traverses the study area from north to south, dividing it into an eastern two thirds and a western one third. The flood plain of Sandy Creek progressively widens from the north to the south edge of the study area, and the uplands rise abruptly from the valley of the creek. These uplands are dissected by several small canyons. At the head of each canyon are springs that drain into Sandy Creek. Six of these canyons have been dammed, resulting in eight clear-water lakes. A 61-acre field in the southeastern flood plain of Sandy Creek has been maintained as cropland where alfalfa, winter wheat, and white sweet clover are planted. The soil is a silty, sandy loam of red color, reflecting its origin from the underlying strata of Permian age.

Barber County is typically an area of rolling, mixed-grass prairie dissected with shallow, sand-bottomed streams with wide flood plains. Woodlands are limited principally to the banks and flood plains of the streams, although, since the 1930's, many miles of narrow shelter belts of trees have been planted at the north and south edges of cropland. Prior to the settlement of the County in the 1860's, the uplands probably supported a dense stand of mixed and tall grasses, with scattered thickets of Chickasaw plum (*Prunus augustifolia*). Much of this native grassland subsequently has been plowed and the remainder used for range for cattle and, to a lesser extent, sheep. Information obtained from the Barber County office of the United States Production and Marketing Administration, at Medicine Lodge, Kansas, indicates that, in 1953, 60.6 per cent of Barber County was used as range land, 36.1 per cent was planted to crops (principally winter wheat), and 3.3 per cent was classified as non-agricultural (streams, ponds, railroads, towns). The thickets of Chickasaw plum, once perhaps the only woody vegetation in the uplands, seemingly have been reduced in number and size and, in some areas, exterminated. Erosion by wind and water has removed much of the original topsoil, reducing the productivity of the land for native grasses, wildlife, and domestic livestock and crops.

Climate in Barber County is characterized by hot, dry summers and mild, dry winters. The following climatological data regarding Barber County is from Flora (1948). Average annual precipitation is 25.47 inches. Greatest and least amounts of precipitation are received in the months of May and February, respectively. Average annual snowfall is 12 inches. Average annual temperature is 57.9° F. Prevailing winds are from the south throughout the year, and the average annual velocity of the wind (recorded at 3 p. m., the time of greatest velocity) is 14 miles per hour. The average length of the growing season is 191 days. The average date of the last killing frost in the spring is April 14, and that of the first killing frost in the autumn is October 22. Average annual relative humidity (interpolated, data from Wichita and Dodge City) at 12:30 p. m., the time of lowest relative humidity, is approximately 50 per cent.

In some respects the study area is not typical of the rest of Barber County. In general, the study area is characterized by dense vegetation in both upland and lowland situations. The density of the vegetation is due primarily to the absence of grazing by domestic cattle. In 1946, when the study area was acquired by Mr. Amsden, it was typical of the surrounding countryside. The northeastern quarter of the study area was eroded as a result of intensive farming without regard for soil conservation. The remainder of the study area was over-grazed. Even the woodlands bordering the creek and in the canyons had been reduced to park-land with little or no understory of woody shrubs.

The study area slowly regained a native aspect following the removal of cattle and the cessation of farming in the uplands. By 1951, the northeastern portion, previously planted to crops, supported a sparse stand of short grasses and weeds; the sandy washes in the old fields had been reduced in extent; a dense understory of vines and woody shrubs had developed in the woodlands; in the over-grazed uplands of the western part of the study area the vegetation was a community of mixed grasses; and in some areas pure stands of sand bluestem (*Andropogon hallii*) were found. By 1953, the sandy washes supported short grasses and weeds, the stands of short grasses in the less eroded parts of the old fields was more dense, and the pure stands of sand bluestem in the old pastures were more extensive.

VEGETATION OF THE STUDY AREA

In the summer of 1951, Dr. Howard J. Stains, then a graduate student in Zoology at the University of Kansas, studied the ecology of the area. He prepared a map of the vegetation and I am indebted to him for allowing me to use it.

Stains' original map of the study area delimited 10 types of vegetation. I altered this map with respect to the boundaries of some of the types, and increased the number of types to 12 (see fig. 1). For the sake of convenience each type of vegetation hereafter will be termed a habitat, and given a number and brief descriptive name.

To determine the total area of each of the habitats, a map delimiting each was prepared on cardboard of uniform thickness. This then was cut along the lines marking the boundaries of the habitats. The pieces of cardboard representing each of the habitats were weighed to the nearest milligram on an analytical balance. The weight of the pieces of cardboard that represented each of the habitats was divided by the weight of all the cardboard included

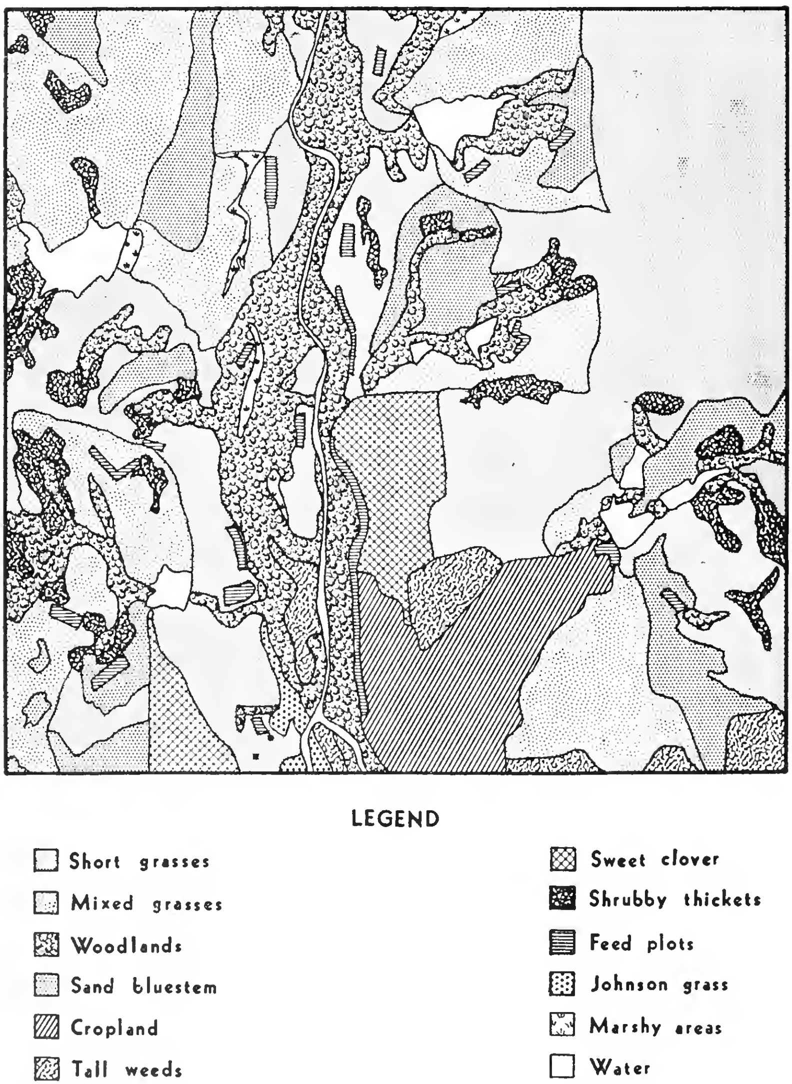

FIGURE 1. Map of the vegetation of the study area. Taken, in part, from Plate 1, fig. *a*. Drawn by Barton C. Kelley.

in the map, giving a percentage of the total for each habitat. From this the acreage of each of the habitats was computed. At a later date, the acreage of each of the habitats was determined by means of a compensating polar planimeter. The results of the two methods of determination of area were identical, for all practical purposes.

From 1951 to 1953, I collected plants from each of the habitats on the study area. The plants were prepared as herbarium specimens and submitted to Dr. Ronald L. McGregor, Department of Botany, University of Kansas, who kindly identified them. In the following descriptions of the habitats, scientific names of plants follow, whenever possible, Fernald (1950). Common names of plants follow principally the American Joint Committee on Horticultural Nomenclature (1942).

SHORT GRASSES (HABITAT 1).—The grasses and weeds making up this habitat comprise 215.7 acres (33.7 per cent) of the study area. This is the most open type of vegetational cover on the study area and is found, for the most part, in the uplands that were cultivated prior to 1946. Habitat 1 is characterized by a wealth of species and numerous "disturbance" plants. The average height of the stand is approximately six inches.

Of the 39 species of plants identified from this habitat, three grasses are the most abundant. Blue grama (*Bouteloua gracilis*) seems to be the dominant species, comprising approximately 70 per cent of the total cover. Red three-awn (*Aristida longiseta*) and Scribner's panicum (*Panicum scribnerianum*) each comprise approximately 10 per cent of the total cover of this habitat. The following 36 species of plants comprising the remainder of the vegetation in habitat 1 are, for the most part, annual weeds.

Achillea lanulosa—western yarrow
Ambrosia psilostachya—western ragweed
Andropogon saccharoides—silver bluestem
Aristida oligantha—prairie three-awn
Artemisia caudata—sage
Artemisia vulgaris—mugwort
Berlandiera texana—berlandiera
Bouteloua curtipendula—sideoat grama
Bromus japonicus—Japanese brome
Cassia fasciculata—senna
Cassia marilandica—wild senna
Chloris verticillata—windmill grass
Cirsium ochrocentrum—thistle
Elymus canadensis—Canada wild rye
Euphorbia dentata—toothed euphorbia
Gnaphalium obtusifolium—fragrant cudweed
Helianthus petiolaris—prairie sunflower
Hymenopappus tenuifolius—hymenopappus
Lepidium densiflorum—prairie pepperweed
Lespedeza capitata—roundhead lespedeza
Lespedeza sp.—lespedeza
Liatris punctata—dotted gayfeather

Lithospermum incisum—puccoon
Lotus americanus—deervetch
Monarda punctata—spotted beebalm
Opuntia sp.—prickly pear
Petalostemum villosum—silky prairie clover
Physalis lanceolata—groundcherry
Plantago purshii—woolly Indian wheat
Psoralea tenuiflora—slimflower scurfpea
Ratibida columnifera—prairie coneflower
Silene antirrhina—sleepy catchfly
Specularia perfoliata—Venus' looking-glass
Sporobolus cryptandrus—sand dropseed
Strophostyles leiosperma—wild bean
Yucca glauca—small soapweed

MIXED GRASSES (HABITAT 2).—Second largest in area, this habitat comprises 125.2 acres (19.4 per cent) of the study area. The grasses of this habitat are found principally in the uplands that were grazed or mowed, or both, prior to 1946.

One of the mid-grasses, hairy grama (*Bouteloua hirsuta*), is the dominant species, comprising approximately 80 per cent of the total vegetation of habitat 2. This habitat is characterized by a dense mat of grasses approximately eight inches in height, with widely scattered annual and perennial weeds. One of the bunch grasses, little bluestem (*Andropogon scoparius*), is limited to, and may be considered an indicator of, this habitat (see Pl. 2, fig. *a*). The following is a list of the remaining 32 species of plants identified from Habitat 2.

Amaranthus retroflexus—redroot amaranth
Ambrosia psilostachya—western ragweed
Artemisia caudata—sage
Asclepias sp.—milkweed
Aster sp.—aster
Bouteloua curtipendula—sideoat grama
Bromus catharticus—rescue brome
Castilleja citrina—Indian paintbrush
Chenopodium album—lamb's quarter goosefoot
Chrysopsis asprella—golden aster
Crotalaria sagittalis—arrow crotalaria
Desmanthus illinoensis—Illinois bundleflower
Erigeron canadensis—horseweed fleabane
Euphorbia petaloidea—euphorbia
Gaura parviflora—gaura
Glycyrrhiza lepidota—American licorice
Lespedeza sp.—lespedeza
Liatris punctata—dotted gayfeather
Linum rigidum—stiffstem flax
Monarda punctata—spotted beebalm

Oenothera serrulata—evening primrose
Opuntia sp.—prickly pear
Panicum scribnerianum—Scribner's panicum
Plantago purshii—woolly Indian wheat
Prionopsis ciliata—goldenweed
Psoralea tenuiflora—slimflower scurfpea
Sideranthus spinulosus—goldenweed
Silene antirrhina—sleepy catchfly
Specularia perfoliata—Venus' looking-glass
Spermolepis patens—spermolepis
Yucca glauca—small soapweed

WOODLANDS (HABITAT 3).—The woodlands comprise 83.2 acres (13.0 per cent) of the study area. They are limited to the moist lowland situations found along the banks and flood plain of Sandy Creek, and in the numerous spring-fed canyons (see Pl. 2, fig. *b*).

The woodland association is composed principally of three kinds of trees: American elm (*Ulmus americana*), cottonwood (*Populus deltoides*), and common hackberry (*Celtis occidentalis*) in that order of relative abundance. A well defined mid-story is lacking. The understory is composed principally of coralberry (*Symphoricarpos orbiculatus*). The following 25 species of plants also were identified from this habitat.

Agastache nepetoides—giant hyssop
Ailanthus altissimus—tree of heaven
Argemone intermedia—prickly poppy
Cercis canadensis—eastern redbud
Chenopodium leptophyllum—slimleaf goosefoot
Digitaria filiformis—slender crabgrass
Eragrostis cilianensis—stinkgrass
Gaura parviflora—gaura
Heterotheca subaxillaris—heterotheca
Juglans nigra—black walnut
Juniperus virginiana—red cedar
Maclura pomifera—Osage orange
Menispermum canadense—common moonseed
Mirabilis nyctaginea—four-o'clock
Morus rubra—red mulberry
Parthenocissus quinquefolia—Virginia creeper
Phytolacca americana—common pokeberry
Robinia pseudo-acacia—black locust
Rhus toxicodendron—poison ivy
Salix sp.—willow
Sambucus canadensis—American elder
Setaria glauca—foxtail grass
Smilax tamnoides—bamboo greenbriar
Triodia flava—purpletop
Vitis vulpina—frost grape

SAND BLUESTEM (HABITAT 4).—Seemingly the climax community of the upland prairie situations, this habitat comprises 69.1 acres (10.8 per cent) of the study area. It is found principally in the upland situations that had been grazed or mowed, or both, prior to 1946 (see Pl. 2, fig. *b*).

The basal leaves of the bunches of sand bluestem (*Andropogon hallii*) form a dense, tangled mat averaging 10 inches in depth. The stems of the plant average six feet in height, occasionally reaching a height of eight feet.

CROPLAND (HABITAT 5).—One small portion of the study area is cultivated. This 35.2 acre field comprising 5.6 per cent of the study area is situated in the southern lowlands bordering the east side of Sandy Creek. The field is divided into east and west portions of approximately equal area for the purpose of crop rotation. The crops that are planted are winter wheat (*Triticum aestivum*) and alfalfa (*Medicago sativa*). In the growing season wild bean (*Strophostyles leiosperma*) grows in profusion in the cultivated fields.

TALL WEEDS (HABITAT 6).—In the lowlands are small areas that were cultivated prior to 1946, but have lain fallow since that time. The vegetation now occupying these situations is composed of tall weeds. This small, but well defined, habitat comprises 22.4 acres (3.6 per cent) of the study area. The dominant species of plant in this habitat is the giant ragweed (*Ambrosia trifida*). The other six species of plants identified from habitat 6 are as follows:

Asclepias incarnata—swamp milkweed
Cirsium undulatum—wavyleaf thistle
Erigeron canadensis—horseweed fleabane
Lactuca scariola—prickly lettuce
Oenothera biennis—common evening primrose
Vernonia baldwini—Baldwin's ironweed

SWEET CLOVER (HABITAT 7).—White sweet clover (*Melilotus alba*) was planted in a field to the north of the cropland, and also appeared as a "volunteer" in certain portions of the uplands. Because of its growth habit and its association with plant communities in the uplands it has been set aside as a separate habitat. Habitat 7 comprises 26.2 acres (4.1 per cent) of the study area.

SHRUBBY THICKETS (HABITAT 8).—Thickets of woody shrubs abound on the study area, although their total area comprises only 20.5 acres (3.2 per cent) of the study area. In the uplands, thickets of Chickasaw plum (*Prunus augustifolia*) are common (see Pl. 1, fig. *b*). In the lowlands, principally bordering the woodlands, the shrubby thickets are composed of either dogwood (*Cornus* sp.) or smooth sumac (*Rhus glabra*). Other plants found in this habitat were hedge cornbind (*Polygonum scandens*) and skunkbush sumac (*Rhus trilobata*).

FEED PLOTS (HABITAT 9).—Twenty-one small cultivated plots are planted each year to provide food for game birds. These plots average 0.5 acres in area and are situated adjacent to woody cover. The total area of these feed plots comprises 9.6 acres (1.5 per cent) of the study area. Sorghum (*Sorgum vulgare*) and foxtail millet (*Setaria italica*) are the domesticated plants grown for feed for game birds. Some of the feed plots have been bordered with shrub lespedeza (*Lespedeza bicolor*) to serve as both shelter and food for wildlife.

JOHNSON GRASS (HABITAT 10).—Small areas in the lowlands have been invaded by the exotic, Johnson grass (*Sorgum halepense*). Because of the difference in growth habit, this type of vegetation has been differentiated from the tall grass of the uplands and set apart as a separate habitat. It comprises seven acres (1.1 per cent) of the study area.

MARSHY AREAS (HABITAT 11).—Associated with the numerous springs and seeps in the canyons and lowlands are small marshy areas. Three species of plants are most numerous in this habitat. They are: American bulrush (*Scirpus americanus*), spikesedge (*Eleocharis macrostachya*), and cattail (*Typha latifolia*). Marshy areas comprise 7.7 acres (1.2 per cent) of the study area. Following is a list of the 14 other species of plants identified from this habitat.

Bidens glaucescens—beggartick
Cyperus esculentus—chufa flatsedge
Cyperus inflexus—flatsedge
Cyperus strigosus—flatsedge
Desmodium illinoense—tickclover
Fuirena simplex—fuirena
Juncus diffusissimus—rush
Juncus interior—interior rush
Lycopus americana—American bugleweed
Mollugo verticillata—carpetweed
Polygonum hydropiperoides—swamp smartweed
Polygonum lapathifolium—smartweed
Rumex crispus—curly dock
Solidago canadensis—Canada goldenrod

MINOR AREAS OF DISTURBANCE (HABITAT 12).—Stripping away of the topsoil during the construction of earth-filled dams on the study area led to the establishment of a distinct kind of vegetation in these denuded areas. Owing to the discontinuity and small size (less than two acres in total area) of habitat 12, no effort was made to determine the exact extent or area of this habitat. The 19 species of plants identified from this habitat are, for the most part, pioneer annuals. They are as follows:

Andropogon gerardi—big bluestem
Artemisia ludoviciana—Louisiana sage
Aster ericoides—heath aster
Boltonia sp.—boltonia
Croton texensis—Texas croton
Cucurbita foetidissima—buffalo gourd
Echinochloa crus-galli—barnyard grass
Eragrostis trichodes—sand lovegrass
Euphorbia marginata—snow-on-the-mountain
Gutierrezia dracunculoides—Tarragon snakeweed
Lolium perenne—perennial ryegrass
Panicum capillare—common witchgrass
Polygonum serpyllifolia—smartweed
Solanum rostratum—buffalo bur nightshade
Solidago rigida—stiff goldenrod
Sorghastrum nutans—yellow Indian grass
Tribulus terrestris—puncture vine
Verbena simplex—verbena
Verbena stricta—verbena

Two other situations were recognized on the study area. Denuded areas, resulting from erosion in the previously cultivated fields or from the stripping away of the topsoil in various construction projects, comprise 3.8 acres (0.6 per cent) of the study area. The eight man-made lakes have a total surface area of 16 acres (2.5 per cent of the study area).

Although the time spent in this study was not long enough to permit the gathering of factual data on plant succession, the knowledge of past land use on the study area gives some clues as to the sequence of succession of plant communities there. Considering each of the habitats as a distinct plant community, the writer feels that three of the 12 habitats represent edaphic climax communities.

In the xeric uplands, a pure stand of sand bluestem (habitat 4) seemingly is the climax community. In the mesic lowlands, composed of the banks and flood plain of Sandy Creek and the numerous canyons, the woodlands (habitat 3) seem to be the climax plant community. The limited marshy areas (habitat 11) associated with the springs situated at the head of each of the canyons support the third type of edaphic climax community.

A scheme of hypothetical plant succession on the study area is presented graphically in figure 2. Each of the habitats, except the three considered as climaxes, may be termed seral stages. The pioneer vegetation of the first seral communities is homogenous whether the area in question is an upland or a lowland situation. It is only after this pioneer vegetation has been replaced by plants of the next seral communities that there is a noticeable difference between upland and lowland situations. In the uplands the pioneer

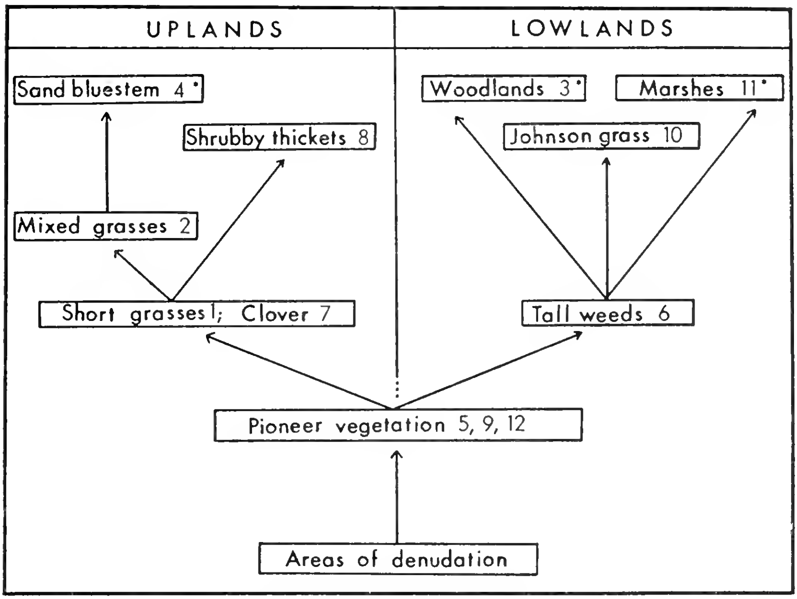

FIGURE 2. Hypothetical scheme of plant succession on the study area. Numbers refer to habitats discussed in text. An asterisk (*) denotes a climax community.

vegetation is replaced by either short grasses (habitat 1) or the exotic, white sweet clover (habitat 7). These, in turn, are replaced by either mixed grasses (habitat 2) or shrubby thickets (habitat 8). The mixed grasses are finally replaced by sand bluestem (habitat 4). Shrubby thickets maintain themselves in the upland climax community but seemingly are incapable of invading an established stand of sand bluestem. Habitat 8 is not considered a climax community.

In the lowlands, tall weeds (habitat 6) replace the pioneer vegetation of the first seral community. Depending upon the relative amount of soil moisture in a given area, the tall weeds are replaced by either woodlands (habitat 3) or marshy areas (habitat 11). Johnson grass (habitat 10) competes successfully with woodlands, but seemingly is unable to invade woodlands once they are established. Habitat 10, therefore, is not considered a climax community.

FOOD HABITS

Perhaps the most extensive, geographically, of the numerous studies of food habits of bobwhites was that by Judd (1905:1-46) in which he reported on the contents of 918 stomachs of bobwhites from 21 states (including Kansas), the District of Columbia, Canada, and Mexico. Outstanding studies of a more local nature include those by Korschgen (1952a) in Missouri, and Handley and Cottam (*in* Stoddard, 1931:113-165) in seven states in the southeastern United States. To my knowledge, the food habits of bobwhites in Kansas have been reported on only once since the study by Judd (*loc. cit.*). In 1941, Jennings published the results of his analysis of the contents of stomachs and crops from bobwhites taken in Osage and Riley counties, Kansas, in the hunting seasons of 1939 and 1940.

The diet of bobwhites usually is studied by analyzing the contents of either crops or stomachs, or both. For an accurate evaluation of diet throughout the year, bobwhites necessarily must be taken each month. It is difficult, and often impracticable, to kill numbers of bobwhites in late spring and early summer (the breeding season) when the population is at lowest ebb, consequently the food habits of the species in the breeding season are poorly known. Korschgen (*loc. cit.*) attempted to overcome these difficulties by examining droppings of bobwhites rather than crops or stomachs.

Food in the crop provides the most accurate picture of the food habits of bobwhites because material in the crop is little changed by enzymatic activity. Mechanical fragmentation of food found in the crop is limited to the action of the bill, and since bobwhites are not normally seed-crackers, food materials are little affected in this respect; even fleshy fruits and invertebrates are readily

PLATE 1

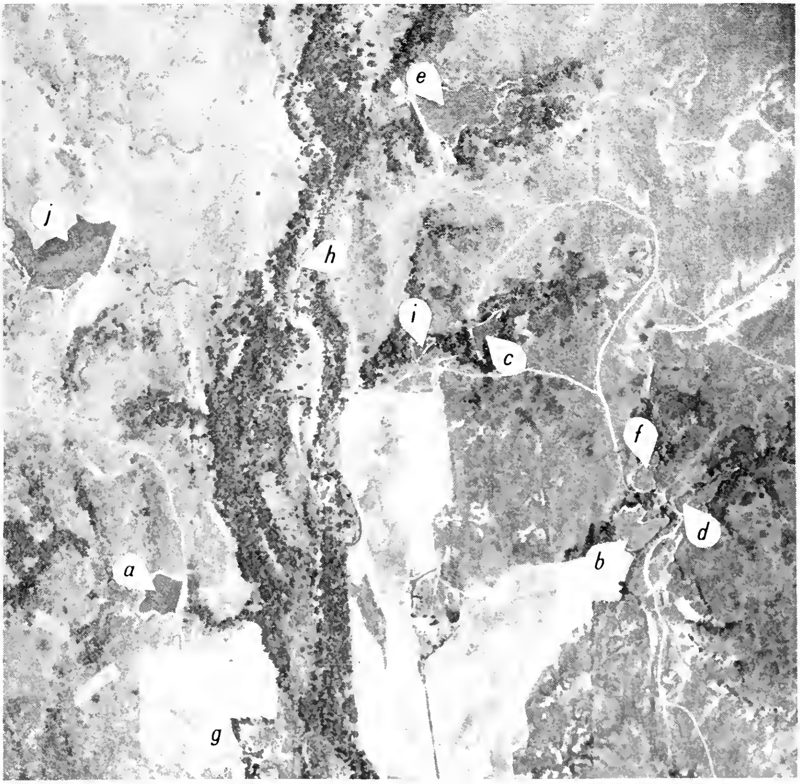

FIG. *a*. Aerial photograph, taken June, 1950, of the study area. North is at top of photograph. Letters on photograph denote the following features:

a. Bittersweet Lake
b. Clear Lake
c. Deep Lake
d. Long Lake
e. Mallard Lake
f. Mud Lake
g. Residence and out-buildings
h. Sandy Creek
i. Stump Lake
j. West Lake

FIG. *b*. Upland prairie in April, 1956. View looking northeast from 200 yards south of east end of Mallard Lake. Dark, disc-shaped areas are thickets of Chickasaw plum (*Prunus augustifolia*).

PLATE 2

Fig. *a*. Mixed-grass habitat in April, 1956. Photograph taken 200 yards east of Deep Lake. The tall, bunch-grass is little bluestem (*Andropogon scoparius*).

Fig. *b*. Woodland habitat in April, 1956. View of a wooded canyon, 100 yards west of dam of Mallard Lake. The tall grass in the foreground is sand bluestem (*Andropogon hallii*).

identifiable. Analyses based on stomach contents or droppings are distorted by digestive action on some food items.

Three principal methods are usually used to determine the diet of bobwhites; volumetric analysis, a count of whole fruits and animals, and calculation of the frequency of occurrence of each food in a series of crops, stomachs, or droppings. The latter method, usually used in analyses of droppings owing to the fragmentary nature of foods therein, at best gives only a rough index to the diet of bobwhites. Counts of the numbers of each kind of food found in the stomach or crop may yield a distorted picture of the diet of bobwhites unless the size of the particles of each food is taken into account; ten grains of corn constitute a relatively enormous amount of food to a bobwhite as compared to ten grains of foxtail millet. Volumetric analysis of food in the crop seems the best method for the determination of the food habits of bobwhites, because it avoids the errors inherent in the other two methods used in analyzing droppings or contents of stomachs, and the results may be treated statistically.

In order to obtain information regarding the food habits of bobwhites on the study area, 37 birds were shot in the period beginning September, 1951, and ending August, 1952. Since bobwhites feed principally in the early morning and late evening each bird was shot, whenever possible, in the midmorning or late evening hours to insure a maximum amount of food in the crop. In addition, 16 bobwhites shot by hunters on the study area on November 22, 1951, were examined. The crops of 43 of the 53 bobwhites examined contained food.

Within one hour after being shot, each bobwhite was weighed, and its age determined by methods reported in Robinson and Baker (1952:288-291) modified after Petrides and Nestler (1943). The crop was removed, weighed, and allowed to dry intact. After drying the crop was opened and the food therein identified. The volume of each kind of food in each crop was measured by means of a graduated cylinder, graduated in tenths of a milliliter. The volume of irregular objects, such as large grasshoppers, was determined by measuring the volume of number nine lead shot that they displaced. The contents of each crop were stored in a rubber-stoppered glass vial provided with anhydrous calcium chloride to keep the food materials dry. The calcium chloride was separated from the food by a cotton plug.

No bobwhites were taken for food habits study in the months of April, May and July, 1952, and only one was taken in June, 1952. These four months represent the principal breeding season of bobwhites. To have taken five or more bobwhites in each of these months would have reduced severely the breeding population on the study area.

Fruits and seeds were gathered from as many of the flowering plants on the study area as possible, and prepared as a reference collection to aid in identification of plant materials found in the crops.

The results of the analysis of the contents of the 43 crops are presented in table 1. The 32 plants identified to genus or species, exclusive of corn, represent 22.4 per cent of the 143 kinds of plants identified on the study area. Animals comprise only a minor portion of the diet of bobwhites on the study area, making up less than 15 per cent of the total volume of food for all but one of the nine months of record. Of the total volume of the contents of seven crops from bobwhites taken in October, 1951, 34.5 per cent was animal material, principally grasshoppers. Inorganic material, such as sand and gravel, comprised less than a trace (less than 0.1 milliliter) of the contents of each crop. The shells of small snails found in the crops may have been picked up by bobwhites for use as an abrasive in the stomach. The remains of the animals were not found in any of the shells.

Corn (*Zea mays*) was found in the crop of one bobwhite shot at 4:40 p. m., December 27, 1951, 20 yards east of Sandy Creek and 20 yards south of the north boundary of the study area. No corn was present on the study area in the period of the food habits study. On adjacent property a field, approximately 200 yards northeast of the place the bobwhite was killed, had been planted to corn. Probably this bobwhite had been feeding in this field a few hours before being shot.

Considering the number of months each kind of food was taken, and the portion of the total contents of crops for each month that each food represented, three kinds of plants seem the most important in the diet of bobwhites on the study area. These are, in order of importance, sorghum (*Sorgum vulgare*), wild bean (*Strophostyles leiosperma*), and foxtail millet (*Setaria italica*). Two of these, sorghum and foxtail millet, were planted expressly to furnish food for game birds, principally bobwhites.

Table 1. Food of Bobwhites on the Study Area in Per Cent of Total Volume of Total Contents of Crops for Each Month. "t" Signifies "Trace", or Less Than 0.1 Per Cent. "—" Signifies No Records for the Month.

Kind	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Animal												
Snails	t	1.9	t	t	......	......	t	–	–	......	–	......
Spiders	......	......	......	......	......	......	1.1	–	–	......	–	......
Beetles	4.2	3.2	......	......	2.3	0.6	t	–	–	......	–	t
Millipedes	......	......	......	......	......	0.5	......	–	–	......	–	......
Bugs	......	t	......	......	......	......	3.2	–	–	......	–	0.9
Ants	......	......	t	t	......	t	7.5	–	–	......	–	......
Caterpillars	......	......	......	......	......	......	......	–	–	......	–	1.2
Grasshoppers	9.6	29.4	......	......	......	......	1.1	–	–	......	–	7.1
Vegetal												
Amaranthus retroflexus	......	t	......	......	......	t	t	–	–	......	–	......
Redroot amaranth												
Ambrosia psilostachya	......	t	1.7	2.1	1.1	0.6	......	–	–	......	–	......
Western ragweed												
Ambrosia trifida	......	......	......	1.0	t	......	......	–	–	......	–	......
Giant ragweed												
Argemone intermedia	......	......	......	......	t	......	......	–	–	......	–	......
Prickly poppy												
Artemisia vulgaris	......	......	......	......	......	......	t	–	–	......	–	......
Mugwort												
Bromus catharticus	......	......	......	......	......	t	t	–	–	......	–	......
Rescue brome												
Cassia fasciculata	......	......	t	2.4	t	2.9	......	–	–	......	–	......
Senna												
Compositae,	......	......	......	......	......	......	t	–	–	......	–	......
unidentified												
Cornus sp.	6.6	4.6	6.0	0.7	0.2	......	......	–	–	......	–	4.0
Dogwood												

TABLE 1. FOOD OF BOBWHITES ON THE STUDY AREA IN PER CENT OF TOTAL VOLUME OF TOTAL CONTENTS OF CROPS FOR EACH MONTH. "t" SIGNIFIES "TRACE", OR LESS THAN 0.1 PER CENT. "—" SIGNIFIES NO RECORDS FOR THE MONTH.—CONTINUED.

Kind	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Croton texensis Texas croton	...	t	t	2.1	...	0.2	...	—	—	...	—	...
Digitaria filiformis Slender crabgrass	...	...	...	...	...	t	...	—	—	...	—	...
Euphorbia dentata Toothed euphorbia	12.0	7.9	9.1	t	0.2	t	...	—	—	...	—	...
Euphorbia marginata Snow-on-the-mountain	...	...	16.1	4.5	...	...	...	—	—	...	—	...
Grass, unidentified	t	t	t	...	...	...	...	—	—	...	—	...
Green vegetal, unidentified	4.8	5.9	5.0	10.5	0.8	0.8	22.7	—	—	...	—	...
Helianthus petiolaris Prairie sunflower	...	...	5.2	...	...	...	3.8	—	—	...	—	...
Lespedeza bicolor Shrub lespedeza	...	...	...	...	...	30.4	...	—	—	...	—	...
Lespedeza capitata Roundhead lespedeza	...	...	...	t	...	...	...	—	—	...	—	t
Lespedeza sp. Lespedeza	...	...	...	8.3	...	...	...	—	—	...	—	...
Lithospermum incisum Puccoon	...	...	...	...	t	0.2	...	—	—	...	—	...
Lotus americanus Deervetch	...	...	...	...	3.2	2.2	...	—	—	...	—	...
Monarda punctata Spotted beebalm	...	...	...	...	t	...	...	—	—	...	—	...
Morus rubra Red mulberry	...	...	...	...	...	...	...	—	—	97.0	—	...
Panicum capillare Common witchgrass	t	...	...	...	...	...	t	—	—	...	—	t

Table 1. Food of Bobwhites on the Study Area in Per Cent of Total Volume of Total Contents of Crops for Each Month. "t" Signifies "Trace", or Less Than 0.1 Per Cent. "—" Signifies No Records for the Month.—Concluded.

Kind	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Panicum sp. Panic grass	......	......	......	......	t	t	......	–	–	......	–	......
Polygonum lapathifolium Smartweed	......	......	3.8	t	......	t	......	–	–	......	–	......
Polygonum scandens Hedge cornbind	......	......	......	1.0	1.4	0.6	......	–	–	......	–	t
Rhus glabra Smooth sumac	......	......	......	6.9	......	......	60.0	–	–	......	–	......
Rumex crispus Curly dock	......	......	......	......	0.3	t	......	–	–	......	–	......
Setaria glauca Foxtail grass	12.0	t	......	......	0.3	t	t	–	–	......	–	......
Setaria italica Foxtail millet	39.7	6.5	10.5	3.8	1.4	1.4	......	–	–	......	–	18.0
Sorgum halepense Johnson grass	......	......	2.4	......	......	......	......	–	–	......	–	......
Sorgum vulgare Sorghum	7.3	29.4	31.4	41.2	......	......	......	–	–	......	–	68.0
Strophostyles leiosperma Wild bean	t	3.3	5.6	5.5	88.5	58.7	0.5	–	–	......	–	t
Unidentified, seeds	1.9	7.9	2.1	t	......	0.8	......	–	–	......	–	......
Vitis vulpina Frost grape	......	......	......	8.6	......	......	......	–	–	3.0	–	......
Zea mays Corn	......	......	......	1.4	......	......	......	–	–	......	–	......
Number of crops in sample	5	7	5	5	6	6	3	0	0	1	0	5

No one kind of food was taken by bobwhites in every month of record. Wild bean was taken in eight of the nine months; foxtail millet in seven months; and foxtail grass (*Setaria glauca*), sorghum, and western ragweed (*Ambrosia psilostachya*) in five months. If the kind of food taken by bobwhites depends upon availability, as suggested by Handley and Cottam (*in* Stoddard, 1931:123), and Baerg and Warren (1949:10), then the above five kinds of plants represent the plants most important to bobwhites with respect to length of time of availability.

If the relative amount of each kind of food found in the crops is an index to food preference, the foods mentioned in the two preceding paragraphs would be those foods preferred by bobwhites on the study area. It would seem that native plants (see fig. 3) and animals are the principal source of food for bobwhites on the

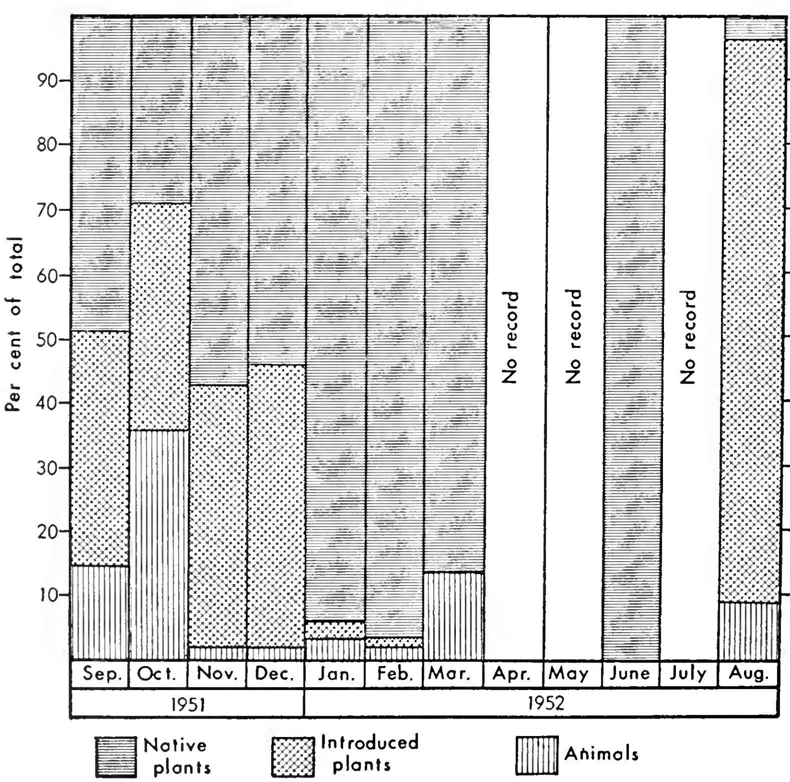

Figure 3. Food habits of bobwhites on the study area. See table 1 for number of crops examined each month.

study area, and that introduced plants are used when they become available.

From the standpoint of management, determination of the kinds of plant communities, or habitats, that furnish the most food for bobwhites seems more important than determination of seasonal or annual preferences. Table 2 illustrates the allocation, by per cent of volume, of each of the plant foods found in the crops, according to the habitats where these plants are found. For the nine months of record, three of the 12 habitats on the study area provided the major part (84.6 per cent) of the food of bobwhites. The greatest amount provided by a single habitat was that by the feed plots (habitat 9). Considering that this habitat comprises only 1.5 per cent of the study area, the use of the feed plots as a source of food by bobwhites is striking.

Second in importance is habitat 1 (short grasses) that provided 28.9 per cent of the food of bobwhites. The proportion of food obtained from habitat 5 (cropland) may be misleading, as only one kind of plant, wild bean, that occurred in this habitat was found in the crops. This legume also occurs in habitat 1, and the total volume of wild beans for each month has been apportioned to both habitats 1 and 5. It is possible that most of the wild bean found in the crops was eaten in habitat 1, thus increasing the importance of the short grass habitat as a source of food for bobwhites.

Two habitats, sand bluestem and white sweet clover, seemingly were not used by bobwhites as a source of food. This is of importance from the standpoint of land management as sand bluestem is the climax community of the uplands. The climax communities of the lowlands, woodlands and marshy areas, each furnished less than four per cent of the total food of bobwhites. Seemingly the bobwhites on the study area depended principally on the early seral community (short grass) of the uplands for food, and on the domestic crops planted in the feed plots. Of secondary importance were the shrubby thickets (habitat 8) and, perhaps, the luxuriant growth of wild bean in the cropland.

The use of grain from domestic crops (sorghum and foxtail millet) planted in the feed plots may be a result of concentration of these foods in small areas, and of the proximity of the plots to woody cover used by bobwhites. The feed plots have been planted each year since 1948, perhaps allowing the bobwhites to establish a pattern of behavior with regard to feeding habits that leads them frequently to the feed plots for food. Since the feed plots were

TABLE 2. DISTRIBUTION OF SPECIES OF PLANTS, IN PER CENT BY VOLUME OF 209.5 MILLILITERS OF CONTENTS OF 43 CROPS OF BOBWHITES, ACCORDING TO THE HABITATS WHERE SPECIES OF PLANTS CONCERNED OCCUR. "T" DENOTES PLANT SPECIES FOUND IN LESS THAN 0.1 MILLILITER OF THE TOTAL CONTENTS IN THE CROPS FOR EACH MONTH.

	Habitat											
	1	2	3	4	5	6	7	8	9	10	11	12
September	15.5	......	15.5	......	T	......	......	8.5	60.5	......	......	T
October	17.7	......	T	......	3.7	T	......	8.9	69.7	......	......	T
November	20.7	1.2	......	......	3.2	......	......	......	49.3	3.1	4.5	18.7
December	4.3	1.1	9.7	......	3.1	1.1	......	12.5	60.5	......	T	7.4
January	50.6	......	0.3	......	45.7	T	......	1.8	1.5	......	0.1	T
February	36.2	T	T	......	30.2	......	......	0.6	32.9	......	T	0.1
March	1.0	T	T	......	T	......	......	99.0	......	......	......	T
April	–	–	–	–	–	–	–	–	–	–	–	–
May	–	–	–	–	–	–	–	–	–	–	–	–
June	......	......	100.0	......	......	......	......	......	......	......	......	......
July	–	–	–	–	–	–	–	–	–	–	–	–
August	T	......	......	......	T	......	......	4.5	95.5	......	......	T
Annual	28.9	0.3	3.2	0.0	15.1	0.1	0.0	7.8	40.6	0.3	0.6	3.1

planted near woody cover known to be used by coveys of bobwhites, it is difficult to evaluate the effect of these plantings on the distribution of coveys on the study area. Seemingly the amount of food provided by the feed plots has had little effect upon numbers of bobwhites occupying the study area; following a peak in 1952, the size of the population has varied from year to year even though the feed plots were present in each of these years (see fig. 6).

In the northern part of the geographic range of the bobwhite heavy snow may cover the food supply, causing the birds to starve. In south-central Kansas winter storms, although often severe, are usually of short duration, and their effect upon the availability of food seemingly is minimal. Present-day farming practices are not conducive to the growth of native plants that furnish food for bobwhites, however it seems more likely that the attendant destruction of vegetation used by bobwhites for cover is more a limiting factor than is the scarcity of food. There is no evidence that food was a limiting factor for bobwhites on the study area.

Information as to competition for food between bobwhites and other animals is difficult to obtain. The truest picture of such competition would be gained by a study of the food habits of each kind of animal present on the study area. Such a task was not within the scope of this research. In the course of field work I have observed animals, other than bobwhites, feeding upon plants that bobwhites use as food. Pocket mice (*Perognathus flavescens copei* and *P. hispidus spilotus*) and kangaroo rats (*Dipodomys ordii richardsoni*) were observed feeding, at night, on heads of sorghum and foxtail millet that were lying on the ground. On two occasions fox squirrels (*Sciurus niger rufiventer*) were observed to bite through the upper stem of sorghum and carry off the whole head of ripe grain. Droppings of cottontail rabbits (*Sylvilagus floridanus llanensis*) and tracks of ring-necked pheasants (*Phasianus colchicus*), crows (*Corvus brachyrhynchos*) and unidentified species of small birds were numerous in the feed plots. Scats of raccoons (*Procyon lotor*), some of which were collected on the study area, contained remains of 10 plants (Stains, 1956:51) used by bobwhites on the study area as food.

Using the publication by Martin, Zim and Nelson (1951), it was possible to determine most of the kinds of vertebrates that might compete with bobwhites for food. In extracting this data, I limited myself to those kinds of vertebrates (principally birds and mammals) that occurred on the study area, and to those kinds of plants known to be used as food by bobwhites on the study area. With these limitations, comparisons were possible for 28 kinds of food plants. It was found that 93 species of animals, other than bobwhites, used one or more of these 28 kinds of plants as food. In foods eaten the ring-necked pheasant showed the most resemblance to the bobwhite; the pheasant used 19 of the 28 bobwhite foods. The effect of pheasants on bobwhites with respect to competition for food probably was minimal, as the total number of pheasants on the study area, to my knowledge, did not exceed 20 in the period of my field work. Cottontail rabbits and mourning doves (*Zenaidura macroura*), both numerous on the study area, were reported as using 13 of the 28 kinds of food. Cardinals (*Richmondena cardinalis*) and song sparrows (*Melospiza melodia*), except in the summer, were present in large numbers on the study area, and seemingly compete with bobwhites for nine kinds of plant food. Each of the remaining 88 species of animals shared less than eight kinds of food with bobwhites. Although it would seem that competition by bobwhites for food would be greatest with those animals using the most kinds of plants that are also used by bobwhites, competition probably is just as great, or greater, with native mice. Although, according to Martin *et al.* (*loc. cit.*), these mice use only a few of the food plants used by quail, the density of the population of small rodents may bring about a marked reduction in a small segment of the food supply of bobwhites. In any event, judging from my experience in the field, competition for food, although a factor in the ecology of bobwhites, is not limiting to populations of bobwhites.

POPULATION DYNAMICS

In the summer of 1952, ten traps were constructed following the specifications of Stoddard (1931:442-444). The base of each trap was made of 4 inch by ½ inch redwood; the tops, sides and entrance of ½ inch mesh hardware cloth. To protect bobwhites from being scalped while in the traps, ½ inch mesh fish netting was tied across the inside of each trap three inches from the top. The traps then were camouflaged with non-glossy green and brown paint.

On September 25, 1952, 40 trapping sites, each measured 4 x 4 feet, were prepared by removing the vegetation and two inches of the topsoil, and leveling the soil. The traps were taken to the stations where trapping was to begin, set to one side of the prepared sites, and propped open. From September 26 to September 30, 1952, each of the 40 trapping stations was baited with one pint of sorghum (milo maize) once each day. On October 1, 1952, the 10 traps were set. At the end of seven to 10 days each trap was moved to a new trapping station, so that by November 14, each of the 40 stations had been used. At the stations where traps were not set, baiting was continued at intervals of approximately three days in the hope that bobwhites would be attracted to the stations and thus be trapped more easily. This plan of trapping was continued to February 26, 1953, begun again on August 8, 1953, and terminated on November 28, 1953.

Trapping was found to be most successful when traps were set from noon to 2:00 p. m., and checked at or soon after sunset. Bobwhites could be handled with greater ease in the hours of twilight or darkness, and could be directed into a two-compartment holding box more easily than in the daylight. In addition, fewer birds attempted to fly or escape while in the traps in the dark, reducing the possibility of injuries.

To aid in the trapping of male bobwhites in the breeding season, 12 bobwhites, 10 females and two males, were obtained from the Calista hatchery of the Kansas Forestry, Fish and Game Commission. Cages measuring 12 inches on each side were constructed of hardware cloth, each cage being provided with pans for food and water, and a protective buffer of burlap that served also as a sunshade. One of these small cages containing a female bobwhite was placed inside of a Stoddard-type trap and placed in cover known to be frequented by males. The traps were moved every two to seven days in order to include as much of the study area as possible.

Each captured bobwhite was banded with a serially numbered aluminum leg band bearing the return address of the State Biological Survey of Kansas. Each time a bobwhite was captured its age was determined by an examination, and measurement when applicable, of the primary flight feathers and their coverts. In addition each bird was sexed, weighed, and its temperature determined by inserting the sensing bulb of a rapid-registering thermometer to a depth of one half inch into the cloaca.

In the entire period of trapping, 193 bobwhites were captured a total of 386 times. A total of 838 trap-days were accumulated with an over-all average of 0.46 bobwhites captured per trap-day. Of the total number of trap-days, 593 yielded 341 captures when sorghum was used as bait, and 245 trap-days yielded 41 captures when live females were used as decoys. Seemingly sorghum was the more efficient means of enticing the birds into traps, as the average number of captures per trap-day was 0.57 and 0.18 when sorghum and live females, respectively, were used. Such a comparison is misleading, because only one male bobwhite was captured in each trap containing a live female whereas multiple captures were the rule when sorghum was used as bait.

Examination of 181 individuals (172 trapped, and nine shot for food habits studies) in the non-breeding season of 1952-1953, revealed that 51 (28.2 per cent) were hatched prior to 1952, and 130 (71.8 per cent) were hatched in the breeding season of 1952. Of the 51 adult birds, 33 (64.6 per cent) were males and 18 (35.4 per cent) were females. Of the 121 young birds that could be sexed, 60 (49.6 per cent) were males and 61 (50.4 per cent) were females. Considering young and adults together, the sex ratio was 112 males to 100 females. This ratio is comparable to that reported by Stoddard (1931:90); for approximately 20,000 bobwhites in Georgia, he found the sex ratio in the winter to be approximately 114-100. The approximation of a 100-100 ratio of the sexes among young birds on the study area suggests that there may be differential mortality between the sexes. The excess males in the sample of the population on the study area were all old birds, suggesting that fewer females live through the winter and/or breeding season than do males.

Comparison of the percentage of young birds in the population on the study area with percentages presented by Robinson and Baker (1952, 1953, 1954, and 1955) reveals that productivity of bobwhites on the study area was below that which is considered optimum. Such comparisons probably are invalid because the percentage of young on the study area was computed from a sample collected from August through January, whereas data in Robinson and Baker (*op. cit.*) are from a more limited period (late November and early December, 1951 through 1954).

Information regarding the composition of the population on the study area in the non-breeding seasons of 1951-1952, and 1953-1954, is inconclusive owing to the small size of the samples. Of 50 bobwhites shot from September, 1951 to February, 1952, in order to examine the food in their crops, five (10 per cent) were adults, and 45 (90 per cent) were young. Four of the adults were males, one a female; 29 of the young were males, and 16 were females. Only seven bobwhites were trapped and examined in the late summer and autumn of 1953. All were young birds; two were males and five were females.

Data on the composition of coveys on the study area were obtained when all members of nine such aggregations were captured in the autumn of 1952. To insure that every individual in each covey had been trapped, each of the coveys was observed before and after trapping to ascertain the total number of birds in each. The composition of these coveys was as follows (all dates are in 1952):

(A) Trapped at Station 5, on October 1, 2, and 3—13 birds
Adults—3 (1 male, 2 females)
Young—10
7 (3 males, 4 females) hatched on June 26
3 (2 males, 1 female) hatched on June 14

(B) Trapped at Station 30, on October 11, 12 and 14—22 birds
Adults—10 (5 males, 5 females)
Young—12
2 (females) hatched on July 10
4 (sex indet.) hatched on August 9
4 (sex indet.) hatched on August 14
2 (sex indet.) hatched on August 23

(C) Trapped at Station 2, on October 14—13 birds
Adults—2 (1 male, 1 female)
Young—11
5 (3 males, 2 females) hatched on June 10
3 (1 male, 2 females) hatched on June 15
3 (females) hatched on June 20

(D) Trapped at Station 31, on October 16, 18 and 23—6 birds
Adults—0
Young—6
3 (2 males, 1 female) hatched on June 18
1 (female) hatched on June 28
2 (1 male, 1 female) hatched on July 3

(E) Trapped at Station 35, on October 23—7 birds
Adults—4 (3 males, 1 female)
Young—3 (2 males, 1 female) hatched on June 25

(F) Trapped at Station 3, on October 27—10 birds
Adults—0
Young—10
5 (3 males, 2 females) hatched prior to June 1
3 (1 male, 2 females) hatched on June 16
2 (1 male, 1 female) hatched on June 23

(G) Trapped at Station 28, on November 2 and 9—12 birds
- Adults—2 (males)
- Young—10
  - 1 (male) hatched prior to June 5
  - 1 (male) hatched on June 21
  - 4 (3 males, 1 female) hatched on June 27
  - 1 (male) hatched on July 7
  - 1 (female) hatched on July 31

(H) Trapped at Station 16, on November 7 and 9—18 birds
- Adults—2 (1 male, 1 female)
- Young—16
  - 15 (6 males, 9 females) hatched prior to June 13
  - 1 (female) hatched June 21

(I) Trapped at Station 36, on November 2 and 9—13 birds
- Adults—5 (4 males, 1 female)
- Young—8
  - 5 (3 males, 2 females) hatched on July 7
  - 1 (male) hatched on July 14
  - 1 (female) hatched on June 23
  - 1 (female) hatched on June 28

The above data reflect the fact that coveys of bobwhites in the autumn are composed of young and adults from a number of family groups. These nine coveys were composed of a total of 27 age-classes of young birds, an average of three age-classes of young in each covey. Since young birds that hatched one or two weeks apart are not readily distinguishable from one another, observations made at a distance in the field may be misleading with respect to the numbers of age-classes of young comprising a covey. Covey A, if seen in the field, might be identified as a single family group with one extra female. Covey I might be identified as composed of two age-classes of young, and covey H might be identified as made up of members of a single family. The composition of coveys D and F indicates that the presence of adults is not necessary for a group of bobwhites to function as a covey. The composition of covey E indicates that adults can outnumber young birds in a covey even as early in the autumn as late October.

In addition to the combination of two or more families to form a covey, as illustrated by the above data, recapture of banded birds revealed that there is interchange of individuals among coveys. Of the total of 386 captures of bobwhites, 45 represented movements of 39 individuals. Of the total movements, 11 were of males in the breeding season of 1953, four were of males banded in the non-breeding season of 1952-1953 and recaptured in the breeding season of 1953, and 30 were of movements of individuals in the non-breeding seasons of 1952-1953 and 1953-1954 (see fig. 4).

The average distance moved by males in the breeding season was 419 yards (a minimum of 110 yards to a maximum of 650 yards). The average time involved in these movements was seven days (1 to 23). Of the four records of movements from the autumn and winter of 1952-1953 to the summer of 1953, the average distance moved was 524 yards (350 to 950), and the average time between captures was 228 days (201 to 255). Movements of bobwhites in the autumn and winter averaged 277 yards (100 to 460), with an

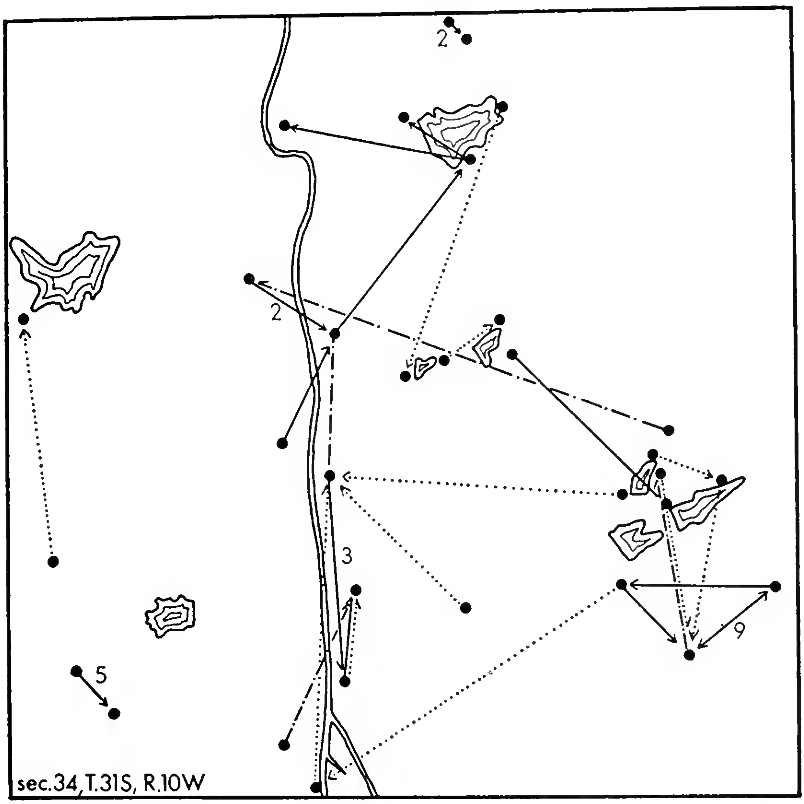

FIGURE 4. Movements of bobwhites on the study area as shown by recovery of banded individuals. Solid line, movements of individuals in the non-breeding season; dotted line, of males in the breeding season; line of dots and dashes, of males banded in the autumn of 1952 and recaptured in the breeding season of 1953. Movements of more than one individual from one locality to another are indicated by numbers, corresponding to the number of individuals, placed near the arrows.

average interval of time of 29.5 days (11 to 54). The distances reported in this paragraph were determined by measuring the least distance between points of capture, and therefore represent the most conservative estimate of distances moved.

Owing to the limitations imposed by the methods used in the trapping and banding operations, comparisons among the averages or extremes of time involved in the movements of individuals are of little or no value.

Distances moved by males in the breeding season (spring and summer) were almost twice as far as in the non-breeding season. In the non-breeding season, males seemingly move farther than do females. Of 18 records of movements of males, the average distance was 270 yards; of 12 records of movements of females, the average distance was 219 yards. The difference between these two averages is not statistically significant, and there may be no real difference in mobility of the sexes in the non-breeding season. The average distance moved by young of the year (226 yards) and by adults (297 yards) also is not statistically significant. However, the difference suggests more permanent bonds between young birds and their covey, than between adults and the covey of which they are a member in the non-breeding season.

All of the returns of banded bobwhites were from the study area. Although neighboring landowners, and hunters in the vicinity of the study area, were advised of the presence of banded bobwhites there, none was reported as killed off the area.

In addition to live-trapping and banding, bobwhites on the study area were censused. Little is known regarding numbers of bobwhites on the study area prior to the autumn of 1946. Mead (1899b: 278), writing of the period, 1859-1869, reported that bobwhites were plentiful in south-central Kansas. He observed (1899a:216) also that there seemingly had been a decrease in numbers of bobwhites in that part of Kansas following settlement of the region. That Barber County provided favorable habitat for bobwhites, at least in the 1870's, is illustrated by McNeal's statement (1922:11) that, "Barber County is unique in that it was fairly well timbered, while north and east of it was a treeless prairie." Mr. Amsden informed me that for many years prior to the time he acquired the study area, bobwhites were hunted in the legal hunting seasons there.

Carefully kept notes, kindly made available to me by Mr. Amsden, provide the first record of numbers of bobwhites on the study area.

In the autumn of 1946, Mr. Amsden censused the area and found only two coveys of bobwhites, totaling 25 birds. A census in the autumn of 1948, revealed 14 coveys totaling 169 birds. The study area was censused each autumn from 1951 through 1955, using excellent bird dogs owned by Mr. Amsden and Mr. Crocker. Each of the censuses involved the direct-count method, care being taken to avoid counting coveys more than once in each census. The censuses of the autumns of 1954 and 1955, were made by Mr. Amsden and Mr. Crocker.

Figure 6 presents the results of the seven autumn censuses made in the period, 1946 through 1955. From 1946 to 1952, the numbers of coveys of bobwhites and of individuals increased on the study area. From 1952 to 1954, the population declined. The population in the autumn of 1955 was larger than that of 1954.

The correlation between climatic conditions in the six months breeding season (April through September) and productivity of bobwhites in the whole of Kansas is in agreement with the correlation between climatic conditions in Barber County, Kansas, and variations in the size of the population of bobwhites on the study area. To summarize the conclusions of Robinson and Baker (1952, 1953, 1954 and 1955) regarding productivity of bobwhites as measured by the ratio of young to old birds in the autumn in Kansas, good productivity occurs when total rainfall in the breeding season exceeds 16 inches. Poor productivity occurs when total rainfall in this period is less than 14 inches. When rainfall in the breeding season totals from 14 to 16 inches, at least in the central third of Kansas, productivity seems to be related to average temperature in the breeding season; moderate temperatures (72° F. or below) are correlated with good productivity, and high temperatures (74° F. or higher) with poor productivity (Robinson and Baker, 1955:357).

In each of three years (1946, 1953 and 1954) of the total of 10 years for which there is record of the size of the population of bobwhites on the area studied, climatic conditions in the breeding season were unfavorable for good productivity of bobwhites. In each of the other seven years, rainfall in the breeding season exceeded 15 inches, and conditions otherwise were usually favorable for good productivity (see fig. 5).

It is difficult to determine whether the small number of bobwhites on the study area in the autumn of 1946 was due to unfavorable climatic conditions in the breeding season of 1946, or to

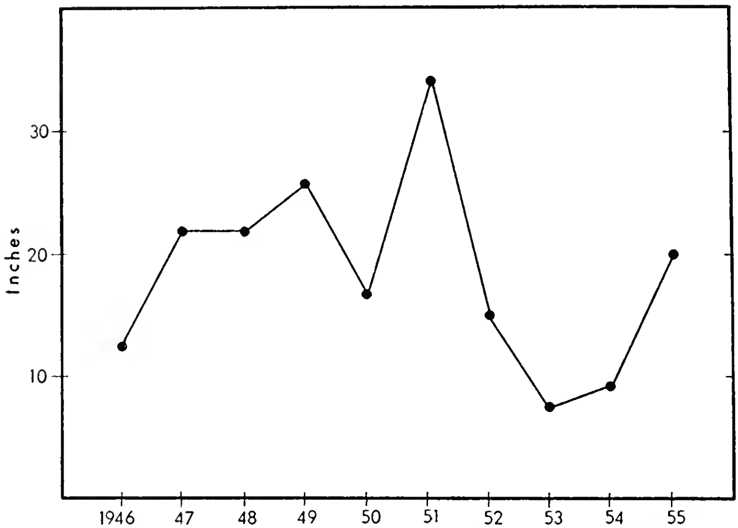

Figure 5. Total rainfall, April through September, received at Medicine Lodge, Barber County, Kansas, 1946 to 1955. (Two miles north and 10 miles west of the study area.)

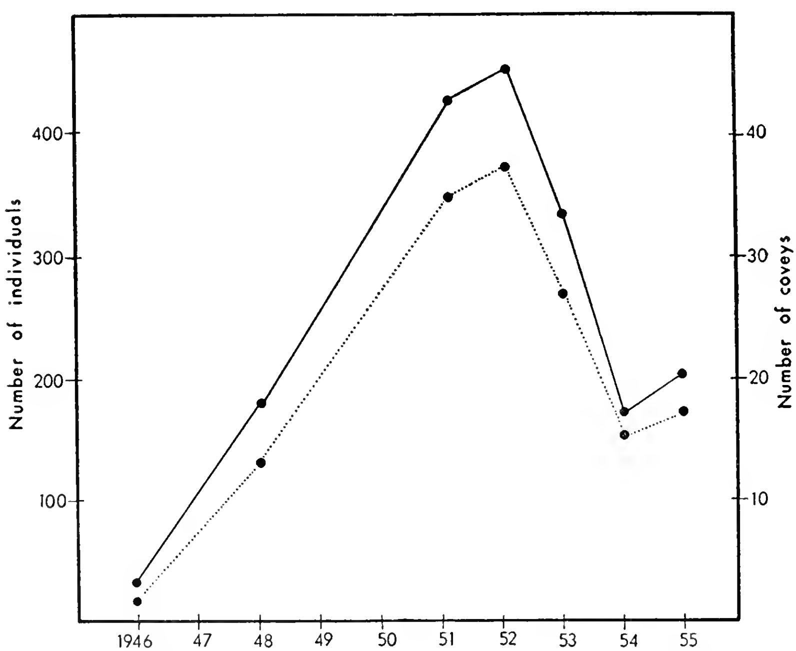

Figure 6. Numbers of bobwhites on the study area in autumns, 1946 to 1955. Solid line, number of individuals; dotted line, number of coveys.

unfavorable habitat resulting from many years of intensive land use. Probably both these factors had a detrimental effect upon bobwhites on the study area. Beginning in 1947, and continuing through the breeding season of 1952, climatic conditions were favorable for good productivity and, as the results of the censuses show, numbers of individuals and of coveys increased to a peak in the autumn of 1952. In the breeding seasons of 1953 and 1954, the study area experienced a severe drought. Only 7.96 inches of rain fell from April through September, 1953, and 9.01 inches in the breeding season of 1954. From the peak population of the autumn of 1952, comprising 462 bobwhites in 37 coveys, numbers of bobwhites decreased to 329 individuals in 27 coveys in the autumn of 1953, and to only 165 individuals in 15 coveys in the autumn of 1954. With the return of climatic conditions favorable for good productivity (19.86 inches of rain fell in the breeding season of 1955) the population increased to 198 individuals in 18 coveys in the autumn of 1955.

Analysis of wings of bobwhites contributed by interested sportsmen in Kansas from 1951 through 1955, yielded information regarding productivity of bobwhites, but not necessarily about changes in numbers of bobwhites. Although good productivity results in more young birds in the autumn than does poor productivity, analyses of wings cannot be used to determine the actual size of the population. However, comparison of climatic conditions in the breeding season with populations of bobwhites on the study area in several autumns throws some light on the effect of climate on numbers of bobwhites. With reference to figures 5 and 6, climatic conditions in the breeding season that seemingly produce good productivity also are correlated with an increase in numbers of bobwhites. Unfavorable climate is correlated with poor productivity and with a decrease in the bobwhite population. Of special interest is the number of bobwhites on the study area in the autumn of 1955. Even though precipitation in the breeding season of 1955 was favorable for good productivity, the increase in numbers of bobwhites over that of the preceding autumn was slight. Seemingly, bobwhite populations cannot attain maximum size in one year following a severe reduction in their numbers in preceding years. This would suggest that not only must the climatic conditions in the breeding season of one year be taken into account, but those of the previous seasons also must be considered if a usable index to numbers of bobwhites is to be found.

It is unfortunate that the effects of climate on numbers of bobwhites on the study area must be compounded by another series of complex factors, that of the progressive change of the habitat on the area. Vegetation on the study area seemingly became increasingly favorable for bobwhites following the acquisition of the area in 1946 by Mr. Amsden. If the study area had been used as intensively by man from 1946 to 1955 as it had in the years before 1946, numbers of bobwhites probably would not have increased so markedly from 1946 to 1952, even with favorable climatic conditions, and possibly the decline in the population, as seen in the autumns of 1953 and 1954, would have been more severe.

There is evidence that the increase in area of the climax plant community (sand bluestem) of the uplands on the study area may have confused even further the relationship between climatic conditions and size of the population. Analysis of food habits of bobwhites on the area indicates that they do no eat sand bluestem. Field observations indicate that bobwhites did not use this habitat for any of their other normal activities. Seemingly the climax plant community of the uplands is not suitable habitat for bobwhites. It follows that any increase in the extent of this type of vegetation reduces the carrying capacity of the study area for bobwhites. Just when this supposed reduction began, I am unable to say. Possibly the peak population in the autumn of 1952 may not represent the maximum carrying capacity of the study area. The decline in the population, as seen in the autumns of 1953 and 1954, may have been accentuated by the increasing extent of the sand bluestem habitat, and the increase in numbers of bobwhites, seen in the autumn of 1955, might have been more marked if the sand bluestem had been more limited in extent. If this supposed effect of the sand bluestem habitat is real, moderate land use in the form, perhaps, of grazing might increase the carrying capacity of the area for bobwhites.

In addition to the autumn censuses, counts were made of bobwhites in the winters and breeding seasons of 1951 through 1953 (fig. 7 presents the results of these censuses). The estimate of the population on the study area in late November, 1951, is based on a count of approximately two-thirds of the total population. On November 20, 22, and 23, 1952, 26 bobwhites were killed by hunters on the area. Of these, 10 were banded. From October 1 to November 23, 1952, 154 bobwhites had been banded on the area. If the proportion of banded to non-banded birds killed by hunters

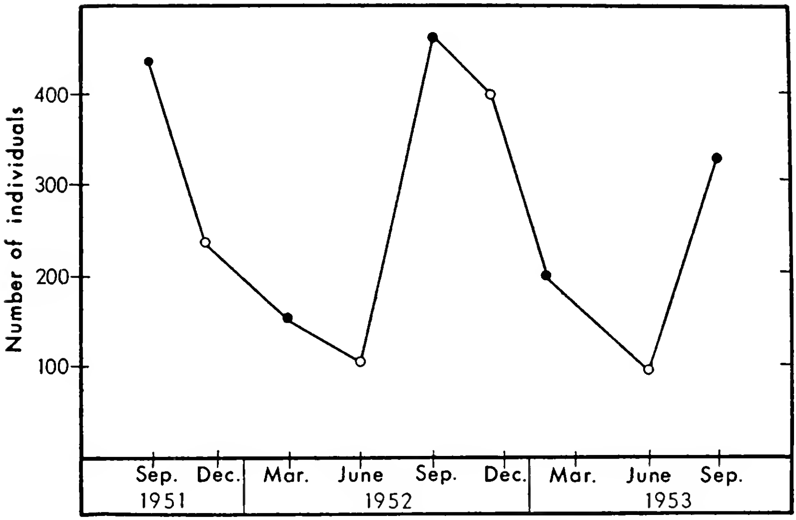

FIGURE 7. Numbers of bobwhites on the study area, September, 1951, through September, 1953. Solid dots, actual counts; open circles, estimates.

was the same as the proportion of banded to non-banded individuals in the entire population (the Lincoln index), there were approximately 400 bobwhites occupying the study area in late November, 1952. Although the Lincoln index often may be unreliable in estimating the size of populations of animals, the result obtained from its application in this case does not deviate markedly from the expected; thus this estimate is included in figure 7.

The numbers of bobwhites estimated to occupy the study area in the breeding seasons are based on the number of males heard whistling on the study area in those seasons. Stoddard (1931:339) believes that, usually only the unmated cocks whistle, and Bennitt (1951:13) presents data to substantiate Stoddard's conclusions. Stoddard (*op. cit.*:340) indicates that the number of unmated cocks is a function of the sex ratio; the larger the excess of males, the larger the number of whistling cocks in the breeding season. Evidence, although inconclusive, that mated males whistle in the breeding season may make the following system of computation invalid. The sex ratio of the adult bobwhites live-trapped in 1952-1953 was 183-100, or a ratio of unmated to mated males of 83-100. In the breeding season of 1952, 30 male bobwhites were heard whistling on the area. On the basis of the percentage of excess males in the autumn, there seemed to be 36 mated males on the area in the breeding season in addition to the 30 unmated birds; an additional 36 females, it is assumed, were present as mates for the mated males. The resulting estimate of the breeding population would be 102 birds (36 mated pairs, and 30 unmated males).

Too few individuals were captured in the autumn of 1953, to permit the computation of the sex ratio, and I have assumed that the sex ratio for adults in the breeding season of 1953 was the same as that in the breeding season of 1952. In the spring and summer of 1953, 27 males were heard whistling on the area. Using the same system of computation as presented in the preceding paragraph, the resulting estimate of the breeding population in 1953 was 91 birds (32 mated pairs, and 27 unmated males).

The estimate of the 36 mated pairs on the study area in the spring and summer of 1952, seemingly accounts satisfactorily for the 37 coveys of bobwhites found in the census of September of that year. That nests of bobwhites are not 100 per cent successful has been established by Stoddard (*op. cit.*:184), Parmalee (1955: 47), and others, indicating that more than 37 pairs of breeding adults would be required to account for the 37 coveys found. However, renesting by pairs that had nested unsuccessfully in the early part of the breeding season might reduce the number of pairs required to produce the 37 coveys. Considering the information on composition of coveys, presented earlier, it would seem that the estimate of 36 mated pairs of bobwhites could not account for all the coveys found in the autumn of 1952. The seemingly disproportionate number of coveys in the autumn probably resulted from the immigration of coveys onto the study area in late summer. The vegetation of lands adjoining the study area is much less dense than that of the study area, and bobwhites may have moved onto the area with the approach of the colder season. I was unable to determine whether bobwhites emigrated from the study area at the onset of the breeding season.

Although the estimate of the breeding population in 1953 may be based on an erroneous assumption (that the sex ratio of adults was the same in 1952 and 1953), the 32 mated pairs supposedly occupying the area in the breeding season of 1953 account somewhat more satisfactorily for the 27 coveys found in the autumn of that year.

Stoddard's (*op. cit.*:339) and Bennitt's (*loc. cit.*) findings that unmated cocks do the most whistling in the breeding season, forming the basis for the determination of the size of the breeding population in 1952 and 1953, may be in error. Data on the correlation between whistling of males and hatching of young, although not conclusive, indicate that mated males whistle more frequently than previously supposed. These data are more logically presented in a later section of this paper.

The results of the censuses and estimates presented in figure 7 show the variations in size of the population through several seasons, and present graphically the loss of individuals to natural causes in the non-breeding season, and the recovery of the population from a low point in the early part of the breeding season to a peak in early autumn.

Figure 8 is the result of an analysis of the data in figure 7, and presents the monthly and seasonal rate of change in the population. Since the data in figure 8 are biased by the time of year that each of the censuses or estimates was made, only generalizations may be made regarding them. Seemingly, the population is in dynamic equilibrium, with loss of individuals equaling gain, only in the early summer and early autumn. At all other times either the gain is greater than the loss, or the reverse is the case, with the period of gain approximately one-fourth as long as that of the loss. That the rate of decrease is greatest when the population is

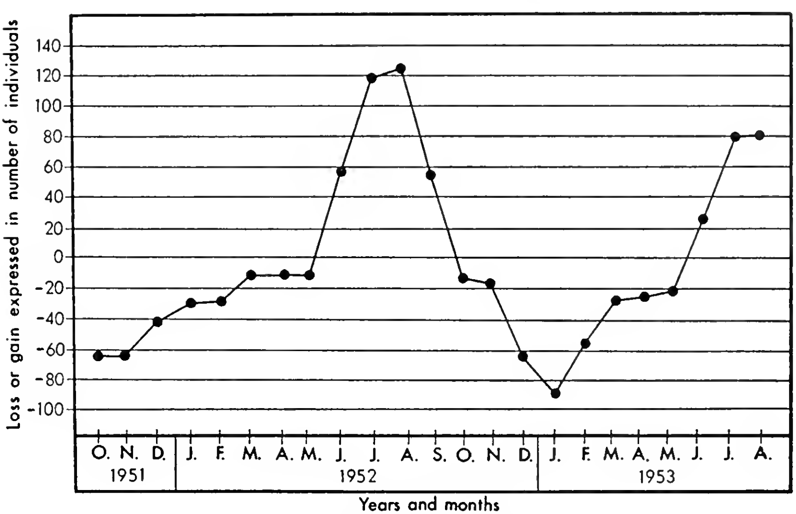

FIGURE 8. Loss or gain per month in the population of bobwhites on the study area, October, 1951, through August, 1953, expressed in number of individuals. Points above the base line of zero indicate an increasing population; points below the base line indicate a decreasing population. See fig. 7 for actual size of the population in different years.

near its peak suggests that mortality is a function of population size. Of interest is the number of bobwhites lost or gained each month. The largest number lost, likewise the greatest rate of decline, was in January of 1953, when 94 bobwhites were lost from the population; the greatest rate of increase was in August, 1952, when 122 individuals were added.

Baumgartner (1944) intensively censused bobwhites on some areas in Payne County, Oklahoma, on April 1, November 1, and January 1, in each of the five years, 1939 to 1943. His data indicate that, from April 1 to November 1, the average increment in size of the population was 250 per cent (a minimum of 174 to a maximum of 320 per cent) on areas that were hunted, and 190 per cent (115-409) on areas that were closed to hunting. From April 1 to November 1, 1952, the population on my study area increased by 293 per cent. From November 1 to January 1, numbers of bobwhites on hunted areas in Payne County, Oklahoma, decreased by an average of 42 per cent (28-51), and by six per cent (5-7) on non-hunted areas. In 1952 and 1953, numbers of bobwhites on my study area decreased, from November 1 to January 1, by an average of 25.5 per cent (13-38).

No particular cause for the decrease in numbers of bobwhites on the study area from late summer to the breeding season could be ascertained. Of the bobwhites examined by me, none was excessively infested with ectoparasites, and none was diseased. Only one injured bobwhite was found; examination of a juvenal male trapped on October 27, 1952, revealed a small twig, four inches in length, imbedded to a depth of one and one-half inches in the muscles of the ventrolateral aspect of the body immediately anterior to the left thigh. The stick was removed, and the wound was suppurating and had a foul odor. The bird was released and not trapped again.

Severe storms seemingly caused no excessive mortality among bobwhites on the area. Reconnaissance of the area during and following storms revealed no dead or injured bobwhites.

Predatory vertebrates of several kinds are numerous on the study area, with raptorial birds comprising the majority of individuals. Investigation of the food habits of predatory vertebrates by Fisher (1893), Dearborn (1932), Errington and Breckenridge (1936 and 1938), Errington, Hamerstrom and Hamerstrom (1940), Latham (1950), Korschgen (1952b), and others has shown conclusively that no kinds of predators, with the possible exception of the goshawk

(*Accipiter gentilis*) and the Cooper's hawk (*A. cooperi*), use bobwhites as a major source of food. I have never seen a goshawk on the study area, and Cooper's hawks are so uncommon there that their effect upon bobwhites would be minimal.

Only a few instances of predation, where the predator could be identified, were recorded on the study area. In the winter of 1950-1951, Mr. Amsden sent to Dr. Rollin H. Baker, Museum of Natural History, University of Kansas, one pellet of a great horned owl (*Bubo virginianus*). This pellet contained the remains of a bobwhite. On December 1, 1951, Mr. Crocker saw a long-eared owl (*Asio otus*) in flight carrying a bobwhite in its talons. On November 24, 1951, I flushed a long-eared owl from a stand of mixed grasses at the edge of one of the canyons; on the ground where the owl had been I found numerous bobwhite feathers. Later in the same day, I found bobwhite feathers beneath a small tree used as a roost by long-eared owls. Examination of approximately 2000 pellets of great horned owls, long-eared owls, and screech owls (*Otus asio*) revealed no bobwhites.

Coyotes seemingly used the wheel-track roads on the study area as pathways in their foraging on the area, judging from the numerous droppings of these animals found in the roads. Examination of approximately 150 such droppings revealed that coyotes were feeding principally on mammals, chiefly rabbits; no bobwhites were found in the scats. Examination of droppings of raccoons (*Procyon lotor*) by Stains (1956:50), many of which droppings were collected on the study area, revealed no bobwhites. Seven bobwhites were killed in the traps in 1952 and 1953. Five were killed by opposums, and two by unknown predators.

On the morning of January 3, 1953, while I was observing a covey of bobwhites feeding in the short grass near the east end of Mallard Lake, a female marsh hawk (*Circus cyaneus*) dived at the covey, causing it to flush and scatter. The hawk dived twice more at the bobwhites, each time approaching to within five feet of the ground, but did not attempt to strike any of the birds. Following the "attack" of the marsh hawk, the covey retired to a dense thicket of smooth sumac near the edge of the lake.

My data are inconclusive regarding predation on bobwhites. However, the density of the cover, and the abundance of small mammals that served as prey for carnivores seemingly combined to reduce the extent of predation on bobwhites. It would seem that a number of causes were involved in the loss of bobwhites in the non-breeding season, and that no one of these causes brought about a serious reduction in numbers of bobwhites.

The Breeding Season

Towards the end of winter, or the beginning of spring, coveys that have survived the colder months begin breaking up; this process is termed the spring "shuffle" by most investigators. During and following the disintegration of coveys, the first "ah-bob-white" whistles of males are heard. The first such whistles heard usually are considered as signaling the beginning of the breeding season. Stanford (1952:82-83) indicates that the breeding season in Missouri begins from late March to late April. Parmalee (1955:45) heard the first whistling of males in east-central Texas in 1950 on April 1, and Stoddard (1931:16) states that the first whistles usually are heard in the first week in April; however, in the "advanced" spring of 1927, the first mate heard whistling was on February 16.

On the study area, in 1952, the first whistle of a male bobwhite was heard on April 3, although a neighboring farm boy reported hearing a male bobwhite whistling, one mile south of the study area, on March 16. By mid-March, 1952, coveys on the study area were becoming increasingly difficult to find, indicating that the spring shuffle was in progress. In 1953, March 23 was the date of the first whistling by male bobwhites on the area.

In the breeding season of 1952, males were located on the study area by triangulation when they were heard whistling, and by observation. In addition, intensive efforts were made to locate nests. A flushing-bar constructed by M. F. Baker, illustrated in his publication (1953: pl. 4a, facing p. 35), was attached to the front bumper of a Jeep and operated in all habitats except the woodlands, shrubby thickets, and marshy areas, where density of the vegetation or softness of the soil prevented its use. To increase the noisiness, and presumably the effectiveness, of the flushing-bar, tin cans with both ends removed were strung on the bar that was dragged over the ground. In those habitats where the flushing-bar could not be used, bird dogs were employed to locate nests. In addition, I walked through much of the woody and marshy vegetation beating the low vegetation with a stick in hopes of flushing adult bobwhites from their nests. None of these efforts was successful in locating nests of bobwhites. The operations were repeated in the breeding season of 1953, with similar results.

On the evening of July 31, 1952, Mr. Crocker informed me that, while mowing in the sand bluestem habitat in the northwest quarter of the study area that day, he had flushed a female bobwhite from a nest containing 12 eggs. On the morning of August 1, I investigated the nest and found that it had been visited by some predator, all of the eggs being opened and the contents eaten. This was the only nest of bobwhites found on the study area.

Fortunately, data provided by aging of young bobwhites live-trapped in the autumn and winter of 1952-1953, yielded information regarding some of the events in the breeding season of 1952. The results are presented in figure 9. Hatching began in mid-May, reached a peak in late June, declined to a low point in early August, reached a secondary peak in mid-August, and declined thereafter. More than half of the young bobwhites that were live-trapped and aged in the non-breeding season of 1952-1953, were hatched in the last half of June, 1952.

It is known that the period of incubation for bobwhites is approximately 23 days, and that an average of one egg is laid per day until the clutch, averaging 13 eggs, is completed. Adding an additional two days for selection of a nesting site and construction of the nest gives a period of approximately 38 days from initiation of nesting to hatching. The frequency of the initiation of successful nesting on the study area was determined by adding, in figure 9, a curve identical to the one for frequency of hatching, but oriented

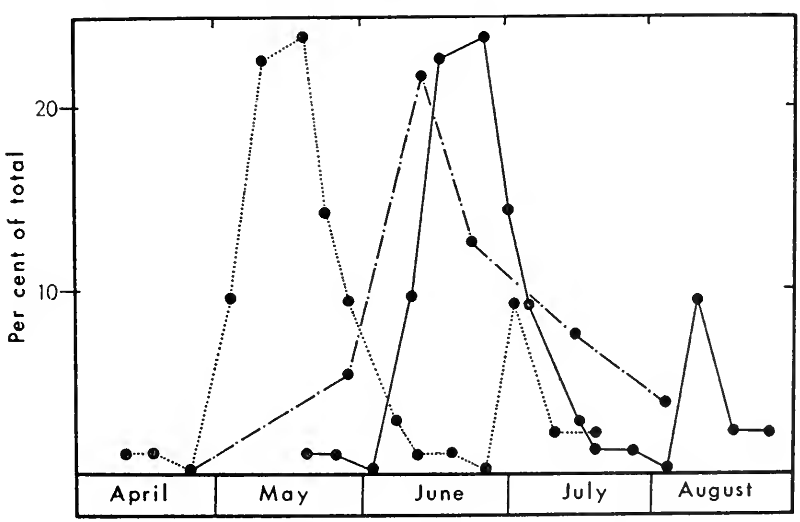

FIGURE 9. Events in the life history of bobwhites in the breeding season of 1952. Solid line, hatching of young; dotted line, initiation of nesting that was successful; dotted and dashed line, numbers of males whistling (in the Figure, numbers of whistling males are reduced by one-half).

38 days earlier in the breeding season. Nesting that resulted in successful hatching seemingly began in mid-April, reached a peak in mid-May, declined to a low point in late June, reached a secondary peak in early July, and declined thereafter. The finding of a nest on the study area on July 31, 1952, indicates that nesting was still in progress at that time. More than half of all the nests that resulted in successful hatches were begun in a two week period in mid-May.

Stanford (1952:83) presents graphically the frequency of hatching in a "normal" breeding season in Missouri. His graph indicates that the peak of hatching occurs in mid-July. No secondary peak, as seen in the hatching curve for the study area, occurs in Stanford's graph. That the peak of hatching in Kansas may be earlier (late June) than in Missouri is suggested by data from the study area, and by results of analyses of wings of bobwhites contributed by Kansas sportsmen in 1951 and 1952 (Robinson and Baker, 1952 and 1953).

There is evidence that the secondary peak seen in the hatching curve for the study area may be of fairly common occurrence in Kansas. Similar secondary peaks, occurring in mid-August, were found in the hatching curves of bobwhites in Kansas in 1951 and 1952 (Robinson and Baker, *op. cit.*). Parmalee (1955:49) suggests that "immature" hens (females in their first breeding season) may nest later than do "adult" hens (females in their second or succeeding breeding seasons). Judging from information regarding the longevity of bobwhites (Bennitt, 1951:33-34), it seems improbable that late nesting, resulting in a secondary peak in the hatching curve, could be attributed to females less than two years old. If late nesting was principally by females in their first breeding season, the peak of hatching would be later than late June, or even mid-July, as females of that age far outnumber older females. The secondary peak of hatching for the study area, occurred approximately 39 days after the major peak of hatching, a period approximating the time involved from the initiation of nesting to the emergence of the young. It is my opinion that most late nesting is by pairs of bobwhites that had their nests disrupted earlier in the breeding season.

In order to learn the date or dates on which the largest number of males were whistling, I made road counts. The route chosen began one mile south of the study area, proceeded two miles west, thence seven miles north; the entire route being on secondary county and section-line roads. The counts were begun one-half hour before official sunrise, and were limited to mornings that were clear, or had cloud-cover confined to the western one-fourth of the sky. At each of the stops, one mile apart, the number of males heard whistling in a three minute period was counted and recorded. Two minutes were required to drive from one stop to the next, and each entire road-count took approximately 50 minutes to complete. The results of the road counts in 1952 are presented in figure 9.

The largest number of males heard whistling was in mid-June, suggesting a relationship between whistling of males and hatching of young. Such a relationship seems incongruous if whistling is done wholly by unmated males, although it is possible that the relationship is accidental. My limited data suggest, however, that in addition to unmated males, mated males whistle in the breeding season, especially at the time of emergence of the young.

Counts of whistling males were made in 1953, at the same stops, and the same times with respect to official sunrise, as in 1952. As in 1952, the largest number of males heard whistling was in mid-June. Comparisons between whistling of males and other events in the breeding season of 1953, are not possible because too few bobwhites were live-trapped and aged in the autumn of that year to permit determination of frequency of hatching and nesting.

It seems to be the general consensus among other investigators that the beginning of the breeding season depends, to some extent, on climatic conditions that prevail at that time of year. If the attainment of breeding condition in bobwhites is a function of the photoperiod, as demonstrated by Baldini *et al.* (1952), it would seem that bobwhites are physiologically capable of initiating search for mates, and mating, at approximately the same time each year; the photoperiod is independent of local climatic conditions. It would seem that the initiation of nesting, and not the actual beginning of the breeding season, is controlled to some extent by local climatic conditions.

Weight of Bobwhites

Bobwhites that were live-trapped on the study area were weighed with spring scales; the birds were confined, head down, in a funnel of known weight and suspended from the hook of the scales. In addition, bobwhites shot for food habits studies were weighed within one hour after death.

Aging of young birds by examination and measurement of the molting primaries allowed me to obtain weights of a number of age-classes of young. Although young birds may be aged accurately only if they are between the ages of eight and 22 weeks, the recapture of bobwhites that had been trapped and aged prior to the completion of the postjuvenal molt resulted in weights of age-classes up to 29 weeks old.

The results of weighing of young birds are presented in figure 10; the data are grouped in two-week intervals to obtain a smoother curve. Rate of growth of young birds decreases progressively with increasing age, maximum size being attained at approximately 22 to 23 weeks of age, the age at which the postjuvenal molt is completed. The attainment of adult appearance, with the replacement of the juvenal plumage, seemingly is correlated with the attainment of maximum, or adult, weight. The average of 79 weights of adults examined in the months of October through December was 193.5 grams; that of 122 young birds that had completed the postjuvenal molt, examined in the same period, was 193.8 grams, indicating that not only is adult size attained, but that adults and young of

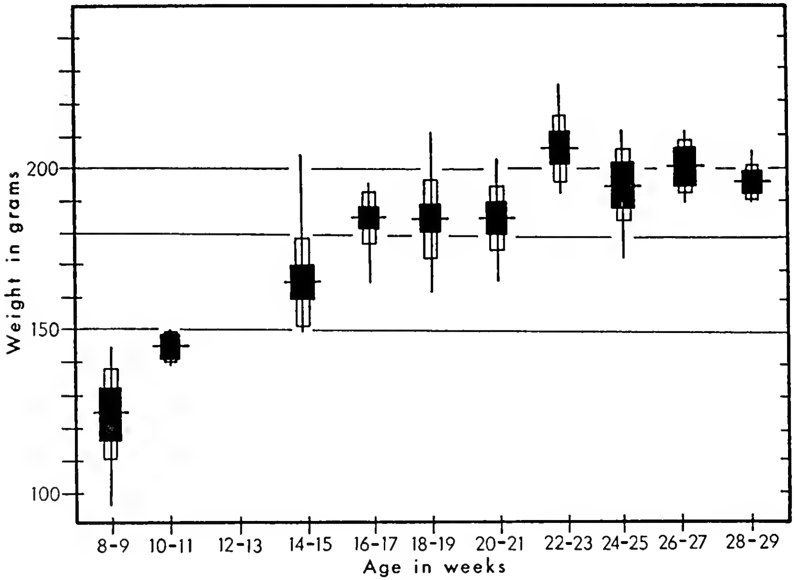

FIGURE 10. Weight of young bobwhites on the study area. The vertical line indicates the range, the horizontal line indicates the mean, the open rectangle indicates one standard deviation either side of the mean and the blackened rectangle indicates two standard errors either side of the mean.

the year that have completed the postjuvenal molt do not have significantly different weights. It was also determined that there is no significant difference in weights of fully-grown males and females.

Stoddard (1931:72) reports the weights of young bobwhites from southwestern Georgia. Comparing his data with those from the study area indicates that bobwhites from south-central Kansas, when from eight to 16 weeks old, average approximately 35 grams heavier than do bobwhites of comparable age from Georgia.

A total of 255 weights of fully-grown bobwhites (young that were 22 weeks old or older, and adults) were obtained, and the monthly averages of these are presented in figure 11. Fully-grown bobwhites on the study area attain maximum size in mid-winter, and weigh the least in June and July. Such differences in weight might result from the fact that bobwhites trapped in the non-breeding season had food provided for them in the traps, whereas those trapped in the breeding season were not so provisioned. This, however, is unlikely judging from the weights of crops examined by me for food habits studies; the maximum weight of a fully engorged crop did not exceed 12.4 grams, of the 43 crops containing food that I weighed.

That bobwhites should weigh the least when the food supply is most abundant, and the most when the food supply is at low ebb seems incongruous, and points to some factor, or factors, other than food as being responsible. As seen in figure 11, the weight of fully-

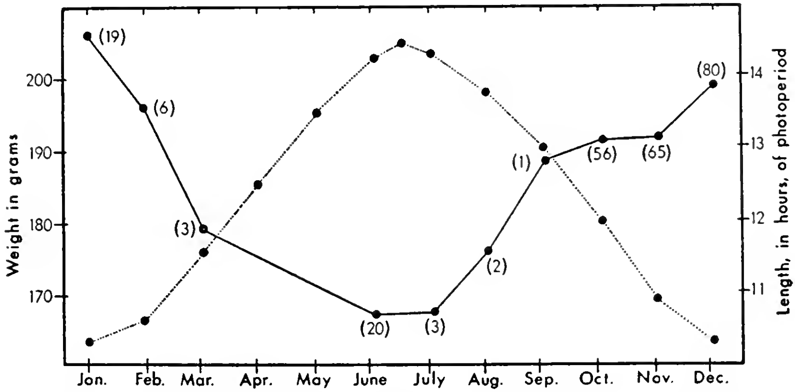

FIGURE 11. Comparison of weight of fully-grown bobwhites on the study area with length of the photoperiod. Solid line, average weight (numbers in parentheses indicate the number of individuals weighed); dotted line, length of photoperiod (data for Dodge City, Kansas, from Weather Bureau).

grown bobwhites seems to be correlated with the length of the photoperiod, weight being inversely proportional to the photoperiod. Data in Kendeigh (1934:333) indicate that birds weigh less in the breeding season than in the non-breeding season. Baldini *et al.* (1952) have demonstrated relationship between attainment of breeding condition in bobwhites and length of photoperiod, and Bissonnette (1938) and Bump and Clark (1939) have shown such a relationship to be true for animals other than bobwhites. Seemingly the weight of bobwhites is related to their sexual activity, and the latter is a function of the photoperiod.

That fully-grown bobwhites vary in size indicates that any comparisons of weights of bobwhites must be made between data obtained in comparable months, or seasons, of the year if such comparisons are to be meaningful. Fortunately, the majority of weights of bobwhites reported in the literature were obtained from birds killed in the hunting season, and the hunting season usually is in the autumn and/or winter. Weights reported by Nelson and Martin (1953) of 1591 bobwhites are accompanied by no information regarding the time of year the birds were obtained, or even the locality from which they came, and thus are of little value.

Stoddard (1931:76-77) and others have shown that bobwhites tend to increase in size from south to north and from east to west in their geographic range. Bobwhites taken in winter in southern South Carolina average 177 grams and in western Tennessee 183 grams (Stoddard, *loc. cit.*). In Missouri the average weight of bobwhites is approximately 184 grams ("6-7 ounces"; Stanford, 1952: 5), and in south-central Kansas 196 grams (average of 164 measurements of fully-grown bobwhites from the study area, November through January). That the plains bobwhite, *C. v. taylori,* is larger than the eastern subspecies is readily apparent. Comparison of size of Kansas bobwhites with that of bobwhites from eastern states lends no support to the dream of Kansas sportsmen of the "big old Virginia bobwhite" of the east. These comparative data also should serve to alleviate concern regarding the effect of the introduction of the "Mexican" bobwhite, *C. v. texanus,* on the size of bobwhites in south-central Kansas. From 1910 to 1925, 233,587 bobwhites from northern Mexico were imported, alive, into the United States (U. S. Tariff Commission, 1952:2); many of these were released in Kansas. Seemingly these introductions have had little or no permanent effect on the size of bobwhites in south-central Kansas.

Temperature of Bobwhites

A total of 43 measurements of cloacal temperature was obtained from live-trapped bobwhites. The mean of the measurements was 41.7° C. (a minimum of 38.4° C. to a maximum of 43.2° C.). In conjunction with these measurements, the temperature of the immediate environment of each bird also was determined. Comparisons were made between cloacal temperature and: environmental temperature, age of the birds, sex, weight, and season. No significant correlation could be found between cloacal temperature of the bobwhites and any of the other variables. Bobwhites, although having variable cloacal temperatures, are true homoiotherms, and their temperature is independent of age, sex, and season of the year. This statement is made with the reservation that the confinement, in traps, of up to seven hours and excitement of the birds caused by handling and examination may have caused greater variation in cloacal temperature than normally occurs. These unnatural conditions might have obscured the actual relationships between cloacal temperature of bobwhites and the other variables mentioned above.

Covey Range and Territoriality

Thirty eight areas that I regarded as covey "headquarters" were selected on the study area, based on observations in the autumns of 1951 through 1953. It was in these situations, without exception in woody cover, that coveys of bobwhites could be found with fair regularity in the midday "loafing" periods in the non-breeding season. Each covey tended to return to its headquarters after the early morning period of foraging in the open, to remain there in the woody cover until late afternoon, and then to return to the open habitats for food in the evening. Each covey usually roosted near its headquarters, although using more open vegetation than in the midday period of "loafing."

My observations suggest that the use of headquarters areas as a base of operations can be accounted for on the basis of habit of the individuals comprising each covey, as well as on the basis of territoriality. I did not observe bobwhites fighting in the non-breeding season, and more than one covey feeding in the same feed plot was a common sight in the late evening. The exchange of individuals between coveys indicates that individuals are not bound to their covey, or their covey headquarters, by permanent psychological bonds.

That there is mutual avoidance between coveys in the midday hours is suggested by the spacing of headquarters areas on the study area. Spacing of many of the covey headquarters was due to discontinuity of the woody vegetation. However, in situations where two or more headquarters were in continuous woody vegetation, the mean distance (of 10 measurements) between adjacent headquarters was 138 (110-220) yards. These distances were determined by measuring, on a map, between headquarters.

It has been stated several times in the literature that the maximum carrying capacity of land for bobwhites is one bird per acre. Using this figure, the study area could have a maximum carrying capacity of 640 bobwhites, or approximately 53 coveys averaging 12 birds each in the autumn. The minimum area necessary for the presence and survival of a covey in the autumn would be 12.1 acres. A small part of this must be the covey headquarters, composed of dense, woody vegetation. There are few reports in the literature on the minimum area of a covey headquarters; Lehmann (1939:3) found that, in Texas, bobwhites seemed to fare well in dense, woody cover where a clump of vegetation was from six to seven feet in diameter. My observations on the study area indicate that a more favorable covey headquarters would be approximately 225 square yards in area (15 yards on each side).

Male bobwhites seem truly territorial in the breeding season. My observations indicate that the territories of the whistling males are ephemeral and that males will move long distances to locate a calling female. I have observed males in pursuit of one another, but never in actual combat. Owing to the ephemeral nature of the territories of the males, I was unable to determine the extent of such territories.

My observations suggest that unmated females in the early part of the breeding season are territorial, and that their characteristic calls attract males, rather than that the females are attracted to the whistling males. It was fairly common, after I placed a trap containing a caged female near a whistling male and concealed myself in adjacent vegetation, to see the male come flying or running to the caged female; she invariably began calling as soon as I was out of sight. Male bobwhites were frequently attracted to hatchery-reared females kept in cages in the yard of my field residence. My observations suggest that the "ah-bob-white" whistle of the males in the breeding season may be principally an announcement of occupation of an area as a territory, and may have little to do with attracting females.

BEHAVIOR AND SELECTION OF HABITAT

The relationships between bobwhites and their environment have received considerable scrutiny, owing to the importance of habitat from the standpoint of management. The accounts of the factors involved have been primarily descriptive, and little or no attention has been given to the causal relationships that exist. Considering the importance of the bobwhite as a game species, it seems unfortunate that the fruitful field of causal ecology has not received greater attention.

Four publications offer detailed information on the behavior of bobwhites, although one of these, Edminster (1954:243-301), seems to be based largely on the other three. Description of behavior of bobwhites by Bent (1932:9-40) is poorly documented, and the excellent account by Stanford (1952) is in a popular vein. From the standpoint of usefulness in research, the information presented by Stoddard (1931) is the best.

Bobwhites have basic daily and seasonal patterns of behavior with respect to their environment judging from my experience in the field, and a review of the above-mentioned works and other publications. In winter the daily pattern of behavior begins with the birds leaving their roosts near the time of sunrise, and foraging in open situations until mid-morning when they retire to denser vegetation and "loaf" until mid-afternoon, when they again return to more open situations for food. This is followed by roosting, beginning soon after sunset. This daily pattern of activity may be disrupted by inclement weather.

The daily pattern of behavior in the breeding season is similar to that in the non-breeding season. Feeding is principally in the early morning or late evening. Midday is spent on or near the nest in herbaceous or grassy cover. At this time of year the activity of males, probably those that are unmated, differs in that they are found in a variety of habitats throughout the day.

Bobwhites usually use woody vegetation as "headquarters" in the colder months. The mobility of individuals and of coveys is less at that time of year than in the warmer months when the birds are found principally in herbaceous and grassy vegetation. In spring, individuals move from dense, woody cover to less dense, herbaceous and grassy cover (the spring shuffle); the autumn shuffle is a movement of individuals and coveys back to denser woody cover.

These patterns of behavior suggest that relationships exist not only between behavior and habitat, but also between behavior and time of day, season, and weather. The effect of the last three factors on the behavior of bobwhites is even more strongly suggested when the effect of vegetation on the immediate environment is considered.

The major variables introduced by vegetation in a local area are microclimatic. The vegetation interferes with incoming solar radiation, thus reducing the illumination beneath the vegetational cover, and affects the temperature there. Velocity of the wind is reduced owing to the resistence offered to the movement of air. The amount of incoming moisture reaching the area below the main canopy of the vegetation is affected by interference by the canopy. The moisture relationships of the plants themselves affect the relative humidity of the immediate environment. All these effects of the vegetation on the environment are controlled, in part, by time of day and season of the year.

In choosing vegetational cover, the bobwhite possibly is selecting a favorable climatic environment, rather than woody, herbaceous, or grassy vegetation. In order to investigate this possibility it was necessary to determine the ranges of each of the measurable factors in the physical environment of the study area, and then to relate them to vegetation, time of day, season of the year, and weather. Finally the results were compared with the behavior of bobwhites on the area.

The excellent work by Geiger (1950) on microclimates has demonstrated the inadvisability of using Weather Bureau data in many ecological studies because of differences in the physical environment between situations near the ground and those at altitudes at which U. S. Weather Bureau instruments are exposed. The relationships between an organism and its environment may best be determined by measuring the physical factors *at the level, or altitude, of that organism.* This is of great importance in dealing with environments that include plants in view of the effect that these plants have upon the climatic conditions. In the case of the bobwhite, the environment with which it is in immediate contact occupies the first four or five inches above the ground, and plants seemingly play an important role in determining the climate of this level.

In order to obtain information on microclimates of the study area, I selected sites, in each of the habitats, that I considered to be "average" with respect to density and distribution of the vegetation and topography. Measurements of microclimatic conditions at the level of the bobwhite were made at these sites at various times. At each site a high-range laboratory thermometer, with a sensing bulb one half inch in length, was suspended so that the sensing bulb was approximately two inches above the ground. Relative humidity was measured with a sling psychrometer. Movement of air was determined by exposing, for three minutes, an eight-vane Biram anemometer of low range at the surface of the ground; velocity of movement of air was measured in an area equal in altitude to the diameter of the vane-surface of the anemometer (four inches). Intensity of light reflected from the surface of the ground was determined with a Weston Master II exposure meter, with the sensing element of the photometer held approximately 10 inches above the ground. Intensity of incident light was measured with the same photometer, with an incident light adapter ("Invercone") placed over the sensing element. All readings obtained on the dial of the photometer were converted to foot-candles of intensity by the use of appropriate conversion factors supplied by the manufacturer. In addition to the measurements made at the selected sites, measurements were made in a variety of situations in each of the habitats in order to determine the maxima and minima of each of the microclimatic factors.

Averages of microclimatic conditions in the various habitats on the study area are presented in table 3. Averages for spring and autumn are not included; microclimatic conditions in spring and autumn are intermediate between those of summer and winter. As a point of reference, for comparative purposes, similar measurements were made of the macroclimate at an altitude of two and one half meters above the surface of the ground. All the data presented in table 3, except that concerning light, are comparisons between conditions at the level of the bobwhite and those at an altitude of two and one half meters.

In the winter, at all habitats, average midday temperatures were higher at the level of the bobwhite than in the macroclimate (table 3). Among the habitats, temperature was highest in the mixed grasses, and lowest in Johnson grass. In summer, the mixed grass was again the warmest of all the habitats, and woodlands the coolest; the latter has a midday temperature lower than that of the macroclimate. Relative humidity varied little between microclimate and macroclimate. In general, relative humidity at the level of the bobwhite was lower than that of the macroclimate. Furthermore, the difference between readings at the two levels was less in winter than in summer. Transpiration of living plants in the growing season tends

TABLE 3. MICROCLIMATIC AVERAGES, AT LEVEL OF THE BOBWHITE, ON THE STUDY AREA.*

Habitat	Temperature		Relative humidity		Wind velocity		Light	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
1	+9.2	+9.2	—14	—5	76%	87%	1,069	1,465
2	+12.0	+15.6	—10	—7	92%	97%	532	995
3	+3.8	—2.9	—9	+6	96%	99%	227	12
4	+3.4	+7.8	—10	—9	97%	99%	31	22
5	+2.9	....	—4	—4	57%	......	1,085	30
6	+4.8	+9.1	—11	......	97%	99%	391	700
7	+6.6	+11.2	—11	—4	85%	93%	823	1,006
8	+7.0	+9.7	—11	0	94%	95%	344	145
9	+2.9	+7.8	—4	—4	57%	71%	1,085	1,550
10	+0.9	....	—9	......	66%	99%	219	567
11	+8.1	....	—9	......	98%	......	78	29
12	+2.9	....	—4	......	57%	......	1,085	700

* All measurements made on clear days between 11 a.m. and 2 p.m. Temperature—deviation, in degrees Centigrade, from that 2½ m. above ground; relative humidity—deviation, in per cent, from that 2½ m. above ground; wind velocity—reduction, in per cent, of velocity of that measured 2½ m. above ground; light—intensity of light, in foot-candles, reflected from ground.

to increase relative humidity in the immediate vicinity of the plants. Relative humidity at the level of the bobwhite was greater than that of the macroclimate only in woodlands, and then only in summer. Reduction in velocity of movement of air is the most striking effect of the vegetation at the level of the bobwhite. Even in the denuded feed plots in winter, velocity of the wind was reduced to less than half that of the macroclimate.

The amount of light reflected from the surface of the ground in each of the habitats may be misleading because several factors are involved. Color and texture of the soil, ground litter, or vegetation, affects the amount of incident light absorbed by those surfaces; however, the variation resulting from these phenomena was found to be of little consequence in measuring reflected light in the various habitats. Although the data presented in table 3 were obtained at the time of highest intensity of incident light each day, the amount of incoming radiation varies with the season, being greater in summer than in winter. This accounts for the differences between summer and winter in intensity of reflected light in habitats 1 and 9.

With the possible exception of wind velocity, all the factors listed in table 3 are related to incoming solar radiation. The temperature of the air at the level of the bobwhite is due primarily to heat radiated from the surface of the soil, ground litter, or adjacent plants; the source of this heat is radiant solar energy. Since radiant energy decreases with the square of the distance from the radiating surface, it is not surprising that temperatures immediately above the soil are higher than temperatures at greater altitudes. Vegetation alters this relationship if the plants, rather than the soil or ground litter, become the principal radiating surface. Measurement of vertical temperature-gradients in the habitats on the study area showed that on calm days, the highest temperatures occur where vegetation is most dense. This is the reason for the temperature at the level of the bobwhite being highest in the mixed grass habitat; the densest part, and thus the major radiating surface of this vegetation, occurs approximately three inches above the surface of the soil. Such a condition is not found in any of the other habitats on the study area. In the thickets of Chickasaw plum, the major radiating surface in summer is the low canopy formed by the upper branches and leaves of the shrubs. In this habitat the maximum of the vertical temperature-gradient is approximately four feet above the ground. The maximum of the vertical temperature-gradient in the woodlands is even farther above the surface of the ground. In such a habitat some incoming radiation passes through the canopy to the ground, causing warming of the lower air mass; nevertheless, the higher temperatures are in the main canopy.

Relative humidity varies with temperature; the same amount of moisture in vapor form in a given volume of air gives a higher value, with respect to relative humidity, in cooler air than in warmer air. For this reason, at the level of the bobwhite, the deviations of absolute humidity from that of the macroclimate are not so great as indicated in table 3. It is surprising that, in the summer, the relative humidity near the surface of the ground is less than that of the macroclimate.

The effect of wind on the character of the microclimate might seem to be great, but actually is of little consequence. Only in the denuded areas, and in the sparse stand of grasses in habitat 1, is the wind velocity great enough to cause exchange between the skin of air near the surface, and the more turbulent air mass of greater altitude. Temperature and relative humidity at the level of the bobwhite thus are little affected by wind.

In general, lowest temperature in any given habitat occurs at, or soon after, sunrise; highest temperature occurs in mid-afternoon, usually at approximately 3:00 p. m. This daily march of temperature is altered to some extent by the vegetation, and by cloudiness. Lowest temperature is found somewhat later in the early morning in dense vegetation than in more open cover, and cloudiness may cause the time of highest temperature to occur later in the afternoon than on clear days. The arrival of cold and warm fronts may disrupt the usual pattern of the march of temperature, but these frontal systems are so infrequent in south-central Kansas as to be of little consequence to one who studies the effects of microclimate on behavior of bobwhites.

The daily course of relative humidity is similar to that of temperature, but with the peaks reversed. Highest relative humidity generally occurs at sunrise, and the lowest usually in the late afternoon. Cloudiness may prolong the morning period of high relative humidity; dense vegetation has a similar effect.

In south-central Kansas, thermal winds are almost entirely diurnal phenomena. Air movement begins soon after sunrise, increases in velocity through the morning and early afternoon, and reaches a peak in late afternoon. Winds of appreciable velocity generally are absent within three hours after sunset. Winds associated with cold and warm fronts are frequently of high velocity, but of short duration. These frontal winds occur at any hour of the day or night, depending on the time of arrival of the front.

The march of intensity of light has little variation on clear days. The peak of intensity of incoming light at all times of the year on clear days occurs between 12:00 noon and 1:00 p. m.; the rate of increase and decrease is greatest in the mid-morning and mid-afternoon, respectively. The vegetation has a profound effect upon the amount of radiant energy reaching the level of the bobwhite, with shading being greater in summer than in winter. Clouds cause marked changes in illumination in all habitats; on summer days when scattered cumulus clouds are in the sky, the illumination in any given area may change abruptly as a cloud casts its shadow on the area for a short period. The amount of incoming solar radiation depends on the season of the year, greatest amounts being received in mid-June and least amounts in mid-December.

In addition to vegetation, topography has some effect on the microclimate at the level of the bobwhite. At night, cool air pools in the lowlands causing these situations to be relatively cooler than the uplands. This cooling also affects the relative humidity of the lowlands. Velocity of wind near the ground is affected by topography; owing to the north-south orientation of the valley of Sandy Creek, winds from the east or west caused less movement of air at the level of the bobwhite in the lowlands, than did winds of equal velocity from the north or south. Similar effects were noted in the canyons. Topography also has some effect upon the intensity of light at the level of the bobwhite. In early morning, or late evening, the uplands receive light of greater intensity than do the shadowed canyons, creek valley, or hillsides facing away from the incoming radiation.

A comparison of the data presented on temperature at the level of the bobwhite, and behavior of bobwhites, does not substantiate the observations in the literature that bobwhites seek warm places in winter and cool places in summer. On the study area in winter, bobwhites were limited almost exclusively to dense and tangled woody vegetation in midday. The situations in which they were found were some of the coldest on the study area. In the summer, bobwhites rarely were observed in these dense, woody situations, which are then cooler than any of the other habitats on the study area.

A review of the daily pattern of behavior of bobwhites indicates little possibility for relationship with temperature. Bobwhites feed in early morning and late afternoon, times that are quite unlike one another with respect to temperature. Variations in temperature that may occur within one day, or between different days, cannot account for the regular pattern of behavior as seen on clear days in the non-breeding season. Measurement of temperatures in microclimates where bobwhites were observed yielded no correlation between pattern of behavior and temperature.

A comparison of daily and seasonal patterns of behavior of bobwhites on the study area, with relative humidity at the level of the bobwhite gives no indication that bobwhites select situations with an optimum range of relative humidity. The time of feeding in open situations in early morning and late evening is not correlated with relative humidity in those situations, or in situations used by the birds before they ventured into the open. That a correlation between behavior of bobwhites and relative humidity does not exist is substantiated by comparison of measurements of relative humidity and behavior of the birds.

Velocity of wind seemingly has little, or no, effect upon the pattern of behavior of bobwhites on the study area. Simply by being close to the ground, bobwhites avoid winds of high velocity. The selection of habitats by the birds on the study area gives no basis for a correlation between velocity of wind and behavior, nor does measurement of velocity of wind at the birds' level where they were observed.

Ephemeral factors of the physical environment have observable effects upon the daily pattern of behavior of these birds. On cloudy days in winter I have observed bobwhites in open situations in the midday hours, a period in which they normally confine themselves to dense cover. Reconnaissance of the study area during snowstorms of moderate severity has revealed bobwhites feeding in the open, likewise during light to moderate rains, and even in a sleet storm. Heavy rains and blizzards seemingly cause bobwhites to retire to vegetation that offers protection from the elements. Following snowstorms, there was no evidence that bobwhites on the study area ventured into the open to feed, even at the usual time of foraging in the early morning.

There is some suggestion, from a comparison of microclimatological data and behavior of bobwhites, that these birds choose situations that offer light of low intensity. This is best seen in the daily pattern of activity when the birds are in open situations at the time of low intensity of incident light, and in dense, woody cover in the midday hours when intensity of incident light is highest. That bobwhites seek situations of low intensity of light is also suggested by the fact that the birds are observed in open situations at midday on cloudy, or partly cloudy, days.

In table 4a it can be seen that, on clear days, bobwhites do, in fact, avoid situations during midday in which the vegetation does not offer shade from incoming light. In midday, when incoming light was at highest intensity, bobwhites were in habitats that provided shade. Vegetation that provided only a moderate amount of shade from incident light seemingly was used only in the mid-morning and mid-afternoon. Table 4b demonstrates that bobwhites were not as restricted in their choice of habitat in the midday hours on cloudy or partly cloudy days; days on which interference of incident radiation was provided not by vegetation, but by clouds.

That the daily pattern of behavior is not due to any timing mechanism in the physiology of the birds is illustrated by table 5. Choice of habitat is a function of intensity of light. Bobwhites were observed in vegetation that provided little or no shade from

TABLE 4. NUMBER OF BOBWHITES SEEN ON THE STUDY AREA IN THE NON-BREEDING SEASON (SEPTEMBER THROUGH FEBRUARY), ACCORDING TO HABITAT AND TIME OF DAY.

(A) clear days.

Habitat	De-nuded	No shade					Moderate shade		Heavily shaded				
		1*	2*	5*	9*	12*	6*	7*	3*	4*	8*	10*	11*
a. m.													
6–7		42	7		25	11							
7–8		6				18							
8–9							17				15		
9–10									14			2	
10–11									23			10	
11–12									20				
p. m.													
12–1									59		5		
1–2											11		
2–3											15		
3–4					1		19	4	33		11		10
4–5							4						
5–6		16			21								15
6–7				4					11				

(B) cloudy or partly cloudy days.

Habitat	De-nuded	1*	2*	5*	9*	12*	6*	7*	3*	4*	8*	10*	11*
a. m.													
6–7	2												
7–8													
8–9					9								
9–10													
10–11		14		6									
11–12						11			4				
p. m.													
12–1							4				7		
1–2		14							7				
2–3							16		16		14		
3–4		10											
4–5													
5–6		31				12							
6–7	1												

*/ Habitats:

1. Short grasses
2. Mixed grasses
3. Woodlands
4. Sand bluestem
5. Cropland
6. Tall weeds
7. Sweet clover
8. Shrubby thickets
9. Feed plots
10. Johnson grass
11. Marshy areas
12. Minor areas of disturbance

TABLE 5. DISTRIBUTION OF BOBWHITES OBSERVED ON THE STUDY AREA IN THE NON-BREEDING SEASON ACCORDING TO HABITAT AND INTENSITY OF INCIDENT LIGHT. OBSERVATIONS INCLUDE ALL HOURS OF DAY, AND A VARIETY OF WEATHER CONDITIONS.

Habitat	De-nuded	No shade					Moderate shade		Heavily shaded				
		1*	2*	5*	9*	12*	6*	7*	3*	4*	8*	10*	11*
Light in thousands of foot-candles 8–9	......	....	....	....	....	....	....	....	11	....	....	....	....
7–8	......	....	....	....	....	....	....	....	49	....	....	....	....
6–7	......	....	....	....	....	....	....	....	36	....	20	10	....
5–6	......	....	....	....	....	....	....	....	36	....	11	....	....
4–5	......	....	....	....	....	....	4	....	24	....	11	2	10
3–4	......	....	....	....	....	....	4	....	....	....	15	....	....
2–3	......	....	....	....	....	....	19	....	29	....	....	....	15
1–2	......	11	....	6	1	18	28	4	11	....	21	....	....
0–1	3	122	7	4	46	22	17	....	....	....	....	....	....

*/ Habitats:

1. Short grasses
2. Mixed grasses
3. Woodlands
4. Sand bluestem
5. Cropland
6. Tall weeds
7. Sweet clover
8. Shrubby thickets
9. Feed plots
10. Johnson grass
11. Marshy areas
12. Minor areas of disturbance

incident light only when the intensity of the incoming radiation was below 2000 foot-candles. When the intensity of incident light was greater than 5000 foot-candles, bobwhites were observed only in situations that were shaded, these being woodlands, shrubby thickets, Johnson grass, and marshy areas.

From the foregoing data and discussion, it seems that bobwhites on the study area were limited in choice of habitat by the intensity of light reaching their level. This restriction imposed by intensity of light also determines the daily pattern of behavior of the birds. Seemingly the bobwhites were not seeking situations that afforded the least possible intensity of light; rather they were seeking places in which the intensity of light was below a certain level. If the birds had been seeking light of the lowest possible intensity, they would not have left the shaded situations in the late afternoon and moved into the open areas, for the intensity of light varies proportionately with incoming radiation in all habitats. From table 5 it might be assumed that the upper limit of favorable intensity of light for bobwhites is approximately 2000 foot-candles. However, several variables enter into the determination of the upper limit of the optimum intensity of light for bobwhites, and this value is in reality too high, as will be pointed out later.

Owing to the range of sensitivity of the photometer with incident light adapter attached, I found it necessary to measure light, in places that I observed bobwhites, by determining the amount of light reflected from the surface of the ground. The intensity of incident light reaching the level of the bobwhite may be calculated from measurements of reflected light by the following proportion:

$$\frac{\text{intensity of reflected light}}{16} = \frac{\text{intensity of incident light}}{84}$$

The average intensity of light reflected from the surface of the ground in all situations where bobwhites were observed in the non-breeding season was 58.8 foot-candles. Since many of these measurements were made in early morning or late evening, or on cloudy days, it is possible that the mean value might be lower than when intensity of incoming radiation is near its maximum. My findings indicate that this was not the case; the mean value of 84 measurements made only on clear days, between the hours of 11:00 a. m. and 1:30 p. m. (the time of highest intensity of incident light) was 51.2 foot-candles; a value lower, rather than higher, than the mean of all the measurements.

The mean intensities of light reported in the preceding paragraph are based on the total number of individuals observed. It is conceivable that a more accurate estimate of the intensity of light most often used by bobwhites in the non-breeding season might be gained by considering coveys, rather than individuals. To determine whether measurements should be weighted according to the size of the covey, I analyzed statistically the correlation between size of covey and intensity of reflected light in the situation in which each covey was found. No correlation was found to exist; the coefficients of correlation (r) varied from 0.03 in October to —0.35 in February, none of which is statistically significant.

Table 6 indicates that there is a slight trend, though not statistically significant, towards higher mean values of intensity of reflected light in situations in which bobwhites were observed as the non-breeding season progressed. This seeming trend suggests that bobwhites were venturing into areas of brighter illumination in the late winter than in the autumn. This trend is not correlated with intensity of incident light in the six months of the non-breeding season. Bobwhites possibly found it necessary to feed in the more open situations at times other than the normal foraging periods of early morning and late afternoon, in order to obtain enough food. As was pointed out in the section on food habits, however, there seems to be no scarcity of food for the birds at any time of the year on the study area.

The increase in variability, as indexed by the standard error (table 6), suggests that as the non-breeding season progresses, bobwhites on the study area had fewer situations to choose from that would offer enough shade; or that their behavior with respect to intensity of light was changing gradually. The latter possibility seems the most likely, for the density of the vegetation did not decrease appreciably from the time of defoliation in the autumn to the emergence of new foliage the following spring.

The relationship between activity of bobwhites and intensity of light in the breeding season differs in some respects from that in the non-breeding season. In the breeding season, coveys, single females, and males and females seen together, all were found in situations in which intensity of light was low. Male bobwhites seen alone or in the company of other males seemed to disregard the intensity of light. The mean intensity of reflected light in situations in which a total of 17 males and females were observed (seven pairs, and two males with one female) was 84.5 foot-candles (a minimum of 6.4 to a maximum of 160); that of three females seen without males was 48.0 foot-candles (40 to 64); and that of 31 individuals, in coveys, was 128 foot-candles (48 to 200). All these means fall within the range of intensity of light used by bobwhites in the non-breeding season. Measurement of light reflected from the surface of the ground where single males, or males accompanied by

TABLE 6. INTENSITY OF REFLECTED LIGHT IN AREAS IN WHICH BOBWHITES WERE SEEN IN THE NON-BREEDING SEASON.

	Month					
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Number of coveys....	11	15	9	9	15	4
Mean light intensity..	23.1	33.2	56.5	36.2	125.2	73.9
Standard deviation of light intensity....	21.0	128.0	25.6	29.6	106.0	104.5
Standard error of light intensity....	6.4	33.1	8.5	9.9	27.3	52.5

other males, were observed yielded results that ranged from 1600 foot-candles to 100 foot-candles, with a mean intensity of 802.5 foot-candles. This latter mean is significantly different from that for the non-breeding season, or for pairs, females, or coveys in the breeding season.

Only males unaccompanied by females in the breeding season disregarded the barrier of bright light, suggesting that the sex drive or, more specifically, the search for a mate, overrides the inherent tendency to avoid light of high intensity. Since only males that were unaccompanied by females seemed unrestricted by light, it is possible that these males may have been unmated.

The disregard of the barrier of bright light by some males in the breeding season may explain, in part, the reason for finding bobwhites in brighter light in the latter part of the non-breeding season. The gradual onset of sexual maturity of males in the late winter may have led them to venture into brighter situations than normally would be used, thus causing the coveys to remain in the open situations longer than in the autumn or early winter. This does not imply leadership by males. Rather, it illustrates that the behavior of the covey depends on the interaction of behavior of individuals comprising the covey.

My data regarding the intensity of light in situations in which male bobwhites were found in the latter part of the breeding season are not numerous enough to permit me to draw any conclusions regarding the return of males to situations in which light intensity is low. That they do return, however, is shown by the data for September.

Seemingly bobwhites, in reacting to light, did not differentiate between direct and diffuse light. This is illustrated by the finding of bobwhites in situations with approximately the same intensity of light on cloudy as well as on clear days.

I feel that the foregoing data and discussion show conclusively that bobwhites on the study area were restricted by light of high intensity. Seemingly the birds were reacting to a threshold stimulus, rather than seeking situations that afforded light of lowest possible intensity.

It is difficult to determine this threshold in terms of foot-candles of light owing to the nature of my data, and to limitations imposed by field conditions. The mean of all the measurements surely does not represent the threshold, nor does the maximum intensity of light used by bobwhites in the period of the study. A clue to the value of the threshold is found in table 5; no bobwhites were found in situations that offered no shade when the intensity of incoming light was greater than 2000 foot-candles. However, topographical features and shading provided by even sparse vegetation, when the sun was low on the horizon, makes the assumption of 2000 foot-candles as the threshold invalid. The majority of bobwhites in the open situations were there when intensity of incident light was less than 1000 foot-candles. This intensity, when converted to the equivalent value of reflected light, approximates that obtained by adding two standard deviations to the mean of all measurements of reflected light. This is the best approximation of the threshold that I have been able to obtain. At best it is an estimate of the actual threshold, in foot-candles, and is probably a conservative one.

The determination of the lower limit of intensity of light used by bobwhites is more difficult than that of the upper limit. A lower limit seems to exist, for bobwhites go to roost in late evening, and leave their roosts in early morning. I spent considerable time in the field attempting to determine the intensity of light at the time bobwhites leave the roost in the morning, and go to roost at night. My attempts in the late evening hours were unsuccessful. Determinations made in early morning I feel to be of little significance owing to uncontrollable variables encountered in the field. My own proximity to the roost in early morning—necessary in order to measure the light in the immediate vicinity of the roost—caused some coveys to fly abruptly from the roost and others to remain "frozen" for periods of time. The minimum threshold, if one exists, seems to be on the order of one foot-candle or less of incident light.

It would seem that bobwhites are more limited by light in early summer than in early winter, for the intensity of incident light is greater in mid-June than in mid-December. Observations of bobwhites on the study area indicate that this is not the case. Bobwhites were more mobile in the breeding season than in the non-breeding season. Coveys could be found with regularity in certain areas in the non-breeding season, whereas there was no assurance that bobwhites would be seen twice in the same locale in the breeding season. The bobwhites on the study area were most restricted by light in autumn and winter, the covey "headquarters" being well-defined in the non-breeding season. This can be explained, at least in part, by the change in the density of the vegetation in spring and autumn. In late spring and summer, situations that provided the proper amount of shade were abundant; in autumn and winter, when most of the woody and herbaceous vegetation had lost its foliage, shaded situations were scarce. Seemingly the intensity of light is more a limiting factor to the local distribution of bobwhites in the non-breeding season than in the breeding season. The number and extent of favorable (shaded) segments of the vegetation in late autumn and in winter may affect, even determine, the carrying capacity of the study area for bobwhites.

Many of the observed phenomena in the daily and seasonal patterns of behavior of bobwhites may be explained on the basis of light intensity as a limiting factor. The feeding by bobwhites in early morning and late afternoon on clear days results from the light intensity being favorable only at those times in the areas where they prefer to feed. My observations in the field, and the results of the analysis of contents of crops indicate that little of the food of bobwhites on the study area came from the dense, dark woody vegetation, habitats in which they spend approximately half of their time on clear days. That bobwhites do not necessarily require a resting period in midday is indicated by the fact that the birds were active in the open situations on the study area in the midday when the sky was cloudy. The midday "loafing" in dense vegetation on clear days seems rather a necessity owing to the unfavorable illumination in all other situations on the study area.

The autumn "shuffle" generally is regarded as a seeking of vegetation that will offer greater protection from the colder weather of the late autumn and winter. This is only partly true, in the light of my findings. The movement seems to be from situations that provided the requisite amount of shade in late summer, to situations that provide the requisite degree of shade in autumn and winter. My observations on the study area indicate that bobwhites made this move at or during the time when the first killing frost defoliated the vegetation in autumn. It is my opinion that bobwhites do not sense the oncoming of cold weather, but rather are forced to move from situations that, although providing shade in the summer, become untenable following defoliation.

The spring shuffle is unlike the autumn shuffle in some respects. The dispersal of coveys over the countryside is probably more a function of mutual antagonism among males, than of increasing amount of available midday habitat. This is not meant to imply that light intensity and density of the vegetation did not affect the local distribution of bobwhites in early spring. On the contrary, the increasing density of the herbaceous and grassy cover of the uplands allowed greater mobility and greater dispersal of the breeding stock of bobwhites.

As stated previously, reconnaissance of the study area following snowstorms revealed that bobwhites did not venture forth in early morning to feed. This may have resulted from too great an intensity of light in open situations, even at the usual time of foraging. A cover of snow on the ground increases the amount of reflected light in all habitats.

Hatchery-reared bobwhites, used in trapping males on the study area in the breeding season of 1953, were confined in cages under a tree in the yard of my field residence. The cages were longer than wide, and were placed under the tree with the long axes oriented in an east-west direction. In mid-morning, when incoming radiation was directly on the cages owing to the angle of the sun above the horizon, the bobwhites huddled in the west ends of the cages; in late afternoon they huddled in the east ends, thus avoiding light of high intensity.

The limiting effect of high intensity of light does not explain a few of the observations made on the study area. The climax plant community, sand bluestem, of the uplands was not used by bobwhites on the study area for any of their normal activities. From the standpoint of light intensity, this habitat was one of the most favorable of all in both winter and summer because light intensity at the level of the bobwhite in the close-ranked stems and basal leaves was below 32 foot-candles in all seasons. Stoddard (1931: 406) made the observation that cover for bobwhites at their level should be open enough for them to run through it easily. Sand bluestem does not meet this requirement. Three birds, from a covey that I flushed from a thicket of Chickasaw plum, alighted in a pure stand of sand bluestem, the only time I have ever observed bobwhites in this habitat. I walked to the spot where I had seen them alight and found all three in the basal leaves of the grass. One took to wing readily; another had difficulty owing to interference from the stems of the sand bluestem; the third I caught by hand as it struggled to free itself from the entangled basal leaves of the plants. Seemingly sand bluestem is too dense for bobwhites to use as cover, even though it offers the proper amount of shade from incoming radiation.

On the study area in the non-breeding season, some situations that provided the proper amount of shade were not used by bobwhites. Microclimatologically they did not differ from the headquarters areas, and I could ascertain no major differences in density of vegetation, or topography between areas used regularly by bobwhites and areas that were unused. The maximum carrying capacity of the study area possibly had not been reached in the period of my field work; all available habitat was not being used. The unused areas might have been used earlier in autumn, or late in summer without my knowledge, the coveys being destroyed or joining with coveys that were nearby. I doubt that all available habitat in the non-breeding season would be used unless the area supported the maximum number possible of coveys of bobwhites.

Choice of roosting areas seemingly was not controlled by intensity of light. The roosts that were found on the study area all shared one characteristic; none was in vegetation that would interfere with sudden flight from the roost. These observations agree with Stoddard's finding (1931:54) that bobwhites show a preference for roosting places that are open to the sky.

It was not within the scope of my field problem to investigate the physiological factors involved in the reaction of bobwhites to intensity of light. Probably the eye is the receptor, and either it or some part of the central nervous system is the measuring device. Baldini *et al.* (1952:92) hypothesized that the photoperiod brings about breeding condition in bobwhites through the pituitary-gonad axis. The role of the endocrine system in the reaction of bobwhites to intensity of light seems, to me, to be a fruitful field of research. Investigation of the role played by vitamin A also is suggested, because of its importance in the physico-chemical processes of vision, and the finding by Lehmann (1953) of a seeming correlation between amount of vitamin A in the liver of bobwhites and periods of greatest abundance of the birds in Texas.

The number of bobwhites and their distribution depend on rainfall and temperature in the breeding season, competition with other animals, distribution of woody vegetation, occasionally the supply of food, man, and probably other factors. Not all these factors are under the control of man; nevertheless, by taking into account the sum total of the known limiting factors, bobwhites in Kansas can be managed with greater efficiency than in the past.

EFFECT OF INTENSITY OF LIGHT ON THE BOBWHITE THROUGHOUT ITS RANGE

Some of my findings may apply only in south-central Kansas, but there is evidence that bobwhites throughout the United States react to intensity of light in a manner similar to that of bobwhites on Plum Thicket Farm.

With respect to daily pattern of behavior in the non-breeding season, Stoddard (1931:55) found that bobwhites in the southeastern United States left their roosts, "as if at a given signal," at approximately the time of sunrise, when objects some 100 yards distant first became distinguishable to the human eye. He notes also the regularity of the daily pattern of behavior, "when the weather is settled" (*op. cit.*:57), and that the time of feeding by adult birds is governed, to some extent, by weather (*op. cit.*:118). An important observation was that captive bobwhites, kept in widely separated pens, left the dense cover that they had used in midday, "as if at a given signal," and started to feed and that a cloud drifting across the sky seemed to be the stimulus for such a change in habitat and activity (*op. cit.*:57). He observed further that when storms were threatening (presumably the sky was cloudy), bobwhites might feed on and off at all times of day, but that on hot clear days the birds fed almost exclusively in the morning (*op. cit.*:60). Baerg and Warren (1949:9) report that bobwhites in Arkansas feed in the morning, and again in afternoon, and that in unfavorable weather the birds may feed at other times of day. Bent (1932:17), writing of bobwhites in general, observes that they are very regular in their feeding habits, and that the morning period of feeding lasts for approximately one to two hours past sunrise, after which time the birds return to some sheltered spot in midday. Stoddard (*op. cit.*:54) states that bobwhites cease activity and go to roost at dusk.

There are few observations, reported in the literature, regarding the daily pattern of behavior of bobwhites in the breeding season. Stoddard (*op. cit.*:45) observed that young bobwhites spend midday in "clumps of oak sprouts, sumac thickets, or similar areas," and that their principal periods of activity are in the early and late hours of the day. He found also that unmated cocks may feed at all times of the day (*op. cit.*:118), and that males in summer spend considerable time in the open (*op. cit.*:53). Parmalee (1955:46) found that bobwhites in Texas tended to avoid dense woody cover and nested in open situations. Bent (1932:10) states that it is not uncommon to find bobwhites (presumably males) perched on fence-posts, or to find them running in open roads in the breeding season.

Bent (*op. cit.*:26) states that bobwhites everywhere become restless in autumn, and wander about "erratically." He observes also that bobwhites move to woods and brush tangles, and may even perform seeming migrations at that time of year (*op. cit.*:25). In Indiana, A. W. Butler (quoted *in* Bent, *loc. cit.*) found that bobwhites deserted the uplands in the autumn and congregated in the valley of the Ohio River. In Arkansas, the autumn shuffle reportedly takes place when young of the year are approximately four months old (Baerg and Warren, 1949:6).

In Texas, Lehmann (1939:3) found that the chief value of woody cover in winter was for midday roosting, and that herbaceous and grassy vegetation furnished roosting areas and supplied the major part of the diet of bobwhites in that season. Simmons (quoted *in* Bent, *op. cit.*:35) noted that, in Texas, the vegetation most frequently used in summer was bushes; in winter the birds used brush heaps and small hollows.

It seems, from the above notes on behavior and habitat selection of bobwhites, that the daily and seasonal patterns of behavior of bobwhites in states other than Kansas are similar to patterns of behavior of bobwhites in Barber County, Kansas. Bobwhites throughout the United States are limited in the daily and seasonal patterns of behavior and in the habitat they select seemingly by intensity of light. This is not meant to imply that the estimated threshold of intensity of light found for bobwhites on my study area is the same throughout the geographic range of the species.

Numerous explanations have been offered for the observed patterns of behavior. Bent (*op. cit.*:30) feels that bobwhites avoid open situations because the birds are too conspicuous there. Stoddard (*op. cit.*:57) infers that bobwhites are seeking escape from the heat on hot days, in their choice of shaded areas. Bent (*op. cit.*: 27) infers that the midday restriction to dense cover is for rest. Stoddard (*op. cit.*:60) states that bobwhites are "lazy" on hot, clear days, and will feed in the cool of the morning, implying that the birds avoid open situations because it is too hot there.

Baerg and Warren (1949:6) infer that the autumn shuffle is a function of the age of the young bobwhites. Bent (*op. cit.*:25) states that the autumn shuffle is an attempt by bobwhites to get to better feeding grounds. Stoddard (*op. cit.*:53), when he observed that males in the breeding season must be good fliers to escape their enemies, implies that predation is a factor in keeping bobwhites out of open situations.

Each of these causal relationships that have been proposed seems logical from some standpoint. However, my findings indicate that bobwhites are not attempting to stay where it is cool in summer, or warm in winter; that they do not move into dense cover in the autumn in order to have a better supply of food; that the midday period spent in dense cover on clear days is not necessarily a period of rest; and that if the time of the autumn shuffle is a function of age of the young birds, coveys would be found still inhabiting the uplands in mid-winter. According to my findings, bobwhites are limited by intensity of light, and this limiting factor seems to operate throughout the range of the bobwhite, at least in those areas where the species has been studied. Too little is known regarding the life history and ecology of the more southern races of the bobwhite to allow me to extend this generalization outside the borders of the United States.

Bobwhites probably benefit in some way by keeping to situations in which the illumination is low. Avoidance of predators, inferred by Stoddard (*loc. cit.*), may be one of these benefits. The shaded situations that bobwhites use when intensity of light is high, and the fact that the birds are practically sedentary when in the shade at such times, would seem to make them less conspicuous to diurnal predators. The kind of cover that they choose at midday in clear weather in the non-breeding season would be difficult for a raptorial bird or a terrestrial carnivore to penetrate. Times at which bobwhites are in the open are not times at which diurnal predators are inactive; however the lower illumination at those times may make bobwhites more difficult for predators to find.

If the males that do not avoid bright illumination in the breeding season are unmated individuals, then the most conspicuous part of the population of bobwhites at that time of year would be the excess individuals. The seeming disregard by these males of the limiting factor of light might concentrate predation on them, thus reducing mortality in the reproductive segment of the population. That predation is of importance in the breeding season is suggested by the disproportionately large numbers of males in autumn, indicating that more females than males are lost in the breeding season. That selection of habitat is based, in part, on escape from predators is suggested by the choice of vegetation for roosting that will not interfere with quick flight.

Avoidance of predation may be a major factor in the selection of situations of low illumination. Seemingly a number of physiological, psychological, and environmental factors have interacted in the adjustment of the species to its environment. The choice of habitat on the basis of intensity of light is not completely efficient with respect to avoidance of predators, but the high reproductive rate of the species allows for such inefficiency.

Intensity of light is probably not a limiting factor for bobwhites in the sense of geographic distribution. The northern limit of the range of the species is approximately the southern edge of the northern coniferous forests, vegetation that provides excellent shade at all times of the year. Limiting factors other than light, such as low temperature and unavailability of food because of snow and ice, in the north seem to limit the distribution of the species. In the west, bobwhites occur almost exclusively in the vicinities of wooded valleys of streams draining the eastern slope of the Rocky Mountains. But, bobwhites do not occur in the westernmost valleys of such streams, even though the woody vegetation is more or less continuous along the courses of the streams. Low precipitation may be a factor limiting the distribution of the species on the western periphery of its range. It has been shown that, in Kansas, productivity and size of the population of bobwhites are correlated with precipitation in the breeding season. Precipitation progressively decreases from east to west on the eastern slope of the Rocky Mountains, and bobwhites may not be able to survive in the arid western part of the rain shadow of these mountains. Not enough is known regarding the relationships between bobwhites and their environment in the southernmost part of their geographic range to enable me to pick out any factor, or factors, that might limit the southern distribution of the species. It is certainly not a scarcity of vegetation that offers shade, for the tropical broadleaf forests that bobwhites supposedly inhabit in northern Central America do not end abruptly at the southern edge of the range of the species. There is no scarcity of rainfall in this region. Possibly some more subtle factors, such as competition with other animals, limit the distribution of bobwhites to the southward.

MANAGEMENT

The carrying capacity of land for bobwhites seems to be a function of the number of covey "headquarters" available in the most critical time of the year—late autumn. To increase the number of bobwhites on an area a management procedure of major importance is the establishment of additional headquarters areas. The chief characteristic of such a headquarters area is that the woody vegetation must be dense enough in the critical season to reduce the intensity of incident light reaching the level of the bobwhite to below approximately 1000 foot-candles in midday.

Woody vegetation, as well as that in open situations, should be open enough at the level of the bobwhite to allow freedom of movement for the birds. Continuous stands of tall-grass prairie should be avoided.

The minimum area necessary to support a covey of bobwhites in the critical season is approximately 12 acres. Dense, woody vegetation should comprise approximately 225 square yards (0.042 acres) of each covey area. An efficient arangement of vegetation would include patches of dense, woody cover 15 yards on a side, separated by not less than 138 yards of open vegetation. An equally efficient arrangement, and one that lends itself to natural contours and fence rows, would include strips of dense, woody vegetation 15 yards wide, separated by strips of open vegetation not less than 138 yards wide. Since a square mile of land probably will not support more than 53 or 54 coveys of bobwhites, planting of more than 54 headquarters areas on a section of land seems unwise.

The vegetation in the open situations should include short grasses, annual and perennial weeds, and, perhaps, small areas of cultivated row crops. The short grasses and weeds may be maintained by infrequent plowing, or controlled grazing by domestic livestock. Experimental burning of areas of tall-grass on my study area indicates that burning is of little value in keeping down the dense growth of sand bluestem.

Several kinds of trees and shrubs provide the necessary shade for covey headquarters. In my opinion, the best species is the red cedar (*Juniperus virginiana*). This evergreen offers excellent shade at all times of year and thrives in all counties in Kansas. Since red cedar is of slow growth, planting of other trees or shrubs, such as Russian olive or tamarack, might enhance the habitability of the proposed covey headquarters in its early stages of development. Planting of multiflora rose in conjunction with red cedar should be done with caution, as the rose may crowd out the slow-growing cedars. Multiflora rose and Osage orange probably should be planted by themselves if they are to constitute the shading vegetation of the covey headquarters. In any event, the choice of the woody plant for planting should be based on the shade that the plant offers at the level of the bobwhite.

The setting of hunting seasons and bag limits for bobwhites in Kansas should be on a realistic basis that recognizes the occurrence of seasonal and yearly variations in the size of the bobwhite population. More bobwhites would be available to sportsmen in Kansas in late September and October when the population of bobwhites is near its peak, than in late November and December, when the population is in decline. It has been shown that productivity of bobwhites, as well as the relative size of the population, may be indexed by climatic conditions in the breeding season. Analysis of climatological data available from the U. S. Weather Bureau takes little time or effort. The use of such analyses as an index to the relative size of the population of bobwhites in Kansas, and thus as a basis for determining the length of the hunting season and size of the bag limit, would be a more economical means than the interview-questionnaire system now used in some states. Hundreds of man-hours, costing the state agency a considerable sum each year, are used in attempting to determine the relative numbers of bobwhites. The money saved by replacing the present system with one using climatological data, could be spent profitably in other needed areas of the agency's game management program.

Release of hatchery-reared bobwhites in the eastern two-thirds of Kansas probably does not increase the number of bobwhites occupying a given area for more than a short time; most likely the maximum number of bobwhites that the area is capable of supporting under existing environmental conditions is already there. Introducing additional individuals into an area increases the population pressure, causing additional and unnecessary hardships for the wild birds already occupying the area, as well as for the released birds.

If sportsmen in Kansas continue to request the release of hatchery-reared bobwhites, the releases might well be made in the hunting season. Such releases would reduce the hunting pressure on the native birds, and more bobwhites would be available in the hunting season for the hunter.

In the western third of Kansas, many covey headquarters are in shelter belts of trees. Owing to the distance between some of these shelter belts, it is unlikely that bobwhites could repopulate rapidly an isolated shelter belt once bobwhites had been exterminated from it. In such an instance, the release of birds there by man might hasten the re-establishment of a covey.

Summary and Conclusions

A three-year field study (1951-1953) was made of bobwhites on one square mile in the prairie area of south-central Kansas. Relationships between physical environment of the microclimate (climate near the ground where bobwhites live) and patterns of behavior and selection of habitat by bobwhites were emphasized. The conclusions resulting from this research are as follows:

1. Food Habits.—Of the 143 kinds of plants identified on the study area, bobwhites used as food 32 kinds (22.4 per cent). Animals made up only a minor portion of the diet. Native plants seemed to provide the major source of food; introduced plants were used as they became available.

Three of the 12 habitats (types of vegetation) on the study area provided more than 85 per cent of the food of bobwhites; these three habitats are early seral stages in plant succession of the region.

Bobwhites competed with approximately 93 species of vertebrate animals for food on the study area. There was no evidence, however, that supply of food was a major limiting factor for bobwhites.

2. Population Dynamics.—The sex ratio of adult bobwhites on the study area in the non-breeding season was 183-100 (males to females); that of young bobwhites in the same season was 98-100; and that of all age classes was 112-100. The ratio of adults to young in the non-breeding season was 28-72. Most coveys were composed of individuals from several original family groups, and adults outnumbered young in one covey in late October.

There seemed to be no difference in mobility of the sexes in the non-breeding season. My data suggest that young bobwhites have stronger psychological bonds to their coveys than do adults. Male bobwhites in the breeding season moved farther than did either males or females in the non-breeding season.

Censuses in autumns, 1946 through 1955, showed that the population of bobwhites increased from 1946 to 1952. The increase seemed to result from a gradual improvement of habitat on the study area following the cessation of intensive land use in 1946. The population declined from 1952 to 1954, this decline being cor-

related with drouths in the breeding seasons of 1953 and 1954. Favorable rainfall in the breeding season of 1955 seemingly was responsible for the population being larger in the autumn of 1955 than in the autumn of 1954. Bobwhite populations seem not to be able to attain maximum size in one year following severe reductions in numbers in preceding years. Size of the population in the autumn is correlated with precipitation in the preceding breeding season.

Increase in the climax plant community (sand bluestem) of the uplands on the study area may have reduced the carrying capacity of the area for bobwhites. The potential maximum carrying capacity of the area may not have been reached in the period of my research.

Estimates of the breeding population on the study area in two years, based on the number of whistling males, do not account for the number of coveys found in the autumns following each of these breeding seasons. Some of the bobwhites are thought to have moved off the area to nest, and then to have returned to the area in the non-breeding season.

Loss of individuals equaled gain only in the early summer and early autumn. The period of increase was approximately one-fourth as long as the period of decrease. Rate of decrease was greatest when the population was of maximum size, suggesting that mortality is a function of size of the population. Greatest rate of decrease was 93 individuals lost in one month; greatest rate of increase was 122 individuals added in one month. Seemingly a number of causes, and no particular one, was involved in loss of bobwhites on the study area.

3. THE BREEDING SEASON.—Whistling by males on the study area was heard first on April 3, in 1952, and on March 23, in 1953. In 1953, nesting began in mid-April, reached a peak in mid-May, declined to a low point in late June, and reached a secondary peak in early July. Hatching began in mid-May, reached a peak in late June, declined to a low point in early August, and increased to a secondary peak in mid-August. More than half the young bobwhites live-trapped in the autumn and winter of 1952-1953 were hatched in the last half of June, 1952.

As to time, number of individual males whistling in the breeding season paralleled the number of clutches that were being hatched, suggesting that mated males whistle more frequently than had been supposed previously.

The secondary peak in nesting and hatching probably is due to renesting of pairs that had nested earlier, but whose nests were destroyed. The probability is small that late nesting is by females in their first breeding season.

Attainment of breeding condition probably occurs at approximately the same time each year, as it seems to be controlled by the number of hours of light per day. Initiation of nesting may be controlled by local climatic conditions.

4. WEIGHT OF BOBWHITES.—Young bobwhites increased in weight until completion of the postjuvenal molt; adult appearance and weight were attained at approximately 22 weeks of age. Rate of growth decreases with increasing age in young bobwhites. There was no significant difference between weights of males and of females. Young bobwhites, eight to 16 weeks old, averaged approximately 35 grams heavier than did young of the same ages from Georgia.

Fully-grown bobwhites weighed more in mid-winter than in mid-summer; these differences were not correlated with the supply of available food. There is a seeming correlation between weight of fully-grown bobwhites and length of the photoperiod, suggesting that the weight of fully-grown bobwhites is correlated with sexual activity.

Weights of fully-grown bobwhites from different geographic areas can be meaningfully compared only if the weights are obtained in comparable seasons. Fully-grown bobwhites from south-central Kansas weigh approximately 19 grams more than do fully-grown bobwhites from South Carolina.

My data lend no support to the idea, prevalent among Kansas sportsmen, that the introduction of Texas bobwhites (*Colinus virginianus texanus*) has decreased the size of bobwhites in Kansas.

5. TEMPERATURE OF BOBWHITES.—Cloacal temperatures of live-trapped bobwhites averaged 41.7° C. No correlation could be found between cloacal temperature and environmental temperature, season of the year, sex or weight of the birds.

6. COVEY RANGE AND TERRITORIALITY.—Coveys of bobwhites used small areas of dense, woody vegetation on the study area as "headquarters" in the non-breeding season. These headquarters were spaced an average of 138 yards apart in continuous woody cover, suggesting that coveys are territorial, at least at midday. Coveys did not seem to be territorial while feeding; two or more coveys feeding together was a common sight.

The minimum area necessary to support a covey in the non-breeding season is approximately 12 acres. In this covey area, patches of dense, woody vegetation approximately 15 yards in diameter were necessary for the headquarters areas.

Male bobwhites in the breeding season are territorial, but their territories are ephemeral. Unmated females may be territorial. Whistling by males may be an announcement of occupancy of a territory, and may have little to do with attracting unmated females.

7. BEHAVIOR AND SELECTION OF HABITAT.—The effect of the physical environment on an organism can be determined only by measuring the factors of the environment in the immediate vicinity of the organism. Use of data published by the United States Weather Bureau may be misleading, or invalid, when dealing with small animals and plants. The physical environment at the height above the ground of the bobwhite differs considerably from that at greater heights. The effect of incoming radiation and of the vegetation on the environment of the bobwhite is pronounced.

There was no correlation between daily and seasonal patterns of behavior of bobwhites on the study area and velocity of wind, temperature, or relative humidity at the level of the bobwhite. Bobwhites seemingly do not select habitats on the basis of these three physical factors. Heavy rains and severe snowstorms resulted in bobwhites seeking shelter in dense, protective cover.

A correlation was found between intensity of light and selection of habitat by bobwhites on the study area; intensity of light also determined, to some extent, the daily and seasonal patterns of behavior of the birds. With the exception of some males in the breeding season, bobwhites on the study area avoided brightly illuminated situations at all times of the day and in all seasons of the year.

The maximum intensity, or threshold, of light that bobwhites tolerate is estimated to be approximately 1000 foot-candles of incident light.

Intensity of light, either direct or diffuse, was a limiting factor for bobwhites on the study area. The most critical time each day was midday, when incoming solar radiation was at its maximum. The most critical time of year was late autumn, when the population of bobwhites is near its peak, and when vegetation that provides shade from incoming radiation is scarce.

The dense, woody cover used by bobwhites at midday on clear days in the non-breeding season (the covey "headquarters") provides shade from incident light. On the study area coveys moved from open situations in the uplands to dense, woody vegetation in the lowlands (the autumn "shuffle") at approximately the time of the first killing frost in autumn. These movements seemingly were due to the herbaceous vegetation of the uplands becoming untenable following defoliation.

Mobility of bobwhites in the breeding season was made possible by numerous shaded situations offered by the herbaceous and grassy vegetation of the uplands at that time of year. Bobwhites, except some males in the breeding season, occupied situations that did not provide shade only when there was a low intensity of incoming radiation; such low intensity was afforded by clouds, or by the acute angle of the sun above the horizon.

Intensity of incoming radiation determines the type of habitat used by bobwhites, and thus affects the daily and seasonal patterns of behavior of the birds.

My data suggest that the threshold for the effect of intensity of light on bobwhites increases as the non-breeding season progresses. This may be due to the gradual onset of sexual maturity in males. Males in the breeding season, seen singly or in the company of other males, seemingly were not restricted to situations that provided shade below the mentioned threshold.

8. EFFECT OF INTENSITY OF LIGHT ON THE BOBWHITE THROUGHOUT ITS RANGE.—Judging from accounts in the literature on selection of habitat by bobwhites, and their patterns of daily and seasonal behavior, intensity of light seems to be a limiting factor for bobwhites throughout the range of the species, or at least that part of it included in the United States. The threshold for the effect of the intensity of light may not be the same throughout the range of the species. Limiting factors, other than light, probably determine the extent of distribution of the species.

Illumination of situations that bobwhites choose may make them less conspicuous to predators, and thus be of significance from the standpoint of survival.

9. MANAGEMENT.—If the season for hunting bobwhites were in the early part of the non-breeding season more bobwhites would be available for harvest than if the season is in late November and December. The length of the hunting season and size of the bag limit should be on a realistic basis that recognizes yearly variations in the size of the bobwhite population in Kansas. A reliable index for such variation can be computed easily on the basis of climatic

conditions in the breeding season. The use of this index (see page 35), in place of the interview-questionnaire system, results in a considerable saving.

Release of hatchery-reared bobwhites may be desirable, under certain circumstances, in the western third of the State, but such releases in the eastern two-thirds of Kansas seem inadvisable, unless they are made immediately prior to, or in, the hunting season.

Maximum carrying capacity of land for bobwhites probably is 53 or 54 coveys per square mile in the critical season (late autumn). Headquarters for coveys should be patches of dense, woody vegetation approximately 15 yards in diameter, not less than 138 yards apart, with the intervening areas in short herbaceous or grassy vegetation. An equally efficient arrangement would include strips of dense, woody vegetation 15 yards wide, separated by not less than 138 yards of open cover. Probably more than 53 or 54 covey headquarters for bobwhites on one square mile of land are not advisable.

In Kansas the red cedar (*Juniperus virginiana*) is good to use in establishing a covey headquarters. This evergreen tree offers excellent shade throughout the year, and thrives in all counties in Kansas.

Woody plants to use in establishing covey headquarters areas should be chosen on the basis of the shade afforded by the plants in the autumn and winter months at the level of the bobwhite.

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