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WISCONSIN QUAIL 1834-1962

Population Dynamics and Habitat Management

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*Dedicated to the memory of Aldo Leopold,
Paul L. Errington, Albert J. Gastrow, Sr.,
and Helmer M. Mattison*

WISCONSIN QUAIL, 1834–1962

Population Dynamics and Habitat Management

By

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Abstract

During the period from 1829 to 1962, the quail population of Wisconsin reached a peak level in the mid-1850's and then steadily declined, interrupted only by recurring peaks each at successively lower amplitudes. The decline from 1937 to 1962 was directly correlated with a loss of hedgerow cover. On the major study area of 4,500 acres at Prairie du Sac, Wisconsin, the population fell from a high of 433 birds in 1933 to 0 in 1959.

The Prairie du Sac quail population averaged 23 birds per mile of hedgerow cover from 1931 to 1950, during which time the miles of hedgerow cover exceeded 1 mile per 450 acres. When the ratio of miles of hedgerow cover to acres of study area declined to 1:650, the quail population disappeared. The correlation of hedgerow cover and quail density together with other population data establishes a guideline for quail habitat management.

Quail food supplies appeared to be ample except in periods of heavy snow. However, modern agriculture is bringing about changes in this condition which may necessitate deliberate efforts to produce quail food in the future.

Mortality rates at the Prairie du Sac study area, subdivided into ecological seasons and based on 100 per cent for the start of each season, were: 50 per cent from November 15 to March 31, 17 per cent from April 1 to July 14, and 63 per cent from July 15 to November 14.

The winter mortality from 1929 to 1950 was directly correlated with the number of months during which 3 or more inches of snow covered the ground. This correlation led to the conclusion that the percentage of winter mortality can be predicted within 15 per cent accuracy from information on weather conditions alone.

Summer mortality of adults was directly correlated with spring density and appeared to be associated with breeding season stress. Field observations on quail and pen studies on pheasants showed that high adult densities prolonged the period of young production, and this was deduced to increase the breeding season stress. Under high densities, pheasants hatched two-thirds less chicks and at later dates. Adult pheasants, 2 or more years old, were superior in all phases of reproduction to 1-year-old birds. Miscellaneous field data indicate that this same adult superiority may exist in the bobwhite quail.

High spring density of quail suppresses summer gain, the difference between spring and fall populations. Low spring density allows summer gain to reach relatively high levels. Intermediate spring densities showed less impact on summer gain, with the same levels of population scoring both high and low rates of gain. At these levels of density apparently other factors such as weather, disease, food and cover control summer gain.

The interrelationship of winter mortality, spring density levels and summer mortality of adults constitutes a three-phase regulating mechanism of bobwhite quail populations.

While density affected the survival of adult quail, no such relationship was found to exist in young quail. Many factors appear to be involved in their survival.

There was no evidence of any synchronized pattern of population fluctuations. There was a direct correlation between spring and fall population levels. However, the magnitude of increase between these two seasons was tempered by the spring density.

The average hatching date of quail from 1944 to 1960 was July 18, with broods hatching from June to October. Age and sex ratios were comparable to those of other studies conducted throughout the United States and showed no correlation with other population data. Variability and irregularity appeared to be the rule. This is understandable in light of the many variables that control quail populations.

Quail weights reached an annual peak in January and then declined to April. Other studies reported a weight increase after April. This weight trend is phenologically similar to that in pheasants where spring and summer weight changes are correlated with breeding, egg laying, incubation and molting.

Quail move an average of 1/4 mile in winter and 1.3 miles in spring. From spring to fall, 79 per cent of the Prairie du Sac quail left the study area. On a 10,000-acre study area in Dunn County, 42 per cent of the quail left the study area in spring.

Wild quail transplanted to areas containing good habitat but surrounded by areas of marginal and quailess habitat disappeared within two to three years. This disappearance was attributed to the spring dispersal habit of quail. They leave good habitat in spring, moving in an unoriented pattern. Thus, if the surrounding area is quailess, breeding fails to occur and the relatively short-lived quail (85 per cent turnover) disappear.

Quail can be maintained in Wisconsin but only with a concerted effort to preserve existing hedgerows and restoration of this habitat feature so that large blocks of land contain a minimum of 1 mile of hedgerow to 450 acres of land. This must be an interagency effort. Fortunately hedgerows have multiple values to other game, songbirds, beneficial insects and also soil and water conservation values. Detrimental effects will have to be appraised against the assets. This must be done now. In some areas quail already have disappeared as at Prairie du Sac. The statewide population has declined from an estimated high of 1 bird per acre in the 1850's to a low of less than 1 bird per 40 acres in 1960.

A complete management program and future research projects are proposed in this report.

ACKNOWLEDGMENTS

In a long study such as this it is impossible to properly credit all of the people who made significant contributions. To all those whose names we cannot list below, we give our humble thanks, especially the many hunters who sent specimens and information on quail they shot during hunting seasons, and landowners for their responses to our various surveys.

Credit goes to the late Aldo Leopold for the inspiration of our studies and to the late Paul L. Errington for the background on which our efforts were based. Aldo Leopold was also responsible for directing and carrying out studies in Dane County from 1927 to 1942, which are included in this report.

We are also most grateful to I. O. Buss for initiating the Dunn County studies, which he personally supervised and carried out with assistance from H. Mattison from 1945 to 1948. Our gratitude for the field work carried out during most of the course of our studies goes to the late Messrs. A. J. Gastrow, Sr., and H. M. Mattison. These dedicated men gave far more than their call of duty required.

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CONTENTS

PERSPECTIVE AND SCOPE

Preservation and increase of any wildlife species can be attained only by acquiring sufficient data to formulate basic concepts on the primary factors that control populations. This report contains a review and an analysis of the data obtained on bobwhite quail *(Colinus virginianus* Linn.) populations particularly in Wisconsin by other authors for the period 1834–1944 and the results of our own studies, 1942–62. Special emphasis is given to the relationship between cover changes and population trends.

Our study is an expansion of those of Errington (1945 and 1957), Schorger (1944) and the unpublished reports of Aldo Leopold. While the bobwhite quail was the species on which most data were collected, the scope and the concepts that evolved were aimed at all wildlife species. For example, laboratory-type studies were needed to supplement the field data collected on quail, and ring-necked pheasants were used to get basic data on the relationship of density and age ratios to reproduction in breeding populations of upland game birds.

Errington (1945 and 1957) compiled, summarized and analyzed in considerable detail the data obtained during the first 15 and 19 years, respectively, of Wisconsin's 34 years of bobwhite quail and general game bird population studies. His later study, while primarily on muskrat populations, included specific projections of his earlier publications on quail and game bird populations. The focal point in Wisconsin was a 4,500-acre study area lying on the east side of the Wisconsin River across from Prairie du Sac (Fig. 1).

Leaning heavily on the Wisconsin study and drawing on many other wildlife population investigations, particularly those on Iowa muskrats, Errington advanced several basic wildlife population concepts. Significant among these and forming some of the bases for the next 14 years of our study were *emergency and nonemergency winter losses, thresholds of security* (formerly called carrying capacity), *inversity* and *depression phases.*

Since Errington's concepts were basic factors in the initiation of our own studies, it is important to present a brief definition of them at the onset in this report, although they involve complex phases of game bird population mechanisms that must be illustrated in detail to be totally understood. We are taking the liberty in the following paragraphs of interpreting the meaning and importance of these concepts, using examples and brief descriptive and explanatory notes, with humble apologies for any differences that may be incident to Errington's original ideas. Any references in this report to these concepts will involve our interpretations.

Emergency winter losses are easily defined as that part of the annual mortality occurring between fall and spring which can be clearly attributed to unfavorable weather. These losses result from food shortages caused by weed and domestic crop seeds being buried by snow or being encased in ice by sleet storms. Conversely, *nonemergency winter losses* are those that cannot be attributed to adverse winter weather and occur in mild climatic periods when food is generally available. The actual factors involved in nonemergency losses were not known but could include density-related stresses and atmospheric influences other than temperature and precipitation.

When wintering quail populations in a given area survive with little or no loss for a relatively long period, they are described as existing under a *threshold of security.* The implication here is that all facets of the environment are sufficiently favorable to permit the resident quail population to be relatively secure from potential mortality factors.

Winter losses from all causes varied from a reported 7 to 84 per cent during the period 1929–51 according to Errington's and our own investigations. Despite heavy losses in some winters, the following fall population always shows a significant increase over the previous spring. This increase is called *summer gain.* Generally the summer gain is highest percentage-wise when spring populations are relatively low; conversely, the higher the spring population, the lower the summer gain. This inverse relationship between spring density and fall population is called *inversity.*

If winter losses were related only to weather and summer gains were inversely proportional to spring densities with little or no exception, the number of birds that could be safely harvested without detrimentally affecting the breeding population could easily be determined. However, Errington's analysis (1945) indicated that, while spring density generally affected the size of the fall and winter population in most years, this was not always the case, and that some factor or combination of factors might be operating to "depress" the thresholds of security and the expected summer gains. He also advanced the theory that these nonconforming years seemed to fit into *depression phases* but that no satisfactory explanation yet seemed to be in sight. However, in a later report (1957) he seemed to give less credence to the importance of the nonconforming years and depression phases to observed population trends.

Errington's reports were based primarily on winter censuses. Leopold (pers. communication) hypothesized that Errington's concepts were sound and that the mechanisms underlying these population phenomena might be revealed through the results of winter trapping and banding studies together with censuses.

Errington's concepts formed the first premise for the early years of our intensive studies initiated as the result of the interest and inspiration of Aldo Leopold. During the period 1929–43, Leopold carried out various banding studies in the vicinity of Madison, Wisconsin through graduate students and other cooperators to determine survival and mortality rates (turnover) in bobwhite quail. The results of his banding studies are included in this report. Our banding study at Prairie du Sac began in the winter of 1942–43. A few years after initiating this project we broadened Leopold's hypothesis and set up a relatively complete population and habitat study aimed toward the substantiation or refutation of Errington's concepts. The additional study phases included habitat requirements and changes, spring and summer movement, early summer censuses (whistling counts) and observations, the collection of fall population data and experimental studies on density and age relationships in breeding populations of penned pheasants.

Although the population behavior studies were expected to provide data for formulating hunting regulations, it was also necessary to conduct habitat studies simultaneously, for the future of quail depends on managing the habitat. Errington and Hamerstrom (1936) described the main component of habitat as brushy cover in proximity to available food, but they did not quantitate the amount of brushy cover needed to support a given population.

Schorger (1944), in his review of historical accounts of Wisconsin quail populations from 1829 to 1902, questioned whether quail could exist in significant numbers in the future in Wisconsin because of the tremendous rate of destruction of brushy cover located primarily in hedgerows. This destruction began with the expansion of agriculture following settlement and was accelerated by the advent of barbed-wire fences. Hedgerow destruction together with periods of adverse winter weather resulted in the decline of quail in mediocre or poor range.

In this study, we endeavored to measure the amount of hedge cover existing in 1937 and lost during the period from 1937 to 1960, to determine the response of quail to this type of habitat change, and to work out the type of habitat management program needed currently to maintain or increase quail populations in the state. Although general information on habitat requirements has been repeatedly studied, probably beginning with Judd (1905), sufficient quantitative data to develop specific management guidelines have not yet been collected. Thus this phase of the study is one of the primary features of our report.

Our research began with a concentrated effort to get data on winter populations and later was expanded to procuring year-round data on special study areas. After 1950 we increased our efforts to get related data on a state-wide basis for comparative purposes and decreased emphasis on the study areas.

In view of the multitude of factors and combinations of factors that affect the numbers and distribution of a wildlife species, even a 34-year intensive study is relatively short when population and habitat data are interpreted for biological signfiicance and translated into management practices. Thus, it was necessary to review past Wisconsin studies on quail density, distribution and habitat changes for purposes of extrapolating and converting these statistics to numerical expressions comparable with ones obtained more recently during the intensive 1929 to 1962 investigations.

The broadening of the scope of the studies determined the manner in which we presented the information obtained. Included in the Methods of Study are the basic approaches and findings related to the development of several techniques. Further details are presented in the Appendix. The material in the Results and Discussion chapters is arranged in a parallel pattern with the following exceptions. Habitat studies are presented as a separate section under Results, but are integrated with other sections in the Discussion. A section on Fluctuations (population changes between years) is included in the Discussion, drawing on all population material previously presented.

The report is concluded with a section on Management. We tried to make this section directly useful to field personnel and conservation program administrators. Recommendations are included here for practices based on quantitative goals for habitat requirements.

METHODS OF STUDY AND EVALUATION OF TECHNIQUES

Population Studies

Trends

All available sources of information had to be evaluated and interpolations made to obtain and express the population status of quail for the entire period from 1834 to 1962. Since quantitative information on abundance based on field counts of quail in Wisconsin did not become available until 1929, population trends up to this time are based on historical accounts and general surveys. Trends from 1929 to 1962 are based on censuses and specific surveys.

Accounts and General Surveys

Leopold (1931) and Schorger (1944) made exhaustive examinations of the literature for historical accounts on quail distribution and abundance, and in addition Leopold conducted general surveys to get some quantitative data on density. While the information from accounts and general surveys lacks the quality of that given by the more recent census techniques, it does provide background for adequately interpreting population changes and habitat relationships.

Leopold used several approaches. General information on early historical distribution was obtained by reviewing published reports of various observers. For density data he obtained records from hunters on the number of coveys flushed by their dogs, and requested selected farmers and sportsmen to estimate the number of coveys on their farms or to report the number of coveys or birds on a sample farm of known acreage. He considered the last method as far superior to the first one.

Schorger meticulously examined the records of other observers documented in technical reports, diaries, historical observations and newspaper accounts.

Our method of expressing distribution and relative density based on the historical accounts and surveys was to enter these dates and note the reported status in general terms on a state map. Since these reference sources usually contained information on only short periods, abundance statistics were necessarily relative and discontinuous.

Quantitative data for the 1800's was general in nature and consisted of records on quail shipments from various areas and through certain railroad centers, a few hunters' records on birds shot, and occasional references to birds seen during a specific time interval. These data together with the material from Leopold's surveys and the results of recent census studies explained later were expressed in a narrative chronology and in tabular form showing population trends.

Unfortunately the best quantitative data obtained by Leopold (1931) were for other states and for the year 1928. However, he was able to project his survey results to an acres-per-bird expression which provided some statistics for comparison with data obtained later through actual censuses on specific study areas.

Conversion of the miscellaneous reports on quail abundance into quantitative expressions of birds-per-unit-area for the period 1834 to 1902 reported by Schorger (1944) for comparison with recent censuses was done through indirect approaches. Quail density was obviously so great in the 1800's that direct comparisons with populations in the 1900's would be almost meaningless. We projected the reported miscellaneous observations of the 1800's and compared them to the 1900's by calculating the approximate density that would have had to exist to permit seeing or shipping as many birds as were reported in the various accounts.

Censuses and Specific Surveys

Two study areas provided the opportunity for obtaining fall, winter, and early summer population dynamics and trend data. The 4,500-acre study area near Prairie du Sac in parts of Columbia and Dane Counties, recommended by Herbert Stoddard and selected by Errington (Errington and Hamerstrom, 1936) for his intensive investigations, was the focal point of our field studies which began in the winter of 1942–43 (Fig. 1). Supplemental information was obtained on a 9,900-acre area in Dunn County selected by Irven O. Buss (Buss, Mattison and Kozlik, 1947). Although outwardly similar, the two areas do show some major differences.

From the standpoint of agricultural crop potential, the soils are similar in both areas; those in Dunn County are grayish-yellow silt loams and, in Prairie du Sac, grayish-brown silt loams. Both areas have an interspersion of hills with Prairie du Sac having bluffs typical of Wisconsin's southwest Driftless region and Dunn County having a rolling-hill terrain showing more recent effects of glaciation. Dunn County has more low land, including a swamp area, but both contain river bottoms. Prairie du Sac is generally surrounded by a quail range with a similar density of birds, while Dunn lies near the northern extremity of the Wisconsin quail range and has forested counties on or near its borders which have much lower quail densities. The agricultural crop acreage varies somewhat with Dunn County having about 30,000 more acres of hay and 24,000 less corn. Otherwise they are similar in this respect.

The study objectives and procedures were generally similar on both areas. However, Prairie du Sac quail were fed only enough to be lured into traps which in some cases meant one meal; censuses were intensive from fall to spring; debrushing of coverts which was heavy and continuous was carefully recorded from 1937 to 1960. On the other hand, the Dunn County quail were fed from fall to spring (except in one year under experimental conditions), censuses were less frequent, and debrushing, though occurring, apparently was not as heavy during the major study years and was not as carefully recorded. The feeding activity was incidental to this study and was not intended to constitute an effort to manipulate the population.

Quail densities on the two areas were very similar on an acres-per-bird basis during the years when both were being simultaneously studied. However, in the early 1930's the Prairie du Sac population was approximately double that on the Dunn County area during the mid-1940's. Also, according to Buss *et al.* (1947), the Dunn County area population was increasing during the period 1945–47 (322–447) while the Prairie du Sac population decreased about 50 per cent from 1929 to 1947.

Fall to spring. The procedure for obtaining fall to spring censuses was the same as the one employed by Errington and Hamerstrom (1936), for which they calculated an accuracy of over 95 per cent. Quail censuses were made by obtaining flush and track counts from fall to spring. The inherent behavior of Wisconsin quail at the population level and habitat conditions prevailing during these years made possible this simple census technique.

Our procedure varied from that of Errington in two somewhat different ways. We usually commenced census operations in October whereas Errington's counts usually started in November and December. The purpose of the early counts was to get data on fall populations at a time when coveys had settled down to use their winter range and before the first fall mortality occurred.

Each fall and winter, censuses of all coveys were made at approximately 2-week intervals from early fall to early spring at Prairie du Sac and somewhat less intensively at Dunn County. An effort was made to get near absolute counts of all quail on the study areas from 1942 to 1951 at Prairie du Sac and from 1947 to 1951 at Dunn County. When it appeared that such intensive efforts were no longer practical, midwinter

Figure 1. Aerial photo of Prairie du Sac quail study area, 1955. (The entire portion east of the river comprised the intensive study area.)

censuses were initiated at Prairie du Sac and conducted in the years 1951–52, 1953–54 to 1955–56 and in November, 1958.

To standardize our information with that of Errington we reviewed all the previous census work beginning in 1937 with Albert Gastrow, Sr., the census-taker who personally made most of the counts or accompanied us in the field from 1929 to 1957. This resulted in slight changes in the winter population figures. Thus, as will be shown later in this report, there are some differences in annual population figures between our analysis and that of Errington for the period 1937–42. These revisions do not change the winter counts to the extent that they should affect any of Errington's basic conclusions.

Early summer. While fall and winter censuses provide valuable statistics for population trends and certain dynamics on study areas, more extensive methods were desirable for county and state-wide surveys.

The early studies on quail whistling by Stoddard (1931), Hawkins (1936) and Bennitt (1943) suggested that this behavior might be adapted for censusing bobwhite quail in summer in Wisconsin. The results of our studies (Appendix A) established the validity of using whistling behavior as a census technique in Wisconsin and showed that the number of males heard whistling in late June and early July on the Prairie du Sac study area closely approximated the number censused in late March (Table 13). Similar results were reported by Ripley (1958).

This agreement is evidence that most males, mated and unmated, must whistle, and is contrary to the conclusion of Stoddard (1931) and Bennitt (1951) that it is generally the unmated males that whistle this late in the breeding season. Bennett's conclusion was based primarily on the deduction from some field observations that the number of males heard whistling on his study area was about equal to the surplus males.

The actual difference between our results and Bennitt's cannot be fully explained. In both studies the seasonal trends in frequency of birds heard whistling and the peak of whistling activity in late June and early July were similar.

Generally, Missouri's quail range supports about five times as many quail as Wisconsin's. The number of males reported whistling by Bennitt was similar to the number heard on our transects. Despite the fact that the Missouri sampling areas included all types of range and Wisconsin only the better range, it would appear that unless there were some differences in behavior their counts should have exceeded ours.

Bennitt preferred to use mid-July for making whistling counts because he believed that behavior was more stable at that time. In contrast, in Wisconsin we preferred to make counts in late June and early July because the whistling behavior was more stable in this period than at earlier or later dates and also because counts at this time provided total population indices which could be used in population dynamics studies.

State-wide Studies

Transects. On the basis of the results obtained on whistling counts in the area studies, a system of county transects was designed to get state-wide information on quail density. Transects were run each year at the time during the season when whistling activity approached a peak.

Automobile routes of 35 miles were laid out through the better quail range in a particular county, avoiding where possible concrete roads and roads less than 1 mile apart. Fairly calm and rainless mornings were selected between June 24 and July 8. Commencing at sunrise, 2-minute stops were made for listening at 1-mile intervals. Two and a half to 3 hours were allowed for each transect. Records were made on standard forms of all birds seen along the route and of weather conditions at the start and end of the transect (Appendix A).

The reason for selecting better quail areas was to get trends in the better parts of the range so that year-to-year changes would be more readily detected. Although we used 35-mile transects in order to cover more range in each county, we selected only the 20 best stops for obtaining the average count, and were thus able to eliminate transects where interference or interrupted range would depress the average. While desirable conditions did not prevail throughout each transect for the entire 35 miles, they did occur in at least 20 of the stops and with these as the base, we had a comparable set of counts for each county. For example, weather factors might delay the start of whistling activity, interrupt or curtail it, but would not affect the entire route. We did not expect, however, that this technique would produce an index that could be used alone to accurately determine the state-wide population trend; other data were also used.

In 1949 about one-third of the original transects were rerouted because it turned out that they sampled poor range. In a few cases discrepancies occurred because of untrained observers. Such counts were not used in final tabulations.

The counts obtained on whistling transects on study areas, when compared with winter census data, provided the means for computing actual quail density levels in the areas covered by transects. A method for determining significant differences between whistling counts obtained on any two transects is shown in Appendix A.

Lemke (1956) compared the results of the annual transects run from 1948 to 1956 with the results of surveys conducted by the Crop Reporting Service for the Wisconsin Conservation Department on quail abundance and distribution (see next section), and found close agreement. This strengthened confidence in the validity of the whistling counts. The comparison was made using only the 20-stop section of these transects, and hence it was deemed that where extensive range information was not necessary, transect length could be reduced accordingly. The greatest variability in the number of males heard whistling on quail transects occurred in the last 15 of the 35 stops due to the decrease in whistling activity as the morning progresses. Thus in 1957 and 1958 the whistling transects were revised and included only 20 stops.

Crop Reporting Service survey. The spring dispersal at the time of covey break-up and the whistling behavior of quail characterized by the widely recognized "bobwhite call" of the male made it possible to obtain inexpensive supplemental information on abundance and additional data on distribution by using the surveys of dairy farmers conducted by the Federal–State Crop Reporting Service. Through the courtesy and interest of Dr. Walter H. Ebling, head of the Crop Reporting Service in Wisconsin, a question on bobwhite quail was included in the July 1, 1948, dairy-farm questionnaire. This was the first of a series of surveys of this type conducted from 1948 to 1961.

The question asked was, "Have you heard any bobwhite quail whistling on your farm this spring?" Space was provided for the farmer to select one of three answers: "yes," "no," and "don't know." The question was based on the expectation that farmers are more apt to hear the sound of the quail whistle than they are to see the birds.

In the initial survey in July 1948, a total of 1,676 questionnaires containing the quail question was mailed to cooperating dairy farmers throughout the state. The number mailed was proportional to the number of dairy farmers in each county. A total of 1,060 reports was returned of which 907 carried answers to the quail question. In later years about 1,000 questionnaires were sent out annually containing the quail-whistling question.

In 1949 the Crop Reporting Service questionnaire was used to determine the relationship between whistling heard in spring and coveys seen in the winter by farmers. The results of these surveys are shown in Table 1, primarily to point out certain features of the technique. Note that district differences within all three surveys were greater than would be expected at the 1 per cent level, thus illustrating the sensitivity of the method.

The ratio of the average number of quail coveys seen in winter to the number heard in spring by farmers in the four districts of the state was 0.66 for 1948 and 0.67 for 1949. These ratios were obtained by dividing the average percentage of "yes" answers on the February survey by that on the July survey. Thus it would appear that only two-thirds of the farmers who hear bobwhites in spring see them during winter. This ratio would vary, of course, with seasonal fluctuations in the quail population, and applies only under the conditions of these surveys.

The ratios for each of the four districts for two years, using the February 1949 survey to compute both sets of ratios, are shown in Table 2.

Note the internal consistency between the years for all districts, except for the southwest area which for both years yielded a much higher ratio. It is not known whether this observation means that quail are more easily seen or less easily heard in the southwest or whether this is simply sampling error.

TABLE 1

Results of Three Crop Reporting Service Questionnaires to Dairy Farmers

District	Spring Whistling (July 1, 1948)		Fall and Winter Coveys (Feb. 1, 1949)		Spring Whistling (July 1, 1949)	
	Total Reports	Per Cent "Yes"*	Total Reports	Per Cent "Yes"*	Total Reports	Per Cent "Yes"*
West	86	64	122	40	93	62
Southwest	69	83	82	63	77	78
Central	71	49	93	32	73	48
South	130	55	147	33	135	56
Totals	356	61.5	444	40.5	378	60.4

*District values differ for all surveys beyond the 1 per cent level of probability (Brandt and Snedecor method, Snedecor, 1946:206).

A comparison of the differences between February and the two July surveys failed to show any significant differences between the two years by district. This was a reflection of a rather stable population over this time period, and also an indication that farmers reported in a consistent manner.

For comparing trends in the quail population by repeat questionnaires of the type discussed here, a numerical change of about 8 per cent in the percentage of "Yes" reports (which represents a proportional change of about 16 per cent) would represent a significant change in quail abundance. To detect a significant change in population in the individual districts, a change of about 16 in the percentage of "Yes" reports would be required. Therefore, it appears that the questionnaires have sufficient sensitivity of results to show major changes of quail abundance in Wisconsin.

In addition to providing population trend information, the Crop Reporting Service survey yielded a distributional pattern of quail in Wisconsin that would not have been practical to obtain through the whistling-count transects. Apparently a small number of farmers were unable to distinguish between quail whistling and the calls of other species, since reports were returned to us on birds whistling in counties where this species is not present. By disregarding the reports emanating from areas obviously without quail, and plotting the plausible reports, a range map showing occupied habitat was prepared (Fig. 4). No attempt was made to correlate whistling reports made by farmers with actual density.

TABLE 2

The Ratio of the Numbers of Quail Coveys Seen in February 1949 to Quail Heard Whistling in July 1948 and 1949 by Farmers

District	July 1948	July 1949
West	0.63	0.65
Southwest	0.76	0.81
Central	0.66	0.67
South	0.60	0.59

Habitat Correlations

The direct relationship between the distribution and amount of shrubby hedgerows and quail populations in Wisconsin provided a means for estimating quail densities even when actual censuses were not conducted.

The method first involved making periodic measurements of the amount of brushy hedges along roads, fences, and streams and of quail densities in the same area over a period of time sufficiently long to determine the relationship. This provided a statistic on the amount of shrubby hedgerow cover required to support a covey of quail in areas having habitat characteristics such as terrain and land use similar to those at Prairie du Sac. This statistic was applied to estimate the quail population at Prairie du Sac for years preceding those when actual quail censuses were made and when habitat conditions were determined.

Hunting Seasons and Kill Data

If hunting seasons are set in accordance with the available surplus and hunting pressure is relatively constant, annual hunting success can be used as a method for following population trends. A study was made of all the readily available information on hunting seasons in Wisconsin.

Sport hunting success or annual kill figures based on report-card returns were available only from 1932 to 1960 (compilations by Otis S. Bersing, in the Wisconsin Conservation Department files).

From 1895 to 1931 there was no open season on quail in Wisconsin. Schorger (1944) reported practically all of the existing records on quail hunting in Wisconsin for the period 1827–95. With the exception of kill records concerning market hunting (railroad shipments and market sales), there are only a few records of hunters bagging quail in a manner representing sport hunting as we view it now.

The fantastically high commercial hunting kill for the mid-1800's serves to show that great changes have taken place in the Wisconsin quail population. For the years between the time quail populations were extremely high and the first hunting seasons in 1932 when census data became available, only relative density information can be presented.

An examination of the length of seasons, counties open to hunting and kill records for 1932–60 (Table 10 and Appendix C) shows that these statistics cannot be used as an index of the Wisconsin quail population. The number of counties open varied from 2 to 31 and season length from 2½ to 44 days. Lemke (1956) compared hunting season kill for 1948–56 with the results of the whistling index. By comparing the percentage change between counties open in successive years, he was able to eliminate the bias that would result from comparing years with varying numbers of counties open. The trend in hunting season kill was generally upward while whistling counts fluctuated in two peaks. The disagreement between the trends of whistling counts and hunting season kill was attributed to the difference in the number of hunters, hunter interest (which for quail is low compared to such species as the pheasant) and length of season.

Mortality and Survival

Winter mortality on the study areas was determined by conducting periodic censuses (flush and track counts) every two weeks as described previously.

Winter mortality records were obtained annually both for the total populations on the study areas and for each individual covey (covey histories). The covey histories for each year were plotted on graphs along with the information on major causes of mortality, particularly weather. Since fox predation has been a controversial subject for decades, estimates were made on winter fox populations and these are included in the figures showing covey histories. The covey histories enabled us to see at a glance the pattern of mortality for each individual covey.

Spring mortality was determined by comparing counts of whistling males in late June and early July with the results of March censuses. While these figures apply directly only to cocks, they were projected to include the hens. Since the peak of whistling activity occurs in late June or early July, we lacked total counts in the interim between the March census and the summer whistling counts. We determined from observation of banded birds that ingress and egress were approximately equal from late March to the time when whistling counts were made. Hence we felt that the populations at the two periods could be compared. This comparison indicated very little mortality in spring, and we therefore did not have the problem of trying to determine the magnitude or causes of interim losses.

Summer mortality information was obtained in only one year. In 1948 we made an effort to find as many young broods as possible in summer, and continued to observe them almost daily up to October 22. The technique consisted of traversing roads by automobile at slow speeds and scanning roadsides and fields for quail broods. Summer mortality was then calculated by measuring brood shrinkage during the period of observation.

Population Characteristics

Ordinarily, reproduction rates for upland game birds are calculated from data on brood hatching and rearing success, brood size, age and sex ratios in the fall population and number of young per adult. Because of the relative ease in censusing quail in spring and fall, however, it is possible to give a direct statement of the increase in the fall population over the spring survivors. This increase was called "summer gain" by Errington (1945). We continued to use this method from 1942 to 1951. However, summer-gain statistics alone do not show the contribution of young birds or adult survivors from the previous spring to the fall population. To get this information we conducted a winter-trapping program.

Winter Trapping

For winter trapping quail, we used variations of existing traps such as those employed by Stoddard (1931) (Fig. 2).

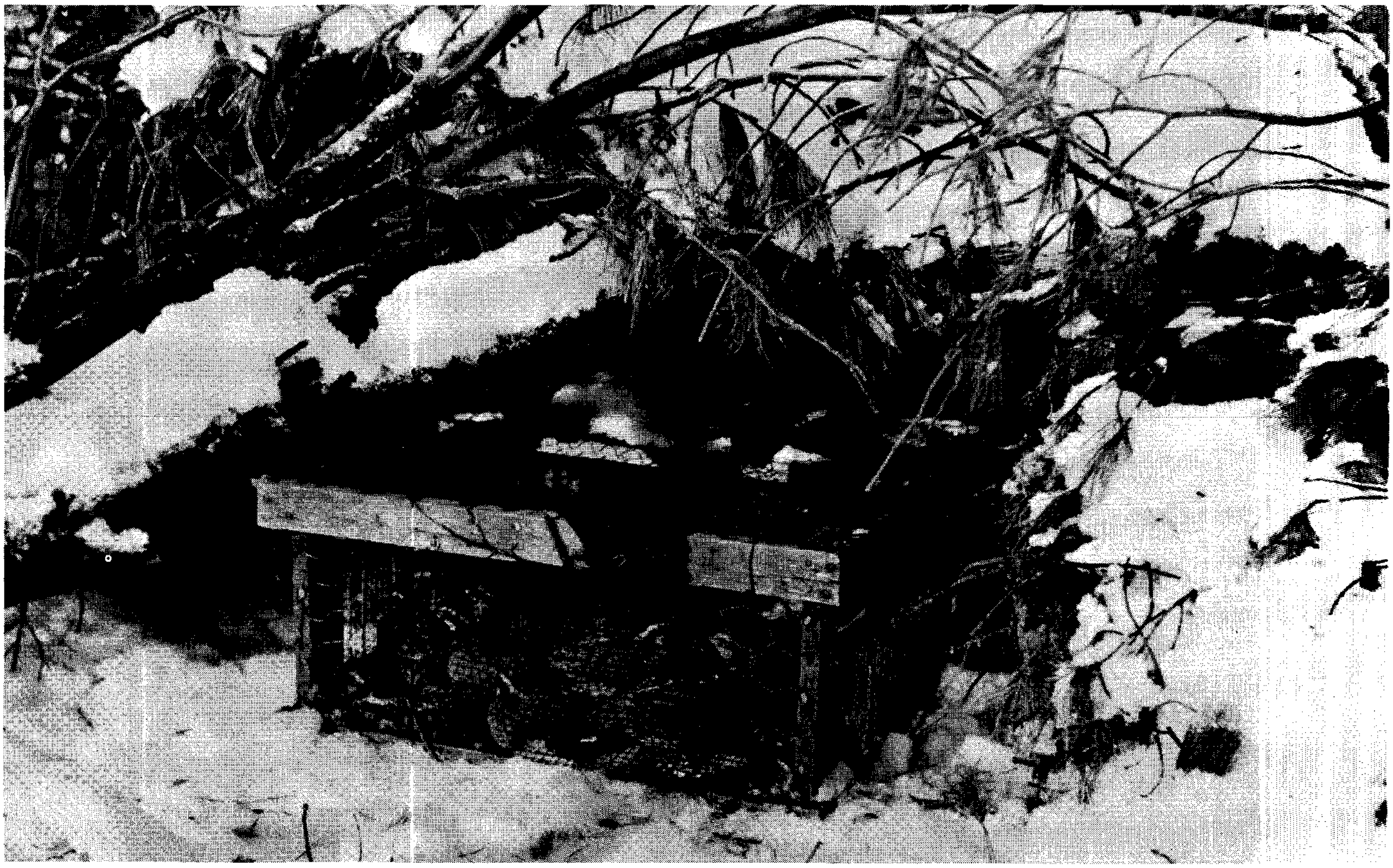


Figure 2. One of the later designed quail traps used on the Prairie du Sac study area.

In the Wisconsin climate where snowfall is frequent, quail enter baited traps readily. We conducted all of our trapping in periods when there was a ground cover of snow. Quail entered traps baited with corn and other grains when there was as little as 1 inch of snow. In the Prairie du Sac area we set traps without prebaiting. This practice decreased our efficiency but prevented the wintering populations from getting artificial feed. In the Dunn County area prebaiting was consistently employed in our trapping efforts.

Aging Techniques

All of the trapped quail were aged, sexed, weighed, banded and released at the trapping site. All juveniles were distinguished from adults by differences in the coloration of the outer primary coverts (Leopold, 1939), and some also by bursa of Fabricius measurements. Data on bursal depths were obtained from several birds that died in traps and from a small sample of live birds. Table 3 shows the monthly shrinkage in the depth of the bursa of juveniles between July and the following March. In adults the bursa is absent or retained as a loose shallow sac which is readily distinguished from the regressed bursa in young birds. Maximum bursa depths are reached in quail by the time these birds reach the age of 60–79 days (Table 4). The average monthy shrinkage rate (October to March) was 1.4 mm.

Although the bursa in quail is relatively shallow, it is nevertheless easily measured and the results of the method show an excellent correlation with the Leopold criterion. Since the bursal aging technique was much slower in practice than the use of the primary-covert characteristic of young and adult birds, we abandoned bursa measurements after 1946–47.

To determine age ratios in fall populations, we obtained wings of quail and aged these on the basis of the advancement of the primary-wing-feather molt and the length of the growing primaries, a technique developed by Petrides and Nestler (1943) and tested on Wisconsin samples by Thompson and Kabat (1950).

Quail wings were collected from birds shot during the hunting season by us or by selected hunters known personally to us. In addition, a sample of quail hunters whose names were selected from report-card returns required by Wisconsin law was contacted by mail and requested to submit wings in the envelopes provided.

We also examined a number of the wings for coloration patterns on the primaries and greater primary coverts to determine if there were some characteristics that could also be used as a method of age determination. Further, we examined several thousand wings donated to us by the late Rudolf Bennitt from his Missouri studies. We concluded that while there was a wide variation of color patterns, these overlapped and varied considerably even for birds from the same brood.

TABLE 3

Bursal Depths in Bobwhite Quail, 1946–47

Month	Adults			Juveniles		
		Depth in Mm.			Depth in Mm.	
	No.	Mean	Range	No.	Mean	Range
July–August	2	0.5	0–1	1	11	11
October	—	—	—	11	10.1	6–13
November	—	—	—	17	9.7	7–13
December	—	—	—	—	—	—
January	5	0	0	17	5.2	2–9
February	7	0.4	0–2	44	3.1	0.5–7
March	1	2	2	14	2.8	0.6

Covey Composition and Hatching Dates

Where possible, we trapped entire coveys of birds as early in fall as possible to determine sex and age composition. We also sampled coveys by collecting 4 to 8 birds from each during the fall season. The number of different-aged young taken from the same covey showed the minimum number of broods composing fall and early winter coveys. These samples had to be obtained prior to the time the young birds had completely molted all of their primary wing feathers.

The wings of all specimens collected in fall provided the sample required to determine hatching dates of Wisconsin quail. To determine hatching dates, the juvenile birds in the sample were aged and back-dated from the collection date.

TABLE 4

Bursal Depths in Juvenile Bobwhite Quail, 1946–47

Age in Days	Number	Depth in Mm.	
		Mean	Range
40– 59	1	13	——
60– 79	5	10.4	7–13
80– 99	3	10.3	8–13
100–119	7	10.3	8–12
120–139	8	9.3	6–11
140–159	5	9.4	6–11

Movement

Fall to spring. All the locations of each covey censused at Prairie du Sac from 1936 to 1951 were recorded. These observations allowed us to calculate the minimum straight-line movement in yards between the time of the first and last census annually for individual coveys.

Spring to summer. Quail were tagged with aluminum leg bands when trapped. In the winter of 1946–47 the birds in two of the trapped coveys were tagged with colored celluloid bands. Unfortunately these colored bands were of poor quality and fell off before any spring observations could be made. By the winter of 1947–48 colored-aluminum leg bands (Chicago–Thrift Co.) became available, and they were used in various combinations to tag the trapped birds.

From March to early summer in 1947 and 1948, we cruised all roads in the study areas two to three times each week by automobile from a half hour before sunrise to 8:00 a.m., recorded all quail seen, and determined whether they were banded or unbanded. All observations were made with 7 x 50 binoculars or a 20 x 60 telescope.

Data on spring movement of quail were obtained by two methods; the first was simply to determine the number of birds that moved off the study areas. The percentage of birds leaving the study area was computed from the ratio of banded to unbanded quail observed in each month from March to July at Prairie du Sac and March to June at the Dunn County area.

The second method, initiated in 1948, was to obtain specific spring locations both on and off of the study area of the birds tagged with the colored-aluminum bands. The distance moved was obtained by plotting the sites of the winter trapping and spring observation points for each color-banded bird, and measuring the straight-line distance between these points.

Density and Age Factors in Reproduction

The correlation of spring density with fall quail populations reported by Errington (1945) suggested pen experiments to study this effect. We used pheasants in these experiments because both birds and pen facilities were available. Further, we believed that we could substitute pheasants because of the similarity of their biology. Also any basic information evolving from the pen experiments would contribute to pheasant management even if it did not apply to quail.

While controlled studies obviously cannot be relied upon completely for interpreting wild bird behavior, they do allow the manipulation of certain conditions affecting the birds. Our pen studies on density relationships consisted of the confinement of varying numbers of birds in each pen, and study of the reproductive behavior. Observations covered both yearling hens and birds two years old or older.

Habitat Studies

Our study of quail habitat was based on the assumption that the qualitative aspects of food and cover requirements were well known. Therefore, we directed our attention to the impact of quantitative changes in land use on the present and future availability of food and cover. In addition we obtained some substantiating information on food requirements from field observations and crop-content analyses reported by Stollberg and Hine (1952) and made by many other people in Wisconsin (unpubl. data). We personally examined about 200 crop samples, obtained primarly from fall and winter collections.

Since quail are almost entirely confined to agricultural land in Wisconsin, we appraised changes in food supply by observing significant changes in farm crop production. Our observations included shifts in land use such as the conversion of a farm to a residential or commercial area, the taking of farm land out of production for two or more successive years, road construction and shifts in the kinds of crops grown.

The first step in determining what changes occurred in the cover conditions in the Prairie du Sac region was to review Errington's numerous reports containing references to habitat. His observations showed that the most obvious cover changes concerned brushy hedges along roadsides and fences. However, he considered that the changes in the quantity of brushy hedgerows from 1929 to 1937 were minor. We traced the history of cover losses from 1937 to 1942 primarily through the records kept by Albert Gastrow and the memories of local landowners. From 1943 to 1960 we documented all of the changes in cover as we personally observed them.

It was not possible to designate hedgerows as useful quail cover on the basis of physical quality. Location frequently determined use. In some cases sparser hedgerows were used as cover while relatively dense hedges at times were unoccupied. Designation of brushy areas as hedge cover was not based on specific dimensions. Generally when Errington began his studies in 1929, hedgerows bordered entire sides of fields or sections of roadsides. All were about one-fourth mile or more in length and were continuous. Only those hedges that were along field edges or roads were included in our measurements. Hedgerows varied from 3 to 12 ft. in width at the ground level.

The short stretches of shrubby growths along woodlands were few in number and were not specifically included in our habitat evaluations. The wooded areas also contained many scattered brushy thickets in which quail were occasionally found. Such sites while important components of the quail cover in the area were definitely transient stops. Only sites containing continuous hedgerows, out of which quail coveys habitually ranged to feed and sometimes just to wander, were classified as individual covey ranges. Coveys occupying these sites occasionally left them for periods varying from a day to a few weeks but normally returned daily. We employed the use of winter cover by quail coveys as the criterion for classifying those shrubby growths along fencelines, field borders or roadsides as hedgerows.

Cover conditions (quantity of hedgerows) were expressed in two categories: completely lost or present. In an earlier analysis (Wis. Conservation Dept., 1951), we used three classifications to identify cover conditions: temporary, completely lost or present. Cover conditions classified as temporary consisted of hedgerows that periodically were debrushed. In the year of debrushing or immediately following the operation, such hedgerows had little quail cover value. This classification was appropriate in 1951 but by 1958, with the exception of a small fraction of the existing hedgerows on the Prairie du Sac study area, all those that had been previously in the temporary category were completely removed.

Maps were prepared of the Prairie du Sac study area showing cover conditions as they existed in 1937, the first year of the period for which we were able to determine cover losses. On these maps we superimposed the areas where cover had been removed by the debrushing of roadsides and fencerows and by road construction. The amount of brushy hedgerow loss could then be determined along with the date when the loss occurred. Then we divided the total quantity of cover lost by the number of years in the observation period and calculated the average annual rate of loss. The rate of cover loss was then correlated with changes in the quail population on the area. This provided us with a statistic which we could use to calculate the cover requirements in terms of quantity of brushy hedgerows per covey of quail.

As a follow-up on the area habitat studies, we traced land-use trends in Columbia County, including road development, to obtain data on the factors that were involved in the statewide distribution and abundance of the quail population from 1840 to 1960. We deduced that land-use trends in Columbia County could be projected to the study area for the period preceding the era of Errington's report and our own research. Conversely, knowing the amount of food and cover required to support the quail populations on the Prairie du Sac study area we could then, through a process of extrapolation, estimate county and state-wide population densities in the past.

We utilized the statistics on agricultural development presented by the Crop Reporting Service (1948 and 1954) based on data from the U.S. census reports. These reports date back to 1850 and are summarized at 20-year intervals. They contain statistics on the trend in farm growth and crop acreage. The earliest records on location and miles of roads were obtained from privately published maps filed in the Wisconsin Historical Library. From these maps the trend in road development was determined by measuring road mileage for the years 1861, 1878, 1926 and 1958. These maps also showed the general types of vegetation and cultivated areas which could be correlated with the crop reports.

Since various historical records showed that little or no agricultural development took place in Wisconsin prior to 1840, the Crop Reporting Service reports together with the existing early maps provided adequate information for estimating quail habitat conditions throughout the years of settlement and subsequent periods. Supplemental information on cover loss relating to agricultural development in southern Wisconsin counties was also obtained from a report on the Town of Jordan in Green County (Curtis, 1959).

RESULTS: POPULATION AND HABITAT STUDIES

Population Studies

The population data are arranged to present a general perspective on Wisconsin quail and related species as well as to report all of the basic data collected from the earliest sources of information through the years of our study. We have attempted to accomplish this by first presenting a historical background on long-term trends and then our data on average seasonal changes.

Long-term Trends

General Distribution

The information on quail distribution in Wisconsin from 1834 to 1927 obtained by Leopold (1931) and Schorger (1944) is shown in Figure 3. The original range in 1834 was generally south of an east-west line running through the center of the state—an area in which the counties or parts of counties containing quail had more than 80 per cent of the land area in farms in 1945 (Ebling, Caparoon, Wilcox and Estes, 1948). Periodically quail were reported in isolated areas north of their original range.

With the exception of the disappearance from an area approximately three counties in width along Lake Michigan, the quail range of 1948 reported by farmers in the Crop Reporting Service survey was similar to that occupied in 1834 (Fig. 4). Actually Schorger (1944) reported quail disappearing from parts of their eastern range as early as 1863, and while quail were reported "gone" in only three of the eastern counties during the period 1863–85 (Fig. 3), we can conclude that this condition prevailed for many of the easternmost counties of Wisconsin.

Also we would expect that periodically a few coveys of quail would spill over into the lake-shore counties after 1900 as was the case in 1905 in Milwaukee. The sporadic appearance of quail outside of their generally occupied range was also indicated by the distribution of quail reported by farmers, although some of the reports of quail in remote counties were undoubtedly due to confusion with other species.

Distribution of quail in 1958 was very similar to that in 1949, again shown by the Crop Reporting Service survey of whistling males. Except in forested areas and at the northern and eastern extremes, quail were found in varying densities in all the townships of the occupied counties. Our intensive studies described in detail later show that quail do not, except occasionally, exist in isolated areas outside of the solidly occupied range.

Hence we concluded that from 1834 to 1927 quail were distributed throughout all the counties within the borders of their original range in those areas where their food and cover requirements were met. The degree to which these requirements were met depended on land-use changes which will be described later.

Relative Density—State-wide (1834–1962)

Accounts and surveys. From 1834, when quail were first positively recorded in Lafayette County, up to 1960, density periodically fluctuated from relatively low to extremely high levels, depending on the changes in environmental conditions. Rough estimates of density for the period 1834–1927 are shown in Figure 3. Table 5 presents a chronology of quail fluctuations from 1834 to 1960.

The all-time peak of quail abundance in Wisconsin since 1834 was reached in the years 1846–55, according to Schorger (1944). The years when the population was reported to be fantastically high in most areas were 1853 and 1854, and, although not shown in Figure 3, this density prevailed throughout the central area where "it ceased to be a sport to shoot them".

As some of the evidence for this peak, Schorger cited the following: In the fall and winter of 1849–50, C. A. Orvis shipped 2 tons of quail from Janesville, and shipments on fall- and winter-harvested birds from Beloit totaled 12 tons which Schorger calculated to represent about 55,000 birds. He also cited fantastic abundance reports such as at Jefferson—"saw about 900,000". Accounts that could be compared to the results of sport hunting of the present day were: "A good shot can bag 50–75 in a day at Milwaukee." . . . "There were on an average three bevies to every 10-acre lot." . . . "At Madison, a

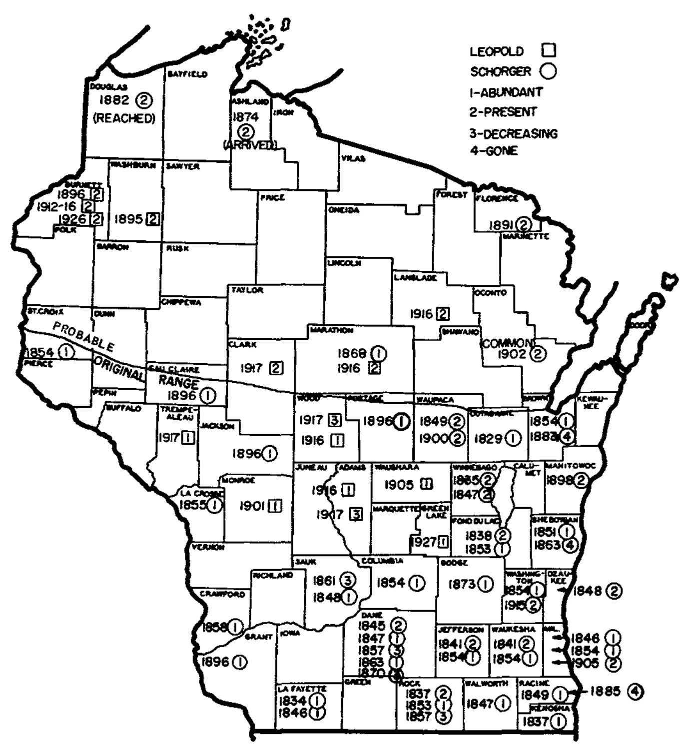


Figure 3. Wisconsin quail distribution and status based on early reports, 1834–1927.

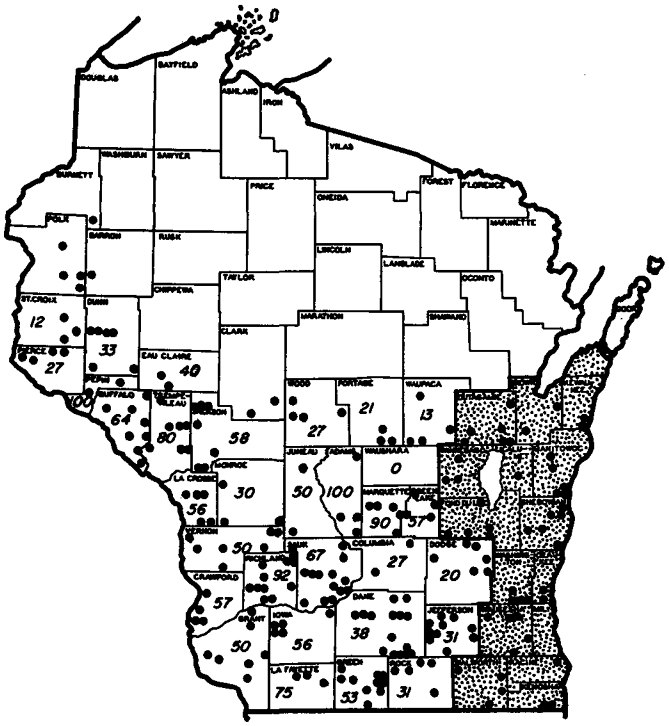


Figure 4. Quail distribution in Wisconsin as shown by a 1949 Crop Reporting Service Survey. (Numbers are the percentage of positive reports by farmers of the occurrence of quail coveys in fall and winter. Reports from stippled area probably are cases of mistaken identity.)

10-minute walk enabled you to put up your first bevy of quails."

Schorger reported the first decline from this peak population in 1855. The decline continued generally to about 1870. The population then apparently leveled off or gradually declined from 1870 to 1895. Kumlien and Hollister (1903) reported that a decrease was gradual to about 1895, and Leopold (1931) further commented that this decline was substantiated by the closing of the Wisconsin hunting season about 1894. That the decline was not general was evidenced by reports for these years from several areas of "more than for many years" (Eau Claire) and "more numerous than usual" (Trempealeau, Black River Falls and Stevens Point).

Area censuses. Leopold (1931) calculated quail densities for several midwestern states based on hunter and landowner questionnaires. The calculations for Wisconsin indicated that quail range contained a density of 1 bird per 4–32 acres in 1929. Forty-five per cent of the range contained 1 bird per 32 or more acres. In Missouri 93 per cent of the range had a density of 1 quail per 0.5–8 acres, with 1 quail per 2–4 acres representing the most common range density (33 per cent). Comparing Missouri to Wisconsin on the basis of Leopold's calculations, we deduced that in half of our state's best quail range, the density was approximately one-sixth of that in Missouri's average habitat during the late 1920's.

There is little or no information on the state-wide quail population from 1929 to 1948. The relative density shown in Table 5 for this period is based on a projection of information we obtained on the study area.

While Leopold (1931) depended on a questionnaire survey addressed to hunters and qualified observers to get his information for calculating quail densities, his estimates were very similar to statistics obtained by Errington (1945) in his intensive censuses on the Prairie du Sac study area. Within the period 1931–35 the fall quail population on this 4,500-acre area ranged from 400 to 433, or an average of 1 bird per 11 acres.

Transects. Trend information on quail densities from 1948 to 1962 obtained from county whistling transects is shown in Table 6. The location of these transects, established in 1948, is shown in Figure 5. The number of birds heard whistling on each transect varied considerably from year to year, but the average per transect for all counties revealed peaks in 1950, 1955 and 1958. The 1958 population, with the exception of that in Buffalo and Green Lake Counties, was almost as high as the 1950 population. From 1959 to 1962 the population has remained very low. This trend (Table 6) is further substantiated by a comparison of the number of tran-

TABLE 5

A Chronology of Wisconsin Quail Fluctuations, 1834–1960*

Period	Relative Density
Prior to 1830's	Present and possibly abundant at times within the original range.
1834–46	Present and locally abundant.
1846–55	Fantastically high in most southern and east central counties.
1856–59	Great decreases in many southern and eastern counties.
1860–65	Numerous locally but not comparable to the 1853–54 peak.
1865–75	Locally abundant but scarce in some areas especially at Madison.
1863–85	Disappeared from the Michigan shoreline in some counties.
1895–1902	Abundant in western and central counties. Appearing in some northern counties.
	Period for which state-wide information is lacking, but Leopold cited some area densities as follows:
1905	Waushara County—Quail spread all over.
1916	Gone by war.
1915	Trempealeau County—Abundant.
1917	Gone.
1916	Mauston—High before war.
1923–27	Lake Puckaway, Green Lake County—Abundant.
1929–35	Populations generally increased from a low to a high level.
1935–38	Relatively low. Adverse winters.
1938–43	Increasing to peak 1942. Decreased sharply in winter of 1942–43.
1943–50	Gradual increase in areas of good range. Decreased or remained the same in heavily debrushed areas. Range extended northward.
1950–52	General reduction in winter of 1950–51. Remained low or declined further.
1953–58	Gradual increase to a peak in good range. Decreased in deteriorating range.
1958–60	Drastic reduction. Population lowest in last 16 years due to adverse winters.

*Schorger's report (1944) covers intensively the period from 1829 to 1902. Leopold (1931) presented some records prior to 1902 and later information on the period 1905–30. For the period 1929–42 our reference source was Errington (1945). Recent records are our own or from the files of the Wisconsin Conservation Department.

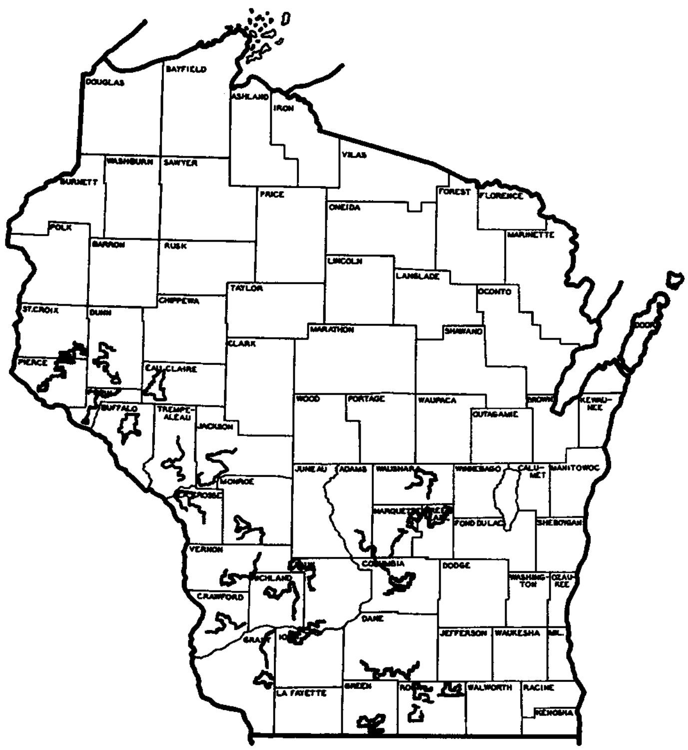


Figure 5. Location of quail whistling transects.

sects showing an increase (up), decrease (down), or a sustaining level (same) between years. The relationships were classified as "up" or "down" when the differences between successive years were beyond the 5 per cent level of probability of no difference (Table 58). When populations were average or above, changes as small as 33 per cent can be detected by this method.

Extreme differences within a transect series from year to year or between the counties in any one year frequently were due to drastic changes in habitat conditions. For example, the decline in counts in the Green Lake County area between 1956–58 was due to road building. However, this lowering of the quail count was not a misrepresentation of the density. Such changes in habitat resulted in net losses to the quail population and since the routes crossed a significant part of the quail range in each county, any change in habitat conditions that drastically lowered the count affected the entire population in this land unit.

Crop Reporting Service survey. The percentage of farmers reporting quail whistling during the spring prior to July 1 in the Crop Reporting Service (CRS) survey for the years 1949–58 is summarized in Table 7. With the exception of 1953 and 1957 the trend is comparable to that shown by the counts made on county transects (Table 6).

We do not regard the CRS survey as being as sensitive a technique as the transects for detecting changes in quail density. The "practical" audibility range of the whistling quail to the human ear is half a mile (Bennitt, 1951). This means that a farmer could hear a whistling male within an area of 640 acres from the center of his farm. Therefore, the chance that a farmer would miss hearing a quail throughout the entire spring would be quite unlikely, particularly since quail move an average of 1 mile each spring.

A broad interpretation of the maximum change in quail density shown in the CRS surveys between the two extreme years of 1950 and 1953 is that there were 7.6 per cent less birds in the areas covered by the questionnaire. On the other hand, the transect counts showed a difference of about 75 percent between the extreme years of 1949 and 1959. The CRS method does provide the advantage of an inexpensive technique for censusing quail where only general trend information is required, or for showing general distribution.

TABLE 6

Total Number of Quail Whistling on County Transects

County	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
Iowa	12	41	47	25	13	14	40	40	39	56	70	12	5	7	4
Adams, Columbia, and Marquette	—	90	57	33	13	—	—	—	—	—	69	9	9	20	6
Buffalo	—	27	19	22	26	20	18	33	4	2	5	1	0	—	—
Monroe	—	36	71	39	24	32	—	—	39	16	18	3	4	—	—
Waushara	—	17	17	36	8	—	17	—	—	—	44	12	8	29	3
S. Dane	—	37	26	8	—	16	—	—	—	—	15	1	4	0	2
Columbia	16	53	23	—	—	10	—	—	41	41	44	23	27	25	39
Richland	41	69	94	61	25	32	65	—	76	45	60	13	13	22	11
Vernon	33	32	38	33	28	25	24	26	37	45	43	12	15	7	—
Crawford	13	44	17	24	18	27	—	—	—	—	40	18	6	7	15
Green Lake	24	8	49	38	25	—	—	47	30	26	8	—	—	—	—
Jackson	65	51	63	—	16	20	36	37	8	12	14	8	5	3	6
Dunn	29	—	—	21	20	26	37	36	6	16	32	32	18	10	7
N. W. Sauk	60	—	63	13	36	26	—	—	—	—	60	—	—	—	—
Grant	14	—	—	49	7	—	—	27	43	38	32	15	5	11	2
Lafayette	—	—	—	—	—	—	46	45	17	29	31	6	7	15	11
Average	31	42	45	31	20	23	35	37	31	30	36	12	9	13	10
Annual changes from previous years* UP		4	2	1	1	0	3	0	0	0	1	0	0	0	0
SAME		2	7	4	8	9	3	6	4	9	9	3	14	12	8
DOWN		1	3	6	3	0	0	0	4	2	1	11	0	0	3

*Based on Table 58.

TABLE 7

Crop Reporting Service Quail Survey*

District	Per Cent of Farmers Hearing Quail by July 1							
	1949	1950	1951	1952	1953	1955	1957	1958
N. W.	25.4	25.0	27.9	22.	29.8	39.8	36.4	37.1
N.	14.9	23.0	13.8	15.	15.2	17.0	13.3	20.5
N.E.	7.7	14.0	10.2	15.9	9.8	5.9	25.7	11.1
W.	61.8	74.0	64.6	60.9	67.9	72.2	59.0	68.8
C.	43.1	59.7	56.3	56.5	46.3	66.7	68.0	58.9
E.	15.3	28.9	22.2	22.	15.2	18.8	23.1	23.6
S.W.	78.1	81.8	82.1	83.9	76.7	89.1	86.6	93.4
S.	53.4	59.8	48.0	47.6	44.2	49.2	48.2	49.0
S.E.	16.9	22.4	18.5	26.8	23.0	15.9	23.3	19.6
Totals	38.0	43.3	38.6	37.4	35.7	40.6	42.4	41.8

*No survey was conducted in 1954 and 1956.

Area Studies (1929–60)

Winter (November 15–March 31). The results of 31 years of censuses of all quail on the 4,500-acre Prairie du Sac area are shown in Table 8. The data from 1929 to 1942 are basically those of Errington (1945) and Leopold (1944).

In the years 1931–35 quail were at their highest level. Following this period, high points were reached in 1939 and 1942. Since 1942 the trend has been downward both in fall and spring. While we lacked spring counts from 1951 to 1958, information was obtained in early summer, as will be shown in the following section, which indicated that the spring trend paralleled the declining low fall population from 1950 to 1958.

Fortunately, the severe decline from a high of 433 birds in 1933 to a low of 19 in 1958 and "0" in the spring of 1960 was not typical for the entire state (Tables 6 and 7). Although quail populations on 3 out of 16 county transects declined severely from 1948 to 1960, with changes comparable to those on the study area, the other 13 transects maintained their population levels through 1958. The drastic decline in 1959 was the result of the very severe 1958–59 winter and was expected to be temporary. However another severe winter, 1961–62, further reduced quail throughout Wisconsin. At this date, we do not have data on this last and wholly unexpected reduction. The magnitude of the variations in fall and spring populations between many of the years at Prairie du Sac was also comparable to that shown by the county whistling transects (Table 6).

Early summer. In addition to the fall-to-spring censuses, quail population trends from 1949 to 1960 with the exception of 1952 and 1953 were obtained from whistling counts in the Towns of Westpoint and Roxbury, which include the Prairie du Sac study area (Fig. 6). For purposes of various studies the whistling counts were divided into three categories and are presented to show the differences in the population of the intensively studied area and the surrounding areas (Table 9).

The peak number of whistling males on the Prairie du Sac study area and in the surrounding two townships occurred in 1950, coinciding with the peak in the state-wide whistling counts (Tables 6 and 7). Following 1950, the quail population declined steadily. The 1957 quail population index in the Towns of Roxbury and Westpoint was equal to 31 per cent of the 1950 index. The eight stops in the Prairie du Sac study area showed a whistling male population that was lower than the surrounding area, but this area still displayed the same downward trend.

Whistling counts are not as accurate as actual counts on

TABLE 8

Fall and Spring Quail Populations on the Prairie du Sac Study Area, 1929–60

Year	Total Birds Present	
	Fall	Spring
1928–29	—	22
1929–30	121	112
1930–31	257	236
1931–32	400	290
1932–33	406	339
1933–34	433	288
1934–35	411	196
1935–36	416	65
1936–37	140	25
1937–38	158	39
1938–39	148	97
1939–40	318	133
1940–41	288	142
1941–42	264	122
1942–43	353	70
1943–44	217	124
1944–45	246	95
1945–46	153	65
1946–47	191	87
1947–48	215	57
1948–49	109	47
1949–50	141	87
1950–51	163	60
1951–52	107	*
1952–53	*	*
1953–54	81	*
1954–55	124	*
1955–56	108	*
1956–57	*	*
1957–58	*	*
1958–59	19	*
1959–60	*	0

*No censuses conducted.

flushed birds, according to Norton, Scott, Hanson and Klimstra (1961). However, these authors evaluated the use of the whistling index as a fall population estimate while we are dealing entirely with a spring population. Hence we believe a crude but usable estimate of the early spring population can be calculated from whistling counts (Table 9). A calculation for the Prairie du Sac and surrounding area was made by converting whistling counts to spring survivors for the period 1949–51 and substituting the average value for these years algebraically for the periods in which there were no spring population censuses. To eliminate some of the error caused by the uncontrollable factors of weather and quail behavior, which caused variations in making whistling counts, the averages for the years 1949–51, 1954–56 and 1957–59 are compared as units and are significantly different at the 5 per cent level for all 3 transect units. The estimated spring population of 46 birds for 1954–56 and 16 birds for 1957–59 is 71 and 25 per cent respectively of the average spring population for the period 1949–51.

Hunting Seasons (1932–60)

Hunting season kill frequently has been used as an index to density for many species. Quail hunting in Wisconsin, however, has not been based on availability but on interest. When quail hunting began in 1932 after a 36-year period of no hunting, only two counties were opened (Table 10). The number of counties open to hunting in 1934 was greatly increased, but only short seasons were allowed. Following the population decline in the winter of 1935–36, a closed season prevailed.

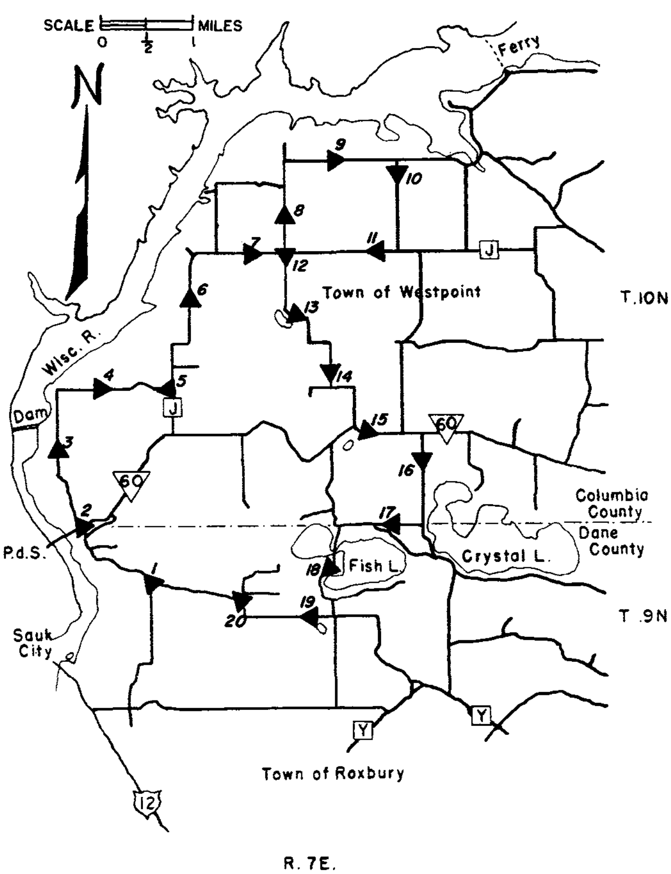


Figure 6. Stops on the whistling transect in the Prairie du Sac study area and the Towns of Westpoint and Roxbury.

TABLE 9

Average Number of Quail Whistling at the Stops Along Transects and Spring Populations at Prairie du Sac and Surrounding Areas

(No. of Stops)	Study Area (8)	Total Area Censused (20)	Westpoint Twp. Only (17)	Spring Pop.* No.	Spring Pop.* Acres/ Quail
1949 (June 10)	2.3	3.2	3.0	47	96
1950 (July 14)	3.5	3.5	3.6	87	52
1951 (June 27)	1.2	1.8	1.9	60	75
Avg.: 1949–51	2.3	2.8	2.8	65	74
1954 (June 23)	1.9	2.1	2.1		
1955 (June 24)	0.4	2.0	1.9		
1956 (July 10)	1.4	1.9	2.1		
Avg.: 1954–56	1.2	2.0	2.0	46†	97†
1957 (July 1)	0.5	1.0	1.1		
1958 (June 19 and June 28)	0.7	0.9	0.6		
1959 (July 6)	0.0	0.2	0.1		
Avg.: 1957–59	0.4	0.7	0.6	16†	281†

*The spring (March) populations from 1949 to 1951 are derived from actual censuses of both sexes (Table 8).

†Based on a conversion of whistling counts to spring population and quail per acre for the "Large Area", from 1954–56 and 1957–59, which includes stops both in the Prairie du Sac area and in the Towns of Westpoint and Roxbury.

Thus while the estimated quail kill increased steadily from 8,592 birds in 1949 to 52,054 in 1957, the population level throughout the state as shown by surveys and censuses did not exhibit a parallel trend. The harvest did, however, reflect the drastic reduction of quail in 1959, following the severe loss in the 1958–59 winter.

The kill for all counties open to hunting in Wisconsin is shown in Appendix C. The 1957 estimated kill, which was the highest for the period 1932–57, is shown by county in Figure 7. The 1957 kill figure provides a general basis for rating and comparing quail densities in Wisconsin counties. All kill estimates are 100 per cent expansions of hunter-report-card returns.

Summary

The distribution of quail in Wisconsin in the 1950's was similar to that of the mid-1850's except for the southeastern quarter of the state where they disappeared after 1900. Generally in the 1900's, quail have been present wherever 80 per cent of the land in a county has been in farms.

Wisconsin quail reached peak population levels in 1845–56. They decreased rapidly for about the next ten years and then entered a gradual decline which has continued to date, interrupted only by re-occurring peaks each at successively lower amplitudes. From 1929–60, the fall population levels of quail in Wisconsin reached peaks in 1934, 1942, 1950 and 1958.

TABLE 10

Wisconsin Quail Hunting Seasons

Year	Counties Open	Dates (Inclusive)	Number of Days	Limit*	Harvest
1895–1931	None				
1932	2	October 1 to October 3	2½	D-4 P-8	551
1933	9	September 30 to October 4	5	D-4 P-8	10,171
1934	17	September 29 to October 2	4	D-4 P-8	12,496
1935	13	October 19 to October 24	6	D-4 P-8	10,848
1936–40	None				
1941	10	November 3 to November 7	5	D-4 P-8	5,058
1942	13	November 11 to November 15	5	D-4 P-8	7,963
1943	5	November 8 to November 12	5	D-4 P-8	3,444
1944	5	November 1 to November 5	5	D-4 P-8	3,741
1945	6	October 31 to November 4	5	D-4 P-8	2,337
1946	4	October 24 to October 28	5	D-4 P-8	6,770
1947	6	October 23 to October 27	5	D-4 P-8	4,986
1948	5	November 2 to November 5	4	D-4 P-8	5,149
1949	12	October 31 to November 4	5	D-4 P-8	8,592
1950	18	October 14 to October 29	16	D-5 P-10	18,487
1951	22	October 13 to November 11	29½	D-5 P-10	14,079
1952	23	Oct. 18 (1 p.m.) to Nov. 11	24½	D-5 P-10	19,182
1953	19	Oct. 17 (1 p.m.) to Nov. 11	25½	D-5 P-10	26,115
1954	17	Oct. 16 (1 p.m.) to Nov. 14	29½	D-5 P-10	25,309
1955	27	Oct. 1 (12 noon) to Nov. 13	43½	D-5 P-10	47,945
		Oct. 15 (12 noon) to Nov. 13	29½	D-5 P-10	
1956	31	Oct. 20 (12 noon) to Nov. 11	21½	D-5 P-10	43,692
1957	30	Oct. 19 (12 noon) to Nov. 25	35½	D-5 P-10	52,054
1958	31 (12, part only)	Oct. 18 (12 noon) to Nov. 30	44	D-5 P-10	49,400
1959	31 (12, part only)	Oct. 24 (12 noon) to Nov. 11	19	D-3 P-6	15,100
1960	26 (12, part only)	Oct. 22 (12 noon) to Nov. 6	16	D-3 P-6	8,500

*D—Daily.
P—Possession.

In this period the quail at the Prairie du Sac study area built up to a peak of 433 in 1934 (1 quail per 10 acres) and fell to 0 in 1959. The general decline was correlated with a loss of brushy cover, and the peaks and troughs with favorable or unfavorable weather conditions.

The trend in the state-wide quail population from 1834–1927 was obtained from historical records as presented by Leopold (1931) and Schorger (1944). From 1929–49 the only specific information on population density was available for study areas at Prairie du Sac and in Dane County through fall-to-spring censuses. Some general information was available from hunting season records after 1932. In 1948 the first state-wide surveys consisting of whistling count transects were initiated; these surveys were followed in 1949 by Crop Reporting Service (CRS) questionnaires.

The CRS surveys, while not as sensitive as whistling counts, provided usable data on distribution and major changes in trends. The transects were estimated to be sufficiently accurate to generally show changes of 33 per cent or less at the 5 per cent level in populations at average or higher levels.

Hunting-season-kill records for quail in Wisconsin were not reliable indicators of population trends because the numbers of counties with open seasons, the length of seasons and hunter interest all varied greatly. The peak kill occurred in 1958. The top-kill counties included Richland, Marquette, Sauk, Trempealeau, and Crawford.

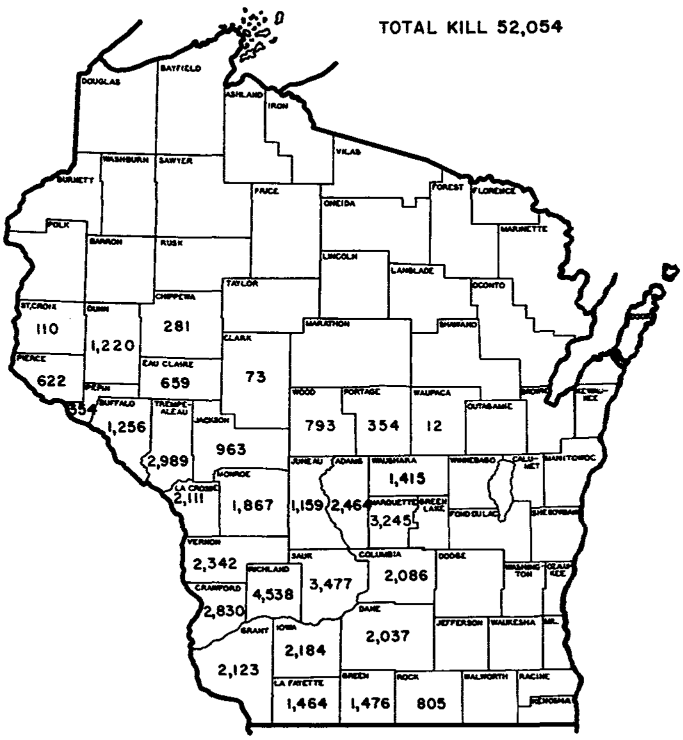


Figure 7. The estimated quail kill by counties in 1957.

Seasonal Losses

The data in this section consist primarily of our findings at the Prairie du Sac study area. Some supporting data obtained in the Dunn County study area, in Columbia County, and on the state-wide population are also presented. The seasons used in this report are based on ecological periods rather than the Gregorian calendar. The ecological relationships include: onset of winter weather, mating season and hatching and rearing of young.

Winter (November 15 to March 31)

The winter losses from 1929 to 1951 ranged from 7 to 84 per cent (Fig. 24). The 1929–44 losses were previously reported by Errington (1945) and included two years, 1942–44, of our study. This graph depicts only total losses for each year and the trend.

From the 29 years of quail censusing on the Prairie du Sac study area, we obtained 15 years of detailed data on winter mortality for all of the coveys in the population. Some of these along with the average are given in Figure 8. This period from 1937 through 1951, featured most of the environmental conditions and variations in quail density that could be encountered in a population study. The individual covey histories, therefore, show at a glance the characteristics of the losses and the role the covey played in the total population losses in winter for any one year. General information on winter weather, food availability and fox populations is also included on these graphs.

The individual covey histories also provided the data needed to calculate a winter survival curve. The percentage quail loss at half-month intervals from October 1 to March 31 is shown in Figure 9 (curve C). Some quail were lost in every month of the period from October to April. The average from October 1 to December 15, prior to the period when adverse winter begins to claim a heavy loss, was 22 per cent. From 1937 through 1951, an average of 55 per cent of the fall population disappeared by late March and for the period 1929–51 the winter loss averaged 50 per cent. The loss of 50 per cent is more representative and will be used in subsequent references in this report.

During most of the years, the census counts began in November or early December. From 1942–43 through 1947–48 (excluding 1944–45), we commenced censuses early to get some data on October losses. These are shown in curve D in Figure 9. Approximately 4 per cent of the loss occurred between October 1 and November 15. From mid-November to mid-December the loss rate increased sharply resulting in an average mortality rate of about 2 per cent per week for the entire fall (Sept. 21–Dec. 21).

The annual winter loss which ranged from 7 to 84 per cent was divided into four classes: Very light (0–29), light (30–49), medium (50–69) and heavy (70 plus) (Table 11). Regardless of the degree of annual loss, some quail were lost every winter from each covey at Prairie du Sac. Annual winter losses for individual coveys varied greatly (Fig. 8). Generally in those years in which losses were classified as very light, there were few coveys that shrank to 0 while in those years when losses were light, medium or heavy, there were almost always some coveys that shrank to 0.

The results of our studies on the relationship of factors responsible for winter losses are reported in the following paragraphs.

Numerous attempts have been made to classify and express winter weather conditions to show their impact on wildlife populations. Errington (1945) presented a series of charts prepared by Aldo Leopold showing daily minimum temperatures and snow depths on the ground at Madison for the years 1929–43. Generally, winter mortality was directly correlated with the amount of snow and the length of time it remained on the ground. However, to analyze all of the effects of adverse weather, it is necessary to have detailed information on all winter conditions. For example, a blinding blizzard of granular snow, an extremely heavy snowfall in a short period of time, or a sleet storm can intensify the mortality effect of snow particularly if available food supplies are limited prior to the precipitation. Conversely, excess snow which has accumulated over a prolonged period and is characterized by fluffiness is damaging only to the extent that it reduces food supplies. Winters with excessive amounts of snow on the ground for prolonged periods (for Wisconsin, those with 6 or more inches on level ground) will also have many days of below-freezing temperatures.

To determine just how closely snow accumulations and quail mortality were related, we compared the percentage winter loss with the total length of time 3 or more inches of snow covered the ground in any one winter (Table 11).

With few exceptions in any one year the number of months of unmelted snow and the degree of winter mortality are closely correlated. The years of apparent exceptions generally need only a more detailed study of conditions to show that adverse weather did occur and was correlated with high quail mortality. For example, the winter of 1936–37 had little snow but the precipitation at times was in the form of sleet, which has a relatively high killing effect on birds, directly or indirectly, by encasing food sources, and making them unavailable.

Immediately after a period in which a winter storm occurred (snow accompanied by driving winds, sleet or heavy wet snow followed by freezing conditions), quail coveys lost birds (Fig. 8). There were no known exceptions in the period 1937–51. The degree to which coveys lost birds as the result of storms depended on the severity of the weather and the amount of exposure. Coveys in poor habitat showed the largest losses.

While we lacked winter census data for 1951–58, the winters that occurred during this period were in the "very mild" or "mild" class. This long period of consecutive mild winters exceeded that for any other series of winters favorable for

TABLE 11

Comparison of Winter Quail Mortality With Snow Accumulation

Mortality Range and Weather											
Very Light (0–29%) (Very Mild)			Light (30–49%) (Mild)			Medium (50–69%) (Moderate)			Heavy (70+%) (Severe)		
Mortality (Per Cent)	Year	Months of Snow*	Mortality (Per Cent)	Year	Months of Snow*	Mortality (Per Cent)	Year	Months of Snow*	Mortality (Per Cent)	Year	Months of Snow*
7	1929–30	1	33	1933–34	<½	52	1934–35	2	84	1935–36	3 sleet
8	1930–31	<½	34	1938–39	1½	58	1939–40	2	82	1936–37	2
28	1931–32	½	43	1943–44	<1	51	1940–41	2	76	1937–38	3
17	1932–33	½	38	1949–50	1	53	1941–42	2	80	1942–43	3
						61	1944–45	2	72	1947–48	3
						60	1945–46	2	70	1950–51	3
						58	1946–47	2	90	1958–59†	3
						57	1948–49	1½			
Avg. 15		½	37		1	58		2	77		3
Average Mortality			←———	50		———		——→			

*Approximate number of months in which 3 or more inches of snow remained on the ground.
†No winter census data were obtained but whistling counts showed drastic reductions.

quail survival from 1929 to 1958 on the study area and on a state-wide basis for the past 110 years. The winter of 1958–59, however, without qualifications fell in the "severe" class.

Generally when winters were "very mild", mortality averaged 15 per cent; "mild", 37 per cent; "moderate", 58 per cent; and "severe", 77 per cent. If we include the winters from 1951 to 1958 as "very mild" or "mild", we have 16 of the 28 years in which mortality averaged between 15 and 37 per cent. In Table 11, however, we averaged only those years for which we had both winter censuses and other records to get an average mortality of 50 per cent for 12 years of mild and moderate winters.

The pattern of losses for individual quail coveys during any one year together with the apparently random occurrence of years of high or low winter mortality clearly shows that the major part of this mortality is directly attributable to weather extremes. The primary mortality factor is lack of food (Errington and Hamerstrom, 1936). Further, these unfavorable conditions appear to act directly on the birds rather than through some indefinable complex of extrinsic factors such as the "great cosmic oscillations" that Elton (1942) suggests may affect rodent populations.

Adverse winter weather apparently has always been a heavy mortality factor for quail throughout the United States. Fall and winter losses of quail were significantly correlated at the 5 per cent level with snow depths in Iowa with losses ranging from 20 to 88 per cent (Kozicky and Hendrickson, 1952). Lay (1952) reported winter losses in Texas in the following percentages: 1946, 44; 1947, 10; 1948, 62; 1949, 45 and 1950, 27. Phelps (1942) in a three-year study of winter mortality in Virginia reported an average loss of 43 per cent on 45 coveys under observation. The covey size of quail in Alabama decreased from 13.9 in November to 7.3 in April (Barkalow, 1948). In Missouri, Crawford (1946) reported that approximately 62 per cent of the fall quail population failed to survive to spring. Oklahoma's average winter mortality was reported as 54 per cent of the fall populations on refuges by Duck and Fletcher (1947). Virginia quail showed a 60 per cent survival in winters having zero days of snow accumulations and 18 per cent with 26 days of snow and an average of 45 per cent (Mosby and Overton, 1950).

Although the southern states generally lack the heavy snows of Wisconsin, ice and rain storms, drastic changes in temperature, drouths and food shortages make heavy inroads on quail populations.

Throughout the Prairie du Sac studies, observations were made in winter on the other major resident or transient wildlife species using the study area to determine whether the behavior or changes in the density of these species were related to quail population changes. Those which were studied intensively for varying periods of time included horned owls (Errington, Hamerstrom and Hamerstrom, 1940), red fox (Errington, 1935 and Richards and Hine, 1953), cottontail rabbits and mice (Hanson, 1943 and 1944).

Population estimates made by Albert Gastrow, or with his assistance, were based on actual observations, trapped and hunter-killed animals, and the presence of tracks and droppings. These estimates, shown for only three years in Table 12, are reliable for indicating major trends, but we have no way of evaluating them in terms of the actual populations.

Several species showed a major change in population trend. Skunk, opposum and raccoon increased; only the gray fox decreased, but this change was paralleled by an increase in the red fox in almost exact proportions. These changes in the mammals were similar to those occurring throughout the state.

Aquatic mammals are limited in the area which has only about five acres of wetlands excluding the river banks. The river banks are steep and generally contain poor aquatic game habitat.

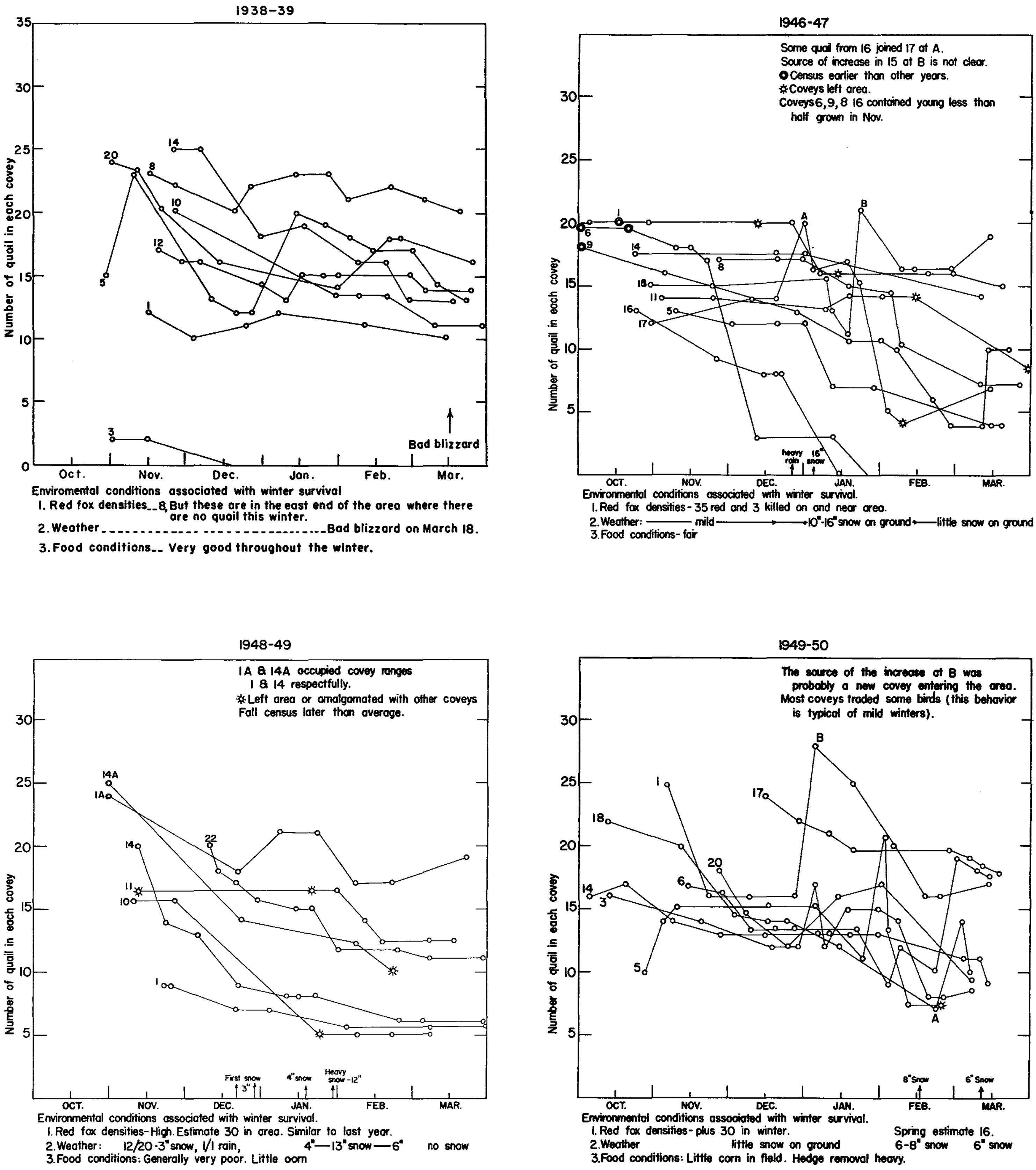
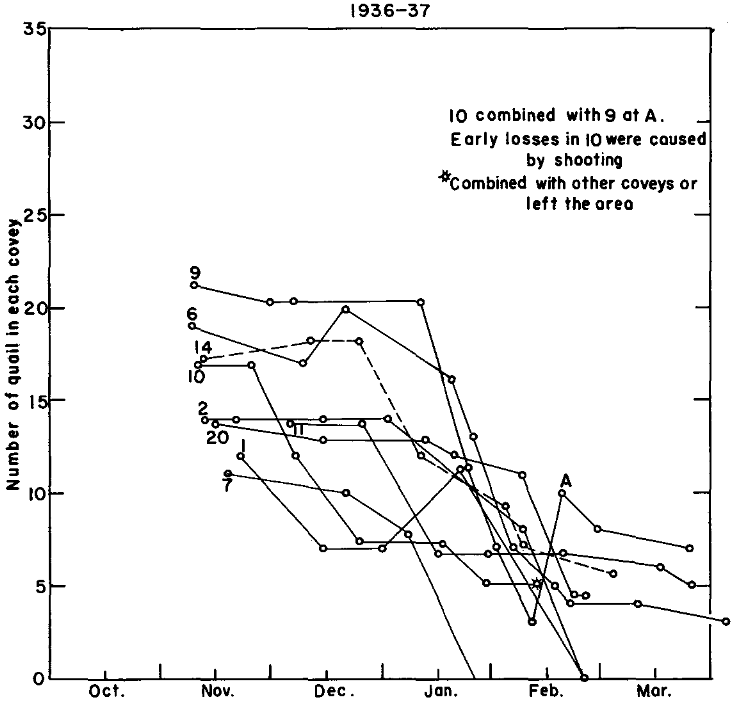


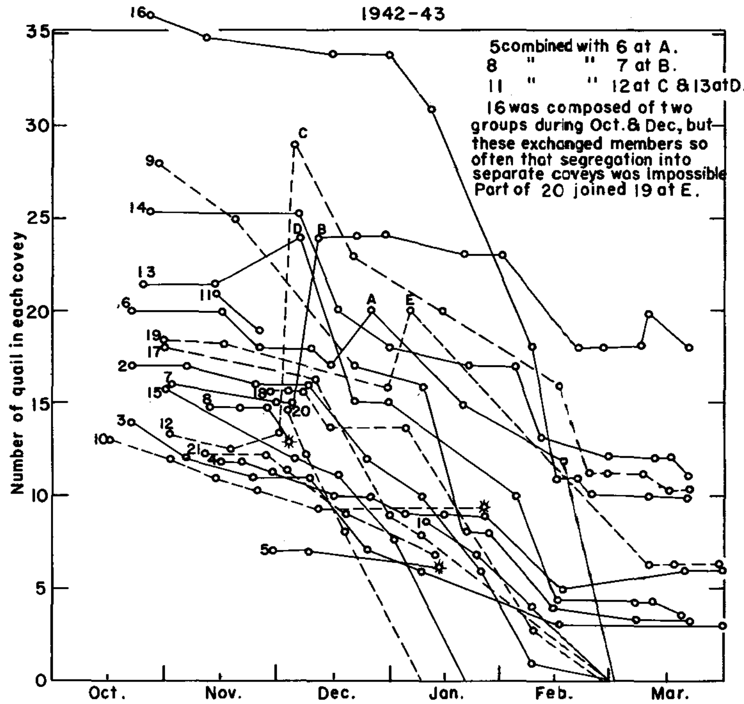
Figure 8. Winter survival of Prairie du Sac quail coveys.

1936-37



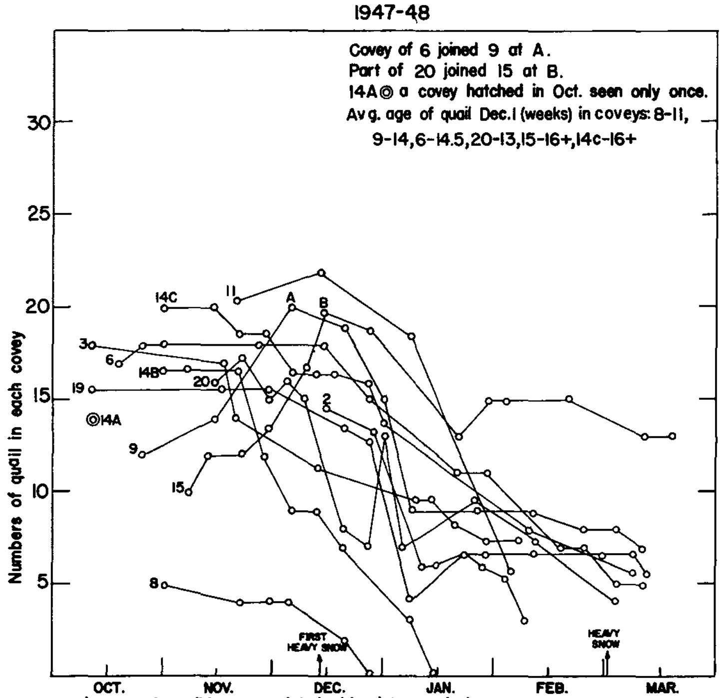
Environmental conditions associated with winter survival
1. Red fox densities -- None in the area this winter
2. Weather ------------------ Sleet storms
3. Food conditions -- Good until January 7, sleet storms coated food sources with ice that remained from January 7 until February 11.

1942-43



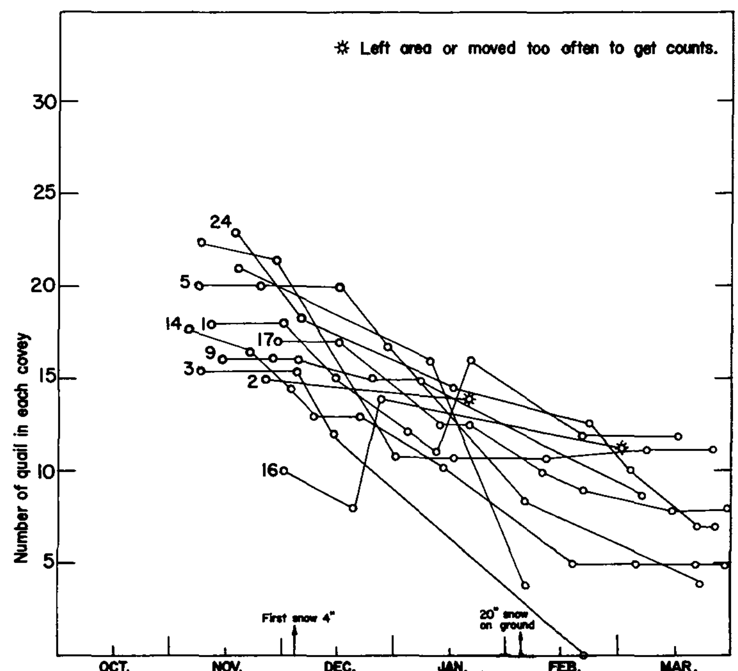
Environmental conditions associated with winter survival
1. Red fox densities -- 10-15 early winter ---------- 5-10 late winter.
2. Weather.---------- | cold snow storms | ----- | cold & snow storms | cold 5-10" of unmelted snow |
3. Food conditions -- Good, despite the deep snow. Corn & soybeans remained in fields until spring.

1947-48



Environmental conditions associated with winter survival.
1. Red fox densities - population high - 25 early winter - 15 late winter
2. Weather snow -4-8"- ———— +12" ———— thaw -snow-
3. Food conditions: poor - buried by snow: few cornshocks.

1950-51



Environmental conditions associated with winter survival.
1. Red fox densities - Winter 23-28
2. Weather: 9" ——— 14" - Frequent heavy snow — 8" ————— 11"
3. Food conditions - Good - fair. Many corn shocks in field.

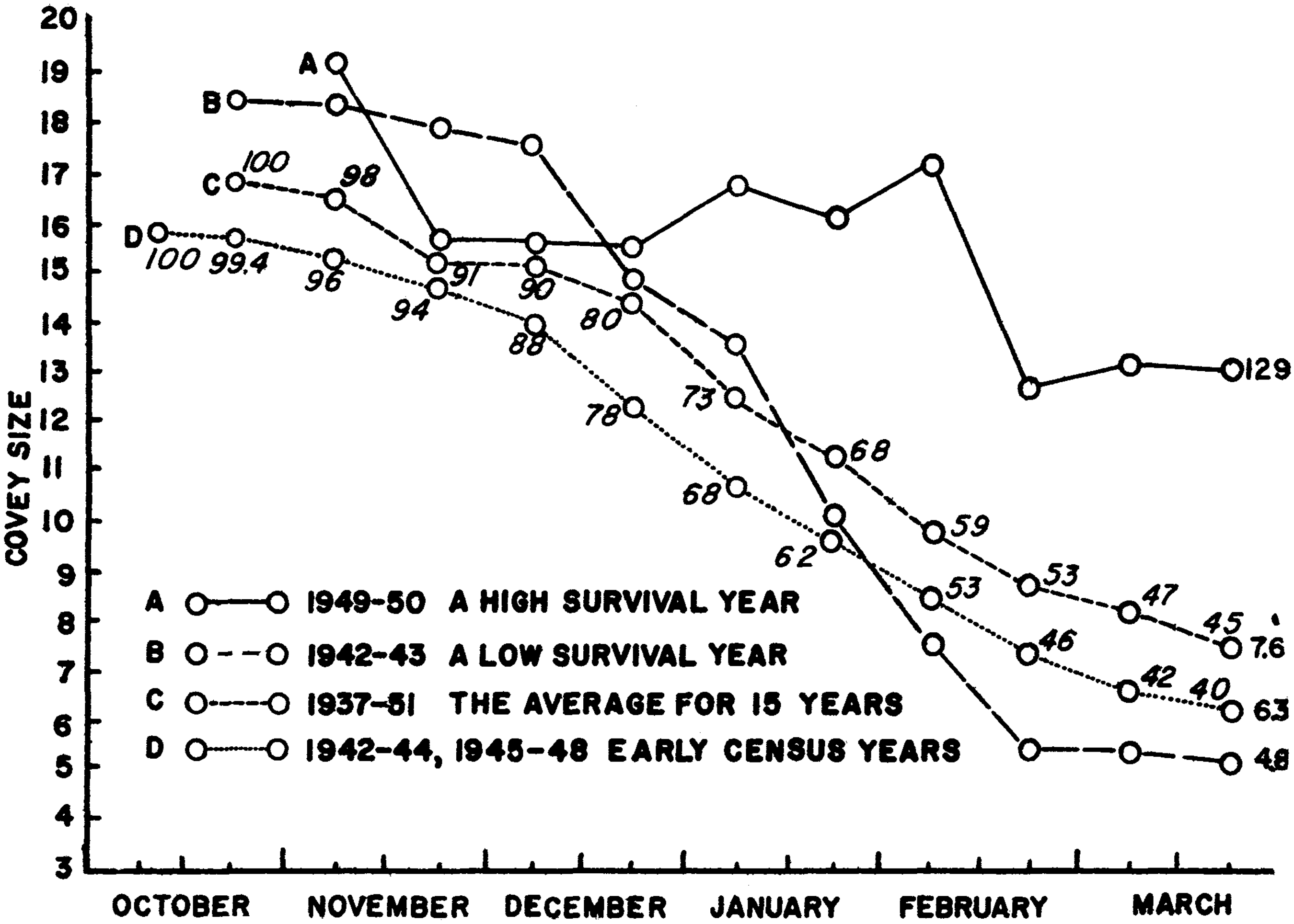


Figure 9. The shrinkage of Prairie du Sac quail coveys in winter. (The numbers on curves C and D express covey survival in per cent.)

Pheasants increased as they did in the rest of the state up to the early 1940's, after which they maintained their numbers at a relatively constant level. The area contains only marginal pheasant range, which has remained fairly constant from 1929 to 1960 with the exception of a steady decrease in the amount of available corn as a winter food source. Pheasants have been artificially stocked on the area since 1939, with 30 to 100 birds being released annually. Hunting pressure on pheasants is moderate. Each winter, pheasants concentrated in a few flocks wherever favorable habitat was created by fortuitous circumstances such as in fields of uncut weedy corn, in unharvested soybeans or on idle farms. Pheasants frequently fed in fields were barnyard manure was spread.

Ruffed grouse increased during this period. Good ruffed grouse habitat is found in the wooded hills, and although most of the wooded hills had been heavily grazed by cattle in the past, decreased grazing and the cutting of trees for use as railroad ties, firewood and lumber have permitted brush to encroach and establish cover.

There was no evidence in the winter covey histories of quail in any year that indicated either a significant loss from predators or the protection from loss due to buffer action of other species.

In the first years in which red foxes began to increase in the early 1940's, a few more quail kills caused by foxes were found. The highest number of quail kills directly attributable to foxes in any one year was six. However, the incidence of quail predation by foxes did not increase in subsequent years even though the red fox population became more abundant, reaching a peak in 1945 and remaining relatively high from 1945 to 1960.

The pattern of winter losses in quail coveys was similar both in the early and late 1940's. The distribution of quail coveys in the area also showed that they were found wherever brushy hedgerows were located regardless of the presence or density of other species. This association, which will be expanded upon later, indicates a greater correlation between quail populations and habitat and weather variations than between quail density and the presence of other species.

Spring to Summer (April 1 to July 14)

Spring losses in quail populations have been an enigma in the quail life equation. On the basis of early winter and spring censuses, Errington (1933b and 1945) assumed that spring and summer losses of adults were negligible. Buss *et al.* (1947), using information from censuses and sex and age

TABLE 12

Estimates of Other Resident or Transient Wildlife Species on the Prairie du Sac Study Area in Early Winter

Species	Year 1935	Year 1942	Year 1949	Red Foxes Year	Red Foxes Number
Pheasant	3	30	18	1937	3
Ruffed Grouse	15	30	50	1938	8
Horned owl	7	6	4	1939	5
Cooper's hawk	*	*	2	1940	4
Red-tailed hawk	6	6	4	1941	8
Rough-legged hawk, Sharp-shinned hawk		Erratic		1942	13
				1943	45
Bald eagle	*	*	3	1944	30
Goldeneye	*	*	25	1945	60
				1946	35
Gray fox	30	2	6	1947	25
Cottontail rabbit	*	*	200	1948	25
Skunk	50	*	100	1949	30
				1950	30
Opossum	12	20	20	1951	26
Raccoon	0	7	15		
Mink	3	2	*		
Weasel	6	4	*		

*No estimates available.

ratios obtained during winter trapping, deduced that adult losses were high in spring. Marsden and Baskett (1958) calculated from data on trapped birds that spring losses were less than 5 per cent.

The whistling-count method provided the first opportunity to measure spring losses directly. During 1946–48 we obtained both early spring censuses on the population and counts on the number of males heard whistling in June. The results of these counts indicated that spring losses in the male component of the quail population on the study area were 5 per cent (Table 13). However, we believe that the actual number of quail whistling was overestimated. Since our counts extended over several days, some of the birds may have moved from one unit to another before the census was complete and may have been counted again. Therefore a 5 per cent spring loss was minimum.

To reduce the effect of the movement factor we ran several daily transects during the next three years covering 60 per cent of the area and projected the number of males heard whistling to 100 per cent. These results showed a maximum loss of 29 per cent (Table 13). For purposes of calculating a life table later in this report, we averaged the maximum and minimum spring-loss estimates (5 and 29 per cent) to get a value of 17 per cent. Although these are still estimates, they represent the best information we have on spring losses.

Summer and Fall (July 15 to November 14)

We obtained information on summer and fall losses of juveniles through observations on 27 broods from early July to late October, 1948, in Dunn County. We plotted the size of each brood observed in the week in which it was sighted. Since our objective was to get a statistic representing the average weekly loss, the approach was to subtract from the number of birds in each brood at the date of the first observation the number remaining at the time of the last count. In some cases broods were larger on subsequent counts than when observed initially. These gains, due possibly to incomplete initial counts, should be compensated for by subsequent observations in which some birds might also have been missed. The total loss in per cent was then divided by the average length of the period of observation in weeks for all broods (Table 14).

The 361 juveniles observed initially shrank to 328 in 4.8 weeks for an average mortality of 9.1 per cent. Computed as an instantaneous mortality rate, *i*, this equals 0.020 for a 1-week interval which is close to 2 per cent per week. This was observed over about a 16-week period, but with most of the observations grouped in the middle part of the period. Thus it is only an approximation of the instantaneous mortality rate of chicks from early July to late October. Applying this mortality rate to 17 weeks, the average age of juveniles in weeks at the time of the opening of the hunting season, we get a juvenile loss of 29 per cent from the time of hatching.

Broods up to 4 weeks of age when first seen were broken down into monthly classes to show the difference in brood size between early and late hatches (Table 15). Only 20 of the 40 broods observed were 4 weeks of age or less when first seen. Late-hatched broods averaged 20 to 30 per cent smaller than those hatching earlier though these differences were not statistically significant. This decline of brood size has been reported for quail by several authors including Lehmann (1946), Errington (1933), Klimstra (1950a) and Pierce (1951a) and for pheasants by Stokes (1954) and Wagner (1961).

TABLE 13

Comparison of Spring Quail Censuses and Early Summer Whistling Counts on the Prairie du Sac Study Area (Males Only)

	1946	1947	1948	Avg. 1946–48	1949	1950	1951	Avg. 1949–51
Spring census	33	56	31	40	30	44	31	35
Summer whistling counts*	42	52	20	38	24	34	17	25
Average loss				5% Minimum				29% Maximum

*For 1949–51, only part of the study area was covered, so a projection to 100 per cent of the area is made for these years.

TABLE 14

Shrinkage in Brood Size (Dunn County, 1948)

	Brood Size (Recorded at Mid-Point of Week of Observation)																			
	July				August				September				October							Observation Period
Brood No.	9	16	23	30	6	13	20	27	3	10	17	24	1	8	15	22	29	Initial	Change	(Weeks)
1	12					10												12	— 2	5
2	20				15	15												20	— 5	5
3	16							12		7		10				12		16	— 4	14
4		9			8			9										9	0	6
5			19					17	7		10	16						19	— 3	10
6				16			17						17					16	+ 1	9
7				16								14						16	— 2	8
8				14	14		15	15										14	+ 1	4
9					7	8	8											7	+ 1	2
10					10	10			6									10	— 4	4
11					11						10	8						11	— 3	7
12					8			8		10								8	+ 2	5
13						14	14	16										14	+ 2	2
14						10	10			10								10	0	4
15						14	18			16								14	+ 2	4
16								10			12	11						10	+ 1	4
17							15		9									15	— 6	2
18								14			12							14	— 2	3
19									11		11							11	0	2
20									8	8	9							8	+ 1	2
21									27					29				27	+ 2	5
22									10	10		6						10	— 4	3
23									5	5		5	5					5	0	4
24									13	13	13	13						13	0	3
25									18		14		9					18	— 9	4
26										14	12	12	11	10		12		14	— 2	5
27													20			20		20	0	3
																TOTAL		361	—33	4.8 Avg.

An inspection of Table 14 suggests that there was no difference in the weekly rate of shrinkage over the time span during which each brood was observed. The average size of the 27 broods listed in Table 14 at the initial observation was 13.4 which is very similar to brood sizes reported by Pierce (1951a) and Klimstra (1950a). An instantaneous mortality rate of 0.020 (1-week basis) would reduce the average brood of 13.4 in summer to 9.5 by late October or 8.7 by late November.

To determine whether this same rate of shrinkage per week held throughout the summer, we compared the size of broods in coveys collected in October and November with those observed from July through October (Table 14). Our data on fall broods were based on samples of young and adults collected from coveys of known size. In addition, we trapped whole coveys and aged all of the birds in them in 1947. These data indicated that the brood size in late October and early November ranged from 7 to 10 with an average of 8.5 which is similar to the value obtained in the calculation above.

Data on summer and fall loss rates of juvenile birds are generally lacking in the literature. Pierce (1951a) estimated that "approximately 25 per cent" of the chicks on a Mississippi study area were lost each month. We assume that this loss included all mortality beginning with the newly hatched chicks. Further, from a study of 31 nests, he reported that the size of chick broods at hatching time was 13 in June, 11 in July, 9 in August and 7 in September. These averages are about 3 birds less per month of hatch than reported in our 1948 study (Table 15).

Klimstra (1950a) reported a loss of 29 per cent from hatching to 8 weeks of age, based on 18 brood observations. The average brood size at hatching was 13.1 birds. Highest losses were observed in the first 2 weeks after hatching.

Therefore, from the results of other studies and our own we concluded that mortality rates in juveniles are highest within the first 2 weeks of life and level off after that to average about 2 per cent per week into the fall.

On the basis of our chronological presentation of losses thus far in this report, we should logically enter here the results obtained on summer and fall loss of adults. However, the supporting data involve a process of extrapolation using

TABLE 15

Average Size of Broods Four Weeks of Age and Under (Dunn County, 1948)

	July	August	September and October
No. of broods	7	5	8
Brood size	16.0	14.2	11.3
Standard error	1.4	1.1	1.7

age ratios with spring and fall censuses. Since age ratios will be discussed later, we are entering here only the basic results on average spring, summer and fall loss for 23 years of data.

The average loss of adult quail from April 1 to November 14 on the Prairie du Sac study area was 69 per cent (Table 40). This loss exceeded the average winter mortality of 50 per cent for adults and juveniles combined.

Summary

The percentage mortality of quail that occurred during the winter (November 15–March 31) when divided into four classes (very light, 0–29; light, 30–49; medium, 50–69 and heavy, 70 plus) was directly correlated with the number of months during which the ground was covered by 3 or more inches of snow. This correlation was so striking from 1929 to 1951 that it appears possible to predict the degree of winter mortality, within an accuracy of about 15 per cent in the quail population, from snow accumulation records alone.

Whistling counts obtained in late June and July were converted into rough estimates of the actual quail population surviving in these months. These data were then used together with early spring censuses to calculate an average mortality rate of 17 per cent for the spring-to-summer period (April 1–July 15).

The size of broods hatched varied in decreasing order with the month of hatch: July—16.0, August—14.2 and September to October—11.3. However, these values are not significantly different at the 5 per cent level of confidence. The mortality rate of broods from July to November, which ranged from 1 to 4 weeks of age when first observed, averaged 9.1 per cent per 4.8 weeks. The value of i, the instantaneous mortality rate, is 0.020 on a 1-week basis or about 2 per cent per week.

Population Characteristics

Hatching Dates

Hatching dates for Wisconsin quail from 1944 to 1960 are shown in Table 16, based on samples taken primarily during late October and early November. The minimum period over which the hatching dates are distributed is 18 weeks. Twenty-four, or 1.3 per cent of the birds had molted their eighth primary juvenile wing feathers and were full grown by the date of the collections. They were classified as hatching in the "Pre-6/1" period, which, on the basis of the distribution of the hatching dates we deduced to be within the last 2 weeks of May. This means that Wisconsin quail hatched during a period of about 20 weeks.

The cumulative percentage of weekly quail hatching shows that half of the birds were hatched by July 13 during a period of approximately 8 weeks. The remainder was distributed over 12 weeks. The week of peak hatching was June 22–28. However, this point is only a few per cent above the weeks immediately preceding and following it.

For purposes of comparing quail hatching dates with those of other Wisconsin species, the hatching distribution is expressed in Table 17 by 4-week classes. In contrast to quail, the majority of Wisconsin pheasants (Buss, Meyer and Kabat, 1951 and Wagner, 1961), ruffed grouse (Hale and Wendt, 1951; Thompson, 1958) and Hungarian partridge (Hickey and McCabe, 1953) are hatched in June, and the peak of hatching is comparatively sharp. The seasonal distribution of quail hatching dates for Wisconsin essentially is almost identical in the span of weeks to that found in most other states, including Missouri (Stanford, 1952b), Florida (Murray and Frye, 1957), Texas (Lay, 1952), Indiana (Reeves, 1954), Alabama (Haugen and Speake, 1958), Kansas (Robinson, 1957), and Massachusetts (Ripley, 1958). However, in an 8-year Iowa study, Stempel (1960) reported that in 2 of the years most of the quail hatched in July, in 2 years hatching extended from June to September and in 4 of the years the hatching period was 1½ to 2 months long. Similar prolonged hatching periods occurred in scaled quail (Schemnitz, 1961) and California quail (Raitt, 1960).

It is expected that a species with a widespread hatching distribution could also have average and median hatching dates that would vary considerably between years. The average hatching date for the period 1944–60 was July 18 and the range of yearly average was July 9 to August 3 (Table 16). The median hatching date was July 13, ranging from July 5 to August 5. Despite the limited samples of quail hatching dates in many years of the study, the extremes of the range occurred in those years when our samples were largest, except in 1960 which was exceptionally early. The size of the sample was not usually proportional to population size.

In analyzing the data in Table 16, it might appear that these figures do not represent true hatching-date distribution because they include only birds alive at the time the samples were collected in late October and early November. Inspection of data in Table 14 suggests that mortality among juvenile quail in summer is relatively uniform. If this pattern of mortality occurred on a state-wide basis and every year, then more of the early-hatched juveniles would have died than those hatching later and therefore would not be included in our fall collections. Thus, the data shown in Table 16 should slightly "under-represent" the early-hatched birds.

To determine the possible error that might occur from using fall collections in calculating hatching dates, we corrected the hatching dates by estimating the mortality occurring between hatching and November (Table 17). These corrections ranged from 0 to 3 per cent in the distribution of hatching dates computed for four-week intervals.

The characteristics of the distribution of quail hatching dates fail to convincingly suggest why young are produced over such a prolonged period. In other species such as pheasants (Buss, 1946; Blouch and Eberhardt, 1953; and Robertson, 1958) and other gallinaceous species (Westerskov, 1957), renesting is common due to large nest or brood losses in early nesting attempts and a second peak of hatching is well defined in some years. Despite the strong renesting drive of pheasants, the length of their brood production pe-

TABLE 16

Bobwhite Quail Hatching Dates in Wisconsin, 1944–60, As Determined by Fall Collections

	No. of Birds																			
Weekly Periods	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	Total	Per Cent	Cumulative Percentage
Pre –June 1	—	1	—	—	—	2	2	—	1	2	1	2	3	3	6	—	1	24	1.3	1.3
June 1– 7	2	—	1	—	4	3	1	1	3	3	5	3	3	10	13	6	4	62	3.4	4.7
8–14	—	—	1	3	8	7	2	1	2	5	2	3	9	16	25	4	2	90	4.9	9.6
15–21	1	—	2	6	11	9	13	5	3	4	2	1	24	42	41	5	5	174	9.5	19.1
22–28	—	1	1	11	15	11	15	4	6	12	8	5	24	51	39	11	6	221	12.1	31.2
29–July 5	1	1	2	15	8	5	11	5	3	9	9	5	24	23	46	11	3	181	9.9	41.1
July 6–12	4	1	2	8	5	13	5	3	1	8	3	5	24	34	35	5	4	158	8.6	49.7
13–19	2	—	1	9	6	9	8	5	1	5	2	3	16	23	21	6	2	120	6.6	56.3
20–26	1	1	1	6	5	8	9	2	1	8	1	3	13	26	22	4	—	111	6.1	62.4
27–Aug. 2	2	—	1	10	6	6	4	2	1	3	3	3	12	24	16	3	2	98	5.4	67.8
Aug. 3– 9	—	—	2	6	5	11	9	1	6	3	3	1	20	13	13	5	—	98	5.4	73.2
10–16	—	—	2	10	5	7	5	2	1	2	7	6	27	14	9	5	2	104	5.7	78.9
17–23	1	—	3	13	5	9	8	2	4	1	2	3	19	6	24	14	2	116	6.3	85.2
24–30	1	1	—	16	3	8	10	1	7	3	3	1	10	22	16	3	—	105	5.7	90.9
31–Sept. 6	1	1	2	11	6	6	10	3	—	1	1	1	13	13	14	3	2	88	4.8	95.7
Sept. 7–13	—	1	—	6	1	9	3	2	1	5	3	—	3	10	5	4	1	54	3.0	98.7
14–20	—	—	1	3	1	2	1	—	—	—	1	—	1	3	—	—	—	13	0.7	99.4
21–27	—	1	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	5	0.3	99.7
28–Oct. 4	—	—	—	2	—	1	—	—	—	—	—	—	—	1	—	—	1	5	0.3	100.0
Totals	16	9	22	139	94	126	116	39	41	74	56	45	245	334	345	89	37	1,827	100.0	
Avg. date	July 16	July 30	July 25	Aug. 3	July 15	July 25	July 23	July 19	July 20	July 13	July 18	July 14	July 21	July 12	July 13	July 20	July 9	July 18		
Median date	July 12	July 23	July 26	Aug. 5	July 6	July 23	July 20	July 13	July 23	July 8	July 8	July 10	July 17	July 10	July 5	July 15	June 29	July 13		

riod is short compared to quail. Possibly the prolongation of nesting in quail concealed any peak of such renesting in many years, yielding a sustained-level curve. Second peaks were apparent in our data only for the years 1947, 1950, 1956, 1958 and 1959. Some of the factors that affect hatching dates for quail and other species are cited below.

The percentage of nest break-up by predators and other factors is high (Stoddard, 1931; Klimstra, 1950a; Lehmann, 1946a), and, although most authors report that quail renest readily, only a few actually observed this behavior. One exception was Stanford (1952b) who described several successful renesting efforts by different hens including one hen which succeeded hatching a clutch in her third effort.

The effect of weather on hatching dates has also been reported frequently for bobwhite quail. Droughts in the summers of 1953 and 1955 in Iowa shortened the period of intensive hatching (Stempel, 1960). Stanford (1961) reported that more lone adult hens were seen in Missouri in June 1960 than usual indicating that many hens were not occupied with nesting and rearing duties. The preceding winter was severe and prolonged followed by a cold, windy and wet April.

A few observations have been reported on the relationship of age of breeding bobwhites and the hatching date of their young. Lehmann (1953) reported that 10 of 16 adults and only 5 of 37 young bobwhite hens were breeding in early spring. Based on an examination of bobwhite ovaries, Parmalee (1955) also suggested that adults may nest earlier than hens of the year. In other gallinaceous species this age differential in the date at which eggs are laid or the number of young produced was more apparent. Genelly (1955) reported that adult California quail laid earlier. Penned adult ring-necked pheasants laid eggs earlier than young hens (Appendix B). In the great tit adults laid eggs earlier than young females and 66 per cent of the adults and only 21 per cent first year hens have a second brood (Kluijver, 1951).

Although bobwhite quail rarely have second broods, two instances of this were cited by Stanford (1953b) but the age of the adult hens was unknown. Quail can lay eggs as early as 19 weeks of age when subjected to artificial light (Baldini, Roberts and Kirkpatrick, 1952), which indicates that sexual maturity is not the only physiological factor in the date of laying.

Heredity is obviously a factor in the date of the first egg of at least some species. Kluijver (1951) reported that some adult females of the great tit laid late every spring, others early.

Other studies by Kluijver (1951) do not shed much light on the hatching dates of bobwhite quail. He reported that day length was a dominant factor in the first egg laying date of the great tit but that this was conditioned by winter temperatures particularly those occuring after January 1. Generally there was a significant correlation between the date when the aggregate of daily temperatures exceeding 0° reached 320° and the peak date of first eggs laid. However, this was qualified by his observation that if the 320-degree "warmth-sun" was reached early in winter, a higher level of this factor was needed to affect the first egg date. Precipitation amounts, humidity and food availability were not correlated with egg laying. Somewhat similar observations were made by Nice (1937) who found that in the song sparrow higher temperatures were required to start egg laying in spring than later in the season.

The possibility that winter temperatures and hatching dates are correlated seems remote for bobwhite quail because of the lapse of time between these two events.

The above factors and conditions all contribute to prolonged nesting. Possibly high nest loss of early attempts, followed by renesting, is an important factor in the prolonged nesting behavior of bobwhite quail. However, the large number of other factors involved suggests that no one factor predominates.

The fact that the over-all distribution of hatching dates for Wisconsin quail is similar to that in states with more moderate climate and different habitat conditions indicates that this population characteristic of a prolonged hatching period is inherent in bobwhite quail wherever they are found. This similarity suggests that summer day length and general food availability (seeds of herbaceous weeds and domestic crops and insects) are dominant factors controlling the average starting date of hatching. Variations in the length of the hatching period are controlled by secondary factors such as density, food quality and weather variations. This speculation is supported by Marshall (1959) who reported that many factors could be involved in all phases of reproduction. He based his conclusion on observations in variations of breeding for different species. For example, waterfowl do not breed if water is lacking, zebra finches produce spermatozoa in darkness if well nourished, and the sooty tern ordinarily has one brood but on Ascension Island it breeds twice.

Data on winter survival of late-hatched birds in Wisconsin were lacking. We used two procedures to acquire such data. The first was to make careful observations on all of the coveys we flushed during the fall-to-spring Prairie du Sac censuses from 1944 to 1948. Our experience in this technique usually allowed us to distinguish between birds that were hatched before and after September 1. When the broods composing coveys were too difficult to classify into these two age groups from size and flight behavior, we collected a bird or two to verify our observations. Some of these birds were also trapped later during our regular banding studies.

Of the 774 quail from 49 coveys we observed using this technique, 99 in 7 coveys were classified as late-hatched (after September 1) juveniles. These 99 birds together with 21 adult and earlier-hatched (before September 1) quail composed 7 coveys. All of the late-hatched juveniles disappeared between early October and late December, whereas the over-all winter mortality of the 654 earlier-hatched juveniles and adults was 58 per cent.

All of the late-hatched birds showed high mortality rates with the advent of the first moderately unfavorable winter weather. Coveys containing full-grown birds showed moderate losses between October and mid-January.

Our second procedure was to trap birds early enough in fall to age them. Since our trapping technique depended on

TABLE 17

Frequency Distribution of Hatching Dates for Quail from 1944 to 1960 (Based on Specimens Collected in Fall and Corrected for Mortality)

(1) Hatching Period	(2) Age in Weeks on Nov. 1	(3) Mortality Rate from Hatching Date to Nov. 1 (%)*	(4) Frequency Distribution of Hatching Dates (%) Based on Table 16	Corrected†
May 16–31	23	37	1.3	1.5
June 1–28	20	33	29.9	32.9
June 29–July 26	16	27	31.2	31.5
July 27–Aug. 23	12	21	22.8	21.3
Aug. 24–Sept. 20	8	15	14.2	12.3
Sept. 21–Oct. 3	5	10	0.6	0.5

*Based on instantaneous mortality rate (i) of 0.020 on a 1-week basis.

†Frequency distribution of hatching dates based on fall specimens corrected for the percentage of mortality occurring between the hatching date and November 1 for each class.

snow cover, we were able to obtain data in only one year, 1947 (Table 18). For comparative purposes we also showed the frequency distribution of hatching dates for the quail obtained during October and early November, the cumulative percentage of birds hatching each week and age when sampled. Further, by projecting these data to December and January, we presented a theoretical age distribution of a quail population in early winter. The assumption here was that all of the quail alive in fall survive into winter.

Though we failed to trap the entire population on the Prairie du Sac study area in 1947, we did get some birds from 8 of the 12 coveys (40 out of a maximum of 215) on the area. The lack of juveniles younger than 13 weeks (hatched after September 6) in our trapped sample, which was obtained between November 29 and December 20, though not statistically significant, suggests that birds of this age class failed to survive beyond the middle of December. The projections from fall wing collections in Table 18 indicates that 9 per cent of the winter population should have consisted of birds hatched after August 31.

Sex and Age Ratios

Sex and age ratios for 2,865 quail collected throughout the state in the fall from 1944 to 1958 do not show any specific trends (Table 19). Little variation is shown in the sex ratios for both adults and juveniles in those years when our samples were largest. The average sex ratios of 61 and 51 per cent for adult and juvenile males respectively are similar to those reported in many states where a preponderance of males has been found repeatedly (Table 20). Possibly the most striking aspect of adult and juvenile sex ratios in quail is this similarity between quail populations located in widely separated states with great variations in habitat and climate.

While it seems unlikely in view of the results obtained in Wisconsin and other states, it is possible that the extreme variations in sex ratios shown in the years when our samples

TABLE 18

Computed Age of Quail (in Weeks) from October to January (Based on Projections from Hatching Dates of Fall Collections Together with a Frequency Distribution of Actual Hatching Dates for a Mid-December 1947 Trapped Sample)

Frequency Distribution (%) of Hatching Dates			Age of Juvenile Quail				Hatching Dates of a Trapped Sample*	
			Actual		Projected			
Period	Weekly	Cumulative	Oct. 15	Nov. 15	Dec. 15	Jan. 15	No. and (Age) on Dec. 15	Per Cent
Pre—June 1	1.3	1.3	20.2	24.4	28.5	32.6		
June 1– 7	3.4	4.7	19.0	23.2	27.3	31.4		
8–14	4.9	9.6	18.0	22.2	26.3	30.4		
15–21	9.5	19.1	17.0	21.2	25.3	29.4	14 (23+)	35.0
22–28	12.1	31.2	16.0	20.2	24.3	28.4		
29–July 5	9.9	41.1	15.0	19.2	23.3	27.4		
July 6–12	8.6	49.7	14.0	18.2	22.3	26.4		
13–19	6.6	56.3	13.0	17.2	21.3	25.4	4 (21)	10.0
20–26	6.1	62.4	12.0	16.2	20.3	24.4	1 (20)	2.5
27–Aug. 2	5.4	67.8	11.0	15.2	19.3	23.4	2 (19)	5.0
Aug. 3– 9	5.4	73.2	10.0	14.2	18.3	22.4	8 (18)	20.0
10–16	5.7	78.9	9.0	13.2	17.3	21.4	4 (17)	10.0
17–23	6.3	85.2	8.0	12.2	16.3	20.4	5 (16)	12.5
24–30	5.7	90.9	7.0	11.2	15.3	19.4	1 (15)	2.5
31–Sept. 6	4.8	95.7	6.0	10.2	14.3	18.4	1 (14)	2.5
Sept. 7–13	3.7	98.7	5.0	9.2	13.3	17.4		
14–20	0.7	99.4	4.0	8.2	12.3	16.4		
21–27	0.3	99.7	3.0	7.2	11.3	15.4		
28–Oct. 4	0.3	100.0	2.0	6.2	10.3	14.4		
							40	100%

*The hatching dates for these birds are shown in Column 1 and they are the same age in weeks as that of the projected sample shown under Dec. 15. The figure in ( ) represents their age in weeks.

were relatively small were biologically significant. The near 50:50 sex ratio found in juveniles in fall and winter did change significantly between spring and the fall in which these birds first became adults. Studies on pheasants by Kabat, Thompson and Kozlik (1950), Kabat, Meyer, Flakas and Hine (1956), and Wagner (1957) indicated that in addition to the direct losses of hen pheasants incurred while nesting and brooding young, the stress of reproductive efforts reduces their stress resistance and thereby further increases mortality. Most biologists agree that nesting and brooding losses in adult quail hens are also responsible for at least a part of the difference between the juvenile and adult sex ratios, and possibly for some of the variation between years.

The age ratios showed greater variation than did the sex ratios (Table 19). Similar variations have been reported for other states. The average percentage of adults for the period 1944–60 is 16.1 with a S.E. of 0.7. The differences in percentage of adults between the average of 16.1 and the averages for 1953, 1955, 1956 and 1958, which showed extreme variation, are highly significant.

The manner in which the percentage of adult population levels, and other population ratios (Tables 6 and 19), bounced from low to high and down again between successive years with little apparent synchronization indicates that many factors affect the production of the young and the survival of the adults from hatching time to fall. The striking increase in the early summer population level of 52 per cent and the difference in the percentage of adults (8 and 20) from 1953 to 1954 might suggest a relationship. However, the percentage of adults in fall from 1955 to 1958 alternated from high to low while the early summer population remained high or gradually increased.

It is difficult to determine the specific effect of spring and summer weather on age ratios. Since the span of the hatching period from May to October encompasses many weather conditions and is characteristic of quail populations over the continent, favorable and unfavorable factors apparently tend to compensate for each other. Biologically a difference of only a few per cent in adult age ratios between years could make a significant difference in the breeding population; however, with the exception of possibly a few years it is doubtful that such precise data are required to evaluate population mechanics for management purposes.

While late-hatched broods appear to contribute little to the size of the breeding population because of their low winter survival, they may affect sex ratios. Westerskov (1957) reported an increase in hens in late hatches of partridges and cited similar observations by Mills (1955), King (1915) and Jull (1923) on rabbits, rats, and fowls respectively.

Winter sex and age data came from studies on two areas located approximately 200 miles apart and revealed almost identical ratios for each area (Table 21). These area winter averages are also very similar to the state-wide fall ratios in Wisconsin and other states (Table 19 and 20).

Some of the differences between individual years are due to chance because of small numbers. With the exception of

TABLE 19

Sex and Age Ratios for Quail Collected in the Fall, 1944–60

Years	No. of Specimens	Per Cent Males Among Adults	Per Cent Males Among Juveniles	Per Cent Adults	Young Per Adult Female [2]	Young Per Adult
1944–46	62	60	42	8	26.5	11.4
1947	345	59	52	14	12.8	6.0
1948	168	71	53	11*	22.0	7.8
1949	222	72	49	14	22.8	6.4
1950	209	67	50	16	12.9	5.3
1951	85	71	52	19	17.5	4.3
1952	80	—[1]	56	13	—	7.0
1953	125	—	57	8†	24.5	11.5
1954	91	40	52	20	6.8	4.0
1955	90	—	64	8†	14.0	11.9
1956	341	61	50	23†	8.9	3.3
1957	405	56	51	14	15.4	6.1
1958	485	61	50	22†	9.1	3.5
1959	107	—	48	12	—	7.2
1960	50	—	57	12	—	7.3
TOTAL	2,865	61.1	51.1	16.1	13.3	5.4
95% C. L.		55.8–65.6	49.0–50.8	14.7–17.5		

[1]No values entered where component of sample is less than 20.
[2]The calculation of the number of young per adult female is corrected for the number of sex-unidentified juveniles.
*Different from average at 5% level.
†Different from average at 1% level. No tests were made for the 1944–46 birds.

1945–46 at Prairie du Sac, we trapped over 50 per cent of the spring survivors each year. Generally we trapped entire coveys, missing only a few birds. The quail at Prairie du Sac, with the exception of 1947–48 were trapped late in the winter, while at the Dunn County study area birds were trapped throughout the winter.

Data obtained from repeat trapping of the same coveys and fall collections showed no change in sex and age ratios between fall and spring. These study results support those of Haugen and Speake (1958) during an 11-week hunting season period and Marsden and Baskett (1958) who demonstrated very convincingly that bobwhite quail age ratios did not change from October to the following summer in their study area. Emlen (1940) reported that this was not true for California quail in which the age ratio changed from 165:100 in November to 99:100 by June and the sex ratio from 105:100 in September to 127:100 in June.

A number of relationships between the ratios shown in Tables 19 and 21 were explored, using information from tables presented in Mainland, Herrera and Sutcliffe (1956), but no statistically significant associations were apparent. For the most part the results for the years which showed extreme variation at Prairie du Sac could be attributed to chance sampling or extreme differences that occur in small-area popu-

TABLE 20

Sex and Age Ratios in Quail from Hunting Season Specimens

State	Author	Years	Per Cent Males Among Adults	Per Cent Males Among Juveniles	Per Cent Adults	Juvenile Per Adult Female	Juvenile Per Adult	Total Birds
Alabama	Haugen & Speake (1958)	1952–53, 1957			16.5–30.0		2.3–5.0	40,616
Indiana	Reeves (1954)	1947–51	62.6	50.2	15.1	17.7	6.6	3,484
Florida	Murray & Frye (1957)	1954	54.3	50.8	22.3	7.2†	3.3†	17,049
Iowa	Kozicky & Hendrickson (1952)	1948			13		6.8	2,327
	Stempel (1960)	1952–59			14			13,206
Kansas	Robinson (1957)	1952–53	64.6	49.6	28.2	6.7	2.4	181
Louisiana	Reid & Goodrum (1960)	1947–57			28.2		2.8	7,762
Massachusetts	Ripley (1958)	1953–55	57.8	50.5	20.7	11.1	3.8	1,465
Missouri	Bennitt (1951)	1944–48	59	50.8	18	11.3	4.7	45,016
	Leopold (1945)	1942–43			17.4			6,067
		1939–43	61.7	50.6	23.2	8.6	3.3	1,633
	Marsden & Baskett* (1958)	1950–57	63	55	18	12.0	5.2	961
Tennessee	Legler (1955)	1951–55			23.9		3.2	14,496
Texas	Lay (1952)	1949–50	59.3	50.5	11.8	11.8	4.5	2,074
		1950–51	53.3	52.5	24	7.3		1,356
Wisconsin	This Study	1944–58	61.1	51.1	16.1	13.3	5.4	2,865

*Data from live-trapped specimens.
†Calculated from other data listed.

TABLE 21

Sex and Age Ratios of Quail Trapped in Winter (December 1 to April 1)

Winter	No. of Trapped Birds	Per Cent Males Among Adults	Per Cent Males Among Juveniles	Per Cent Adults	Young Per Adult Female	Young Per Adult
Prairie du Sac						
1942–43	55	71.4	60.4	13.3	24.0	6.9
1943–44	75	50.0	44.6	16.0	13.0	6.5
1944–45	47	20.0	45.2	10.6	10.5	8.4
1945–46	23	40.0	55.5	21.7	6.0	3.6
1946–47	99	76.5	53.7	17.2	20.4	4.8
1947–48 (1)	141	68.0	52.0	17.7	14.5	4.6
1947–48 (2)*	105	62.5	48.0	17.2	14.8	5.7
Weighted Average	78	63	50.4	15.4	14.4	5.4
95% C. L.		52–73	44.7–55.1	12.5–18.7		
Dunn Co.						
1945–46	275	63.2	53.7	16.0	13.3	5.2
1946–47	318	61.8	53.6	17.3	12.5	4.7
1947–48	348	65.6	45.0	17.5	13.7	4.7
1948–49	332	51.0	54.0	12.3	13.9	7.1
1949–50	307	67.0	49.0	16.6	13.9	6.0
1950–51	238	71.0	49.0	14.3	21.0	6.0
Weighted average	303	62.9	50.9	15.7	14.4	5.4
95% C. L.		57.1–68.4	47.4–52.4	14.0–17.5		

*Data obtained in a bordering area.

lations. The Dunn County data, which revealed less variation, were obtained from a larger area and population and showed no statistically significant differences.

There are many factors which can affect the sex and age ratios of populations on small areas. These include the movement of adults off the study site from year to year, their replacement by ingressing adults from the surrounding area, and the manner in which coveys are formed. The following section shows that the age ratios of different coveys vary tremendously. The presence of one or two coveys containing a proportionately large number of adults or juveniles on the study areas could greatly distort sex and age ratios.

The determination of the relationship of changes in the annual young-per-female and young-per-adult ratios to quail population levels is complicated by several factors. The first of these is the inherent brooding characteristics of males. Stoddard (1931) reported that out of 273 nests, 73 or 27 per cent were incubated by males. While the percentage of males observed incubating nests varied during the four years, our analysis of these data shows the variation is not significant. Only rarely did the sexes alternate incubating. How often males took over the incubation process because the hens were killed or the nest was deserted was not reported. Therefore it is not possible to determine at this time how highly distorted adult sex ratios affect productivity. Also Bennitt (1951) found that in Missouri "the greater the breeding density, as indicated by the call index, the lower the percentage of young in the bag." Lehmann (1946a) reported a similar observation in a Texas study area. However, Stanford obtained a great variation between the call index and the percentage of young for Missouri quail in recent studies (Table 53).

The important point in these sex and age data lies in the fact that there are no clear differences between years that can be attributed to one or two conditions and tested statistically. While the average variation in age ratios and that between years is considerable, it is small compared to the total annual loss of adults from one winter to the next. An analysis of the relationship of population characteristics and changes (Discussion Section) will show why a lack of correlaton between sex and age ratios and density frequently prevails.

Covey Size

The relation of covey size to population dynamics in quail has not been demonstrated to our knowledge. Some authors seem to imply that covey size varies directly with population density, while others seem to regard the covey size as a constant. Stoddard (1931) reported "Coveys tend to keep their organization of normal size." He defined a covey as "an aggregation of individuals of convenient number (10–30)." In a trapping study concerning 78 coveys he found average covey sizes of 12.7 in 1925 and 14.6 in 1926. Errington and Hamerstrom (1936) stated "The average size of a bobwhite covey is 15 birds."

Wilson and Vaughn (1944) reported observations in Maryland from October to January on 18 coveys which averaged 11.7 birds. Some of the coveys were exposed to hunting, hence the 11.7 average is minimum but the indicated hunting mortality seemed to be very light.

Lehmann (1946b) n a Texas study sported a population of 22 coveys, consisting of 284 quail, which averaged 12.9 birds. Population correlations were not given by Lehmann. Reeves (1954) presented some of the better data reported in the literature on covey size and population density on an Indiana study area. His report showed the following average covey sizes from September to November (size of study-area populations shown in parentheses): 1946: 13.3 (319); 1947: 14.0 (335); 1949: 11.3 (329); 1950: 14.9 (357); and 1951: 13.2 (278). Our calculation of the correlation between his covey sizes and populations shows it to be far below significance (r = 0.39; 0.88 required for significance).

The Prairie du Sac area studies provided an opportunity to get accurate information on covey size from early fall to spring (Table 22). According to Errington and Hamerstrom (1936) it was difficult to get covey-size information from 1931 to 1935 when the population was at its peak levels (400–436) because individual quail covey ranges overlapped.

The fall populations for the period 1936–50 differed from those shown in Table 8 because we standardized the procedure for presenting the fall covey-size data. In some years fall censuses were started later than in others. In years when censuses were conducted in early fall, some mortality occurred before the November 1–15 interval for which we have shown covey size. For coveys not found until December we entered the highest covey count for the month as the size of the covey in the November 1–15 period. The fall population shown in Table 22 represents the total of the highest counts for all coveys on the date they were first censused in fall. Coveys that left the area completely or left and returned are not included in the covey averages but are included in the fall population figures.

During the period 1935–51 the population ranged from 81 to 416 and the number of coveys from 5 to 23 or a difference of 414 and 360 per cent, respectively. The average covey size, however, ranged from 14.0 to 19.3 for a difference of 38 per cent. The variation in the average covey sizes in the period 1935–51 is significantly greater than would be expected by chance but when differences between any two given years are compared, only those of the extreme years are significant.

Differences in average covey size as small as 1 bird could be very important if associated with a proportional change in population density. In Figure 10 we compared covey size and summer gain (per cent of population increase from spring to fall) and found that there was not a significant correlation. The correlation of covey size and fall populations (Fig. 11) was also not significant (r = .316 and .497 is required at the 5 per cent level). Although there was a tendency for high populations to have larger coveys, the reverse was also true in some of the years for some low populations.

Despite the presence of slight though nonsignificant correlation, the Prairie du Sac data suggest that the use of quail covey size as a population index has limited possibilities because fall quail populations fluctuated as much as 180 per cent between any two consecutive years while the maximum difference between covey size was only 36 per cent. Apparently quail determine in some way the relative size of the coveys in which they live. Although large populations of quail on an area afford a much greater opportunity for the formation of larger coveys than do those occurring at lower density levels, coveys of similar size were nevertheless found under both conditions. For example, the 1935 fall population of 416 quail or 1 bird per 10.9 acres at Prairie du Sac afforded a much greater opportunity for the formation of large coveys than did the population in 1949 which had 129 birds at a density of 1 bird per 35 acres. Still, the average covey size for these two years was almost identical.

Thus it does not appear that small fluctuations in covey size,

TABLE 22

Fall and Spring Quail Covey Size and Population Statistics at Prairie du Sac, 1935–51

Year	Fall Pop.* Nov. 1–15	No. of Coveys	Average Covey Size Nov. 1–15	Per Cent Summer Gain‡	Average Covey Size Mar. 15–31	Per Cent Winter Loss	Spring Pop.
1935–36†	416	23	18.0				
1936–37	149	9	16.4	100	3.8	77	34
1937–38	138	9	15.3	532	3.2	79	29
1938–39	136	7	19.3	279	13.8	29	97
1939–40	321	17	18.9	228	9.9	48	168
1940–41	293	16	18.3	117	9.2	50	147
1941–42	246	15	16.4	86	8.3	53	116
1942–43	350	18	19.1	189	4.8	74	91
1943–44	222	15	14.0	210	8.3	44	124
1944–45	242	14	16.8	98	6.8	61	95
1945–46	150	11	17.1	61	5.9	57	65
1946–47	202	12	15.3	194	7.1	58	85
1947–48	180	12	15.4	147	4.1	73	49
1948–49	81	5	16.2	85	8.0	51	40
1949–50	129	7	18.4	200	12.9	30	90
1950–51	174	10	17.4	75	6.8	61	68
Totals	3,013	177	254.3	—	112.9	845	1,298
Average	201	11.8	17.0	173	7.5	56.3	81
S. E.			0.4		0.8		

*Highest early fall count and includes or excludes some birds that entered or left the area before or after November 1–15.
†We lacked complete information on the 1935–36 population; these figures are therefore excluded from totals.
‡Computed from data in Table 8.

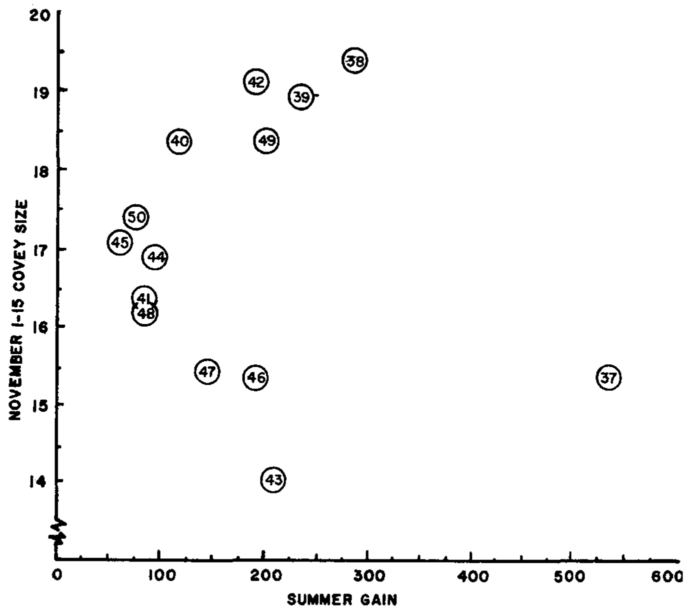


Figure 10. The relationship between covey size and the percentage of summer gain on the Prairie du Sac Study area, 1937–50.

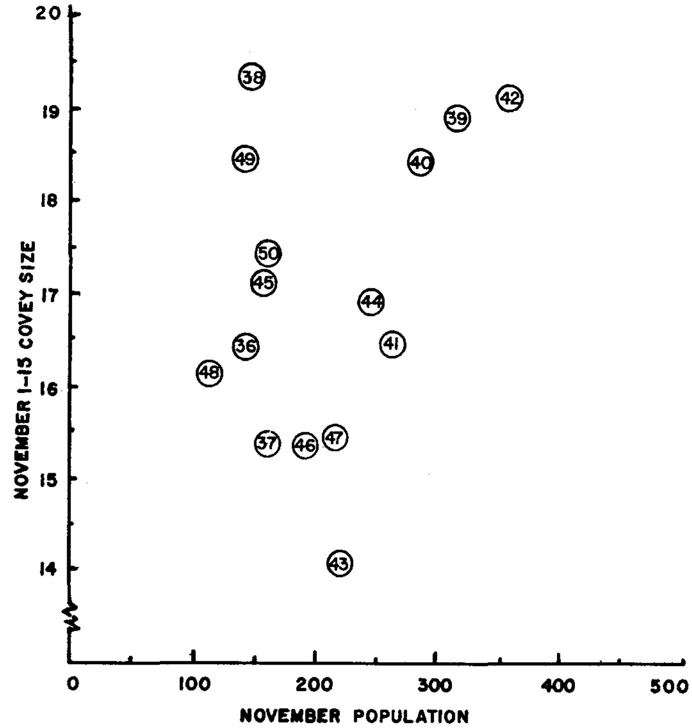


Figure 11. The relationship between covey size and fall population on the Prairie du Sac study area, 1936–50.

even for quail occupying large areas could be used to reliably show year-to-year differences in fall populations.

One possible factor in combination with others that may determine covey size is the roosting behavior involving the familiar "circular roost" pattern. It would be impossible for quail to maintain a tight circle with their heads generally pointed outward, if the covey size was much larger than 15–20. It might appear that observations on larger numbers of birds appearing as seemingly single coveys would contradict this simple hypothesis. But, this may not be a valid contention because while these large groups have been observed as single coveys during the daytime they also have been frequently observed to segregate into smaller groups when flushed or when going into night roosts.

Covey Composition (Winter)

Sex and age ratios for bobwhite quail populations have shown considerable variation between years, particularly on the study areas. The relationship between these variations and population behavior between years was not clear. Therefore, we looked to winter covey composition as a source of additional information, since coveys are the basic units which make up quail populations.

Although a considerable amount of quantitative information is available on sex and age ratios for populations of quail, reference to covey composition is scarce and at best only of general nature. Stoddard (1931), on the basis of observations in the field and during banding studies, concluded that "late in summer and in fall quail coveys may be composed of one to three pairs of adults and their surviving young, with the addition frequently of one to several unmated cocks, or of pairs that failed to bring off broods. In general, the greater the quail abundance, the more mixed is the relationship of birds composing the coveys, probably because birds scattered by shooting or by natural enemies are apt to encounter and join another aggregation while wandering about in search of their own."

During trapping operations from 1943 to 1948 at Prairie du Sac, we were able to catch at least 85 per cent of the quail in 42 coveys. These coveys were divided into four categories based on size (Table 23). The small coveys composed of 5–10 quail in many cases represented the balance of winter survivors, but in this class were also some coveys that were small at the beginning of winter when they were trapped.

The haphazard-appearing distribution of juveniles and adults in coveys indicates that the formation of coveys was not an organized process, at least from the standpoint of age preference or covey size. The two coveys which had the highest percentage of adults (4 out of 8 birds and 10 out of 22) differed greatly in size. Of the 42 coveys trapped there were 31 different combinations of juveniles and adults. Some coveys consisted entirely of juveniles while others contained many adults. The possibility that the adults found in any one covey were drawn into it by some mutual attraction is refuted by the apparent random distribution of adults in coveys and by observations on birds banded one winter and retrapped the following winter. For example, in the winter of 1945–46 in a covey from which we trapped 8 birds there were 4 adults. Three of these adults were returns from previous years' banding, and each came from a different covey.

Similarly there was no evidence of organization in the manner in which males and females occurred in coveys (Table 24). In some coveys females predominated, in others, males, regardless of age. Nor was there evidence of any relationship between covey composition and the size of the fall population.

TABLE 23

Age Composition of 42 Coveys of Various Sizes Trapped in Winter at Prairie du Sac, 1943–48*

Covey Size Range															
5–10				11–15				16–20				21–30			
Coveys				Coveys				Coveys				Coveys			
Size	No.	No. Juveniles	No. Adults	Size	No.	No. Juveniles	No. Adults	Size	No.	No. Juveniles	No. Adults	Size	No.	No. Juveniles	No. Adults
5	5	4	1	11	4	10	1	16	1	15	1	21	1	19	2
5	1	3	2	11	1	9	2	17	1	13	4	22	1	12	10
6	2	5	1	11	1	8	3	18	1	17	1	30	1†	25	5
7	1	6	1	12	1	10	2	19	1	19	0				
7	1	7	0	12	1	9	3	19	1	16	3				
8	1	8	0	12	1	7	5	20	1	15	5				
8	2	7	1	14	3	14	0								
8	1	6	2	14	1	12	2								
8	1	4	4	15	1	14	1								
9	1	7	2	15	1	13	2								
10	1	9	1												
10	1	8	2												
	18	74	17		15	106	21		6	95	14		3	56	17
	(19% adults)				(17% adults)				(13% adults)				(23% adults)		

*Includes only coveys where at least 80 per cent of birds were caught.
†Three coveys combined in late winter into one.

Covey Composition (Fall Broods)

Data on the number of broods per covey are very limited. Agee (1957) reported 2.0 broods per covey; Robinson (1957), 27 broods in 9 coveys for an average of 3.0; and Loveless (1958), 2 to 5. Stoddard (1931) commented that coveys commonly consisted of quail from 2 or more hatchings.

Through the fall collections made from 1945 to 1952, we sampled birds from 76 coveys to get data on the number of broods in coveys. It is possible that a few birds occasionally separated from a brood and joined a different covey. Since there were only a few observations of this, we classified any different-aged young found in a covey as a separate brood.

The average number of broods per covey was 1.7 (Table 25). This is a minimum figure since the technique used involved examination of only the quail shot from each covey sampled. We deliberately limited the sample to 4–8 birds from each covey, depending on its size, in order to leave 10 or more birds in each.

Table 25 also contains the distribution of broods found in eight coveys during trapping operations from November to December in 1947. The average number of broods per covey was 2.4. This average is a better statistic than the one obtained from fall hunting season collections, since we sampled all of the birds in each of the coveys trapped.

Data on the difference in the age of 52 broods composing 23 coveys were obtained from samples collected in 1944–47 (Table 26). We designated classes of age differences by 9-day intervals, since quail differing in age by 9 days could be distinguished from each other when found in the same covey (Thompson and Kabat, 1950). To show the disparity between ages of different broods in coveys, we had to subdivide our data into coveys containing 2 and 3 or more broods. The difference between the ages of broods within coveys varied from as low as 9 to as high as 81 days. While most of the coveys examined were composed of broods whose ages varied by an average of 27 days or less, these broods predominated in the population and hence the opportunity for them to form coveys was greater than for those of other ages. While it reasonably would be expected that the age spread should be larger among the coveys with 3 or more broods, the data are insufficient to demonstrate any such difference statistically. It seems clear that when coveys were formed, there was no tendency for broods of common ages to combine. Thus, covey composition depended largely on whatever broods were present in a given locality when coveys formed.

Weights

On the premise that quail weights might reveal some aspect of population mechanics we obtained weights on most of our collected and trapped samples. Average weights for quail have been obtained for fall hunting season and winter samples by several investigators. The degree to which these data were correlated with the many factors that affect weights, including date of hatch and collection, environmental conditions during the hatching period, and the physical and physiological condition of the parents, was very limited. For example, Buss *et al.* (1947) reported average winter weights for the period 1941–47 and compared the winters of 1945–46 and 1946–47, but lacked data on the age of the birds in their samples. Reeves (1954) obtained data that was partitioned to show quail weights for birds under 20 weeks and over 21 weeks of age but not to show comparisons between quail hatched in the same calendar periods.

We were able to partition our samples of 227 fall juveniles

TABLE 24

Fall Population and Sex and Age Ratios of 37 Quail Coveys Trapped at Prairie du Sac, 1943–48

Winters	Fall Pop.	Covey Size	Juveniles Males	Juveniles Females	Adults Males	Adults Females
1942–43	353	6	1	4	1	0
		11	6	4	1	0
		11	6	4	1	0
		11	8	1	1	1
1943–44	217	5	1	2	1	1
		15	7	5	1	2
		16	6	9	0	1
		17	3	10	3	1
		19	12	7	0	0
1944–45	246	5	2	2	1	0
		7	1	6	0	0
		7	3	3	0	1
		11	5	5	0	1
		14	6	8	0	0
1945–46	153	8	3	1	2	2
		11	3	7	1	0
1946–47	191	8	6	2	0	0
		9	3	4	2	0
		11	6	3	2	0
		12	6	3	2	1
		12	3	4	4	1
		14	9	5	0	0
		30	11	14	3	2
1947–48	215	5	2	2	1	0
		5	4	0	0	1
		6	3	2	1	0
		8	5	2	0	1
		10	4	4	2	0
		11	5	3	3	0
		13	6	7	0	0
		14	7	6	1	0
		15	7	6	1	1
		15	4	9	2	0
		16	7	8	0	1
		16	9	6	1	0
		21	11	7	2	1
		22	6	6	5	5
Total		447	197	181	45	24
Avg.		12.1	5.3	4.9	1.2	0.7
Per cent		100.0	44.1	40.4	10.1	5.4

according to their hatching dates but did not obtain data on environmental conditions or stress relationships of their parents. These results (Thompson and Kabat, unpubl. ms.) show that July-hatched juveniles of the same age groups generally weighed more in fall than those hatched in earlier or later months; also that July-hatched birds predominated in the autumns of some years but not in others. Similarly Stokes (1954) found mid-June-hatched pheasants to have a higher rate of weight gain. If higher weights and more rapid gains indicate superiority in physical condition, those years in which more July birds were hatched may have reflected this advantage in proportionately higher reproductive gains.

We partitioned the weights of quail trapped in late fall and winter at the Prairie du Sac and Dunn County study areas according to the months in which the birds were trapped (Tables 27 and 28). These weights could not be related to date of hatch since the primary molt on which aging is based was complete.

The weights of the quail shown in Table 27 are from different birds in each month. Therefore, the data only simulate a weight series. The sample size and conditions encompassed should be sufficient to show significant patterns if these strongly prevailed in winter quail populations. We found that average weights of adults were slightly but significantly (beyond 1 per cent probability level) higher than in juveniles, as has been shown in other studies (Buss *et al.,* 1947). While there are some differences in weights of borderline statistical significance between years for comparable age and sex groups, these do not reveal the results of any discernible biological or environmental impact.

Quail generally weighed more in January than later in the winter and were lowest in March (differences between months significant beyond 1 per cent probability level). Although food availability was generally restricted by unusually heavy snows in 1942–43 and 1947–48, this was not necessarily manifested in quail weights because only those coveys that were in better habitat survived to be caught later.

Unlike pheasant hens which showed a weight increase in late February and March (Leopold, Sperry, Feeney and Catenhusen, 1943 and Kabat, Thompson and Kozlik, 1950), quail continued to decline in weight. Quail weights in January and February would be expected to vary because of significant differences in the availability of food supplies due to adverse weather, but this factor should not prevail in late March. By the end of winter in March food availability was generally good, as indicated by reduced mortality in this month. Therefore, even though our samples are small and the birds in the

TABLE 25

The Minimum Number of Broods Per Covey Obtained From Fall Collections, 1945–52, and a Trapped Sample in 1947

Broods/Covey	No. of Coveys in 1945	1946	1947	1948	1949	1950	1951	1952	Total*	1947†
1	2	1	4	6	5	7	2		27	1
2	2	3	10	10	6	6	1	5	43	4
3		2		3	1				6	2
4									0	1
Total	4	6	14	19	12	13	3	5	76	8

*Average broods per covey from fall collections = 1.7.
†Average broods per covey from trapping sample = 2.4.

TABLE 26

Age Differences in 9-Day Intervals Between 52 Broods Composing 23 Coveys, October to December, 1944–47.

For Coveys Containing			
2 Broods		3 or More Broods	
Average Difference in Days	Number of Coveys	Average Difference in Days Between the Youngest and Oldest Broods	Number of Coveys
9	3	9	—
18	3	18	2
27	5	27	1
36	1	36	—
45	1	45	1
54	2	54	1
63	1	63	—
72	1	72	—
81	—	81	1
Total	17		6
Avg. difference—32 days		Avg. difference—41 days	

monthly samples were different, we should have been able to detect an upswing in the weight trend in late winter if one occurred. Similar observations were made in Massachusetts by Ripley (1958) who found quail heaviest in January and lightest in late March and early April. After April 9, Ripley's birds showed an upswing in weight to May when his study period ended. Other authors who reported similar weight trends from January to April for bobwhite quail include Wickliff (1932), Hamilton (1957) and Robinson (1957) for Ohio, Missouri and Kansas respectively.

Spring weight increases in bobwhite quail were also reported by Stoddard (1931), but his sample was obtained from April through September (12 birds), and by Hamilton (1957). The increase in the weight of hens has been commonly reported for several species: blue-winged teal (Bennett, 1938), wild turkey (Mosby and Handley, 1943), red grouse (Wilson, 1911) and California quail (Genelly, 1955). Baldwin and Kendeigh (1938) presented weights on 85 species of birds and concluded that the greatest weights are generally reached in winter and the lowest in summer and that these were inversely correlated with temperature.

The difference in the winter weight trend of pheasants and quail is correlated with the time when their reproductive processes begin. Pheasants commence egg laying, incubating and brooding earlier than quail, and are generally through hatching their young early in July in Wisconsin (Buss, 1946, Buss *et al.*, 1951 and Kabat *et al.*, 1950). Quail, on the other hand, begin their reproductive process in May and may not complete it until sometime in September. Therefore, in view of the fact that both female pheasants and quail gain weight in the months just preceding egg laying, there appears to be a physiological similarity between these two species but with a time lag correlated with egg laying and incubation. Further indication that reproduction and weight trends are correlated are shown in the findings that male bobwhites do not gain weight in spring and summer (Stoddard, 1931 and Hamilton, 1957), while the females do. However, other factors may be involved in other species because Genelly (1955) reported that male California quail gained weight in March.

Movement

Winter. Findings on the winter movement of 130 fall-banded quail during a five-month period reported by Stoddard (1931) in Florida were: 74 per cent moved less than ¼ mile, 25 per cent less than ½ mile, and 1 per cent over 1 mile. Errington and Hamerstrom (1936) concluded from observations on approximately 11,650 unbanded quail in coveys in Wisconsin that they usually could be found within a range of ¼ mile and that longer movements resulted only infrequently from the occurrence of various emergencies such as cover removal. A few coveys moved a mile or more for no determinable reason.

Lehmann (1946b) concluded from banding studies and observations in Texas that there was "considerable mid-winter shifting of coveys that did not appear to be under stress of starvation or scarcity of cover. Bobwhites in many areas may not be as sedentary . . . as has been long suspected." His conclusion seems somewhat surprising in view of the fact that the average movement of 105 birds trapped in late autumn in 1942 and retrapped in January and February was only 324 yards. In a similar trapping period in 1944 the average movement for 63 quail was 459 yards.

Other reports on winter movement based on very limited samples of Missouri quail include those of Murphy and Baskett (1952), Lewis (1954) and Agee (1957) who cited movements of less than ¼, less than ½, and .08 miles respectively.

We traced covey movement from fall to spring for the Prairie du Sac quail during the years 1936–51. Generally our findings on winter covey movements are similar to the 440

TABLE 27

Monthly Weight Averages in Grams for Quail Trapped in Winter at Prairie du Sac (1942–48)

Month	Males		Females	
	No.	Weight	No.	Weight
Juveniles				
December	50	187	56	186
January	65	198	72	199
February	67	192	50	194
March	35	190	39	186
Total	217		217	
Avg.		192		192
S. E.		1.1		1.2
Adults				
December	13	205	7	190
January	16	199	6	212
February	10	187	7	205
March	9	190	3	204
Total	48		23	
Avg.		197		202
S. E.		2.1		3.1

TABLE 28

Monthly Weight Averages in Grams for Quail Trapped in Winter in Dunn County, 1948–52

Month	1948–49		1949–50		1950–51		1951–52		All Years	
	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Juvenile Males										
December	58	203	16	213	62	192	—	—	136	199
January	81	202	65	201	29	193	7	202	182	200
February	22	195	38	185	6	196	22	195	88	191
March	—	—	4	175	3	177	—	—	7	176
Total	161		123		100		29		413	
Avg.		201		197		192		197		197
S. E.		2		2		2		2		1
Juvenile Females										
December	54	204	19	213	60	192	—	—	133	200
January	59	206	69	197	34	195	6	201	168	201
February	17	197	38	190	6	190	14	183	75	190
March	—	—	8	173	5	173	—	—	13	173
Total	130		134		105		20		389	
Avg.		204		195		192		188		198
S. E.		2		2		2		4		1
Adult Males										
December	14	211	7	222	16	203	—	—	37	210
January	6	207	11	205	7	207	8	205	32	206
February	—	—	13	197	1	183	7	193	21	195
March			1	169	—	—	—	—	1	169
Total	20		32		24		15		91	
Avg.		210		205		203		200		205
S. E.		3		3		3		3		2
Adult Females										
December	14	215	3	214	4	198	—	—	21	212
January	5	216	8	211	6	214	1	206	20	213
February	3	204	6	189	—	—	—	—	9	194
March	—	—	—	—	—	—	—	—	—	—
Total	22		17		10		1		50	
Avg.		214		201		207		206		209
S. E.		3		4		4		—		3

yards (¼ mile) cited by Errington and Hamerstrom (1936). For Table 29, data were selected for two years each, in which average movement was at a minimum (1940–41, 1943–44) and at a maximum (1938–39, 1946–47). Movement in other years fell between these extremes but even in these cases the differences were not statistically significant. Although quail coveys moved an average distance of 530 yards, there was wide variation in their movement which occurred regardless of weather conditions (Figs. 12 and 13). The 1938–39 and 1943–44 winters were quite mild and the 1940–41 and 1946–47 winters were moderate.

Although the amount of available winter cover decreased significantly from 1936 to 1951, the average distance quail coveys moved did not change perceptibly. Coveys tended to move to better habitat but some moved from good range to starve in poor coverts. Still others remained in poor coverts throughout the winter and gradually starved until all were gone.

There are many factors that could be involved in winter covey movement, but we did not find any predictable pattern or relationship to known factors.

Knowledge of winter movement is basic to habitat management programs, as will be stressed later, for it has a great bearing on the determination and location of the number of winter food patches as well as brush coverts.

Spring. Murphy and Baskett (1952) and Lewis (1954) reported that 88 per cent of their Missouri quail moved less than ½ mile. Quail in Florida moved less than ¼ mile (Loveless, 1958).

We employed two methods of obtaining spring movement data in our studies: observations on the change in the ratio of banded birds (aluminum bands) in known populations during the spring, and observations on movement of individually color-banded birds in spring.

We assumed that changes in the ratio of banded to unbanded birds on the study area represented movement for the following reasons. Whistling counts both on the area and the surrounding lands showed an estimated population reduction of only 17 per cent between April 1 and early July. Also banded birds from the study area were seen in bordering areas (Fig. 14). This proves that the majority of birds alive at the end of winter were still alive in spring. Thus changes in the ratio of banded birds on the area would have to primarily represent movement, and indicate that mortality of banded and unbanded birds was similar.

We were fortunate to be making observations on a population that contained 97 per cent banded birds (Table 30). These data show that 79 per cent of the banded adult quail which survived from late March to November moved off of the 4,500-acre Prairie du Sac area. Sixty-six per cent of this movement occurred before the end of June. The July observations on only 8 birds or 9 per cent of the total seen in spring indicated that spring movement essentially terminated in June. This cessation of movement was expected since nesting activities reached a peak in July.

Changes in the ratio of banded to unbanded birds for late summer and early fall were based on trapped adult birds, the survivors of the previous spring. We were able to trap 66 per cent of the fall population which provided an adequate

TABLE 29

Winter Movement (November to April) of Prairie du Sac Quail*

Movement (Yards)†	No. of Coveys 1938–39	1940–41	1943–44	1946–47	Total
75– 224			5	4	9
225– 374		9		1	10
375– 524	3	2	5		10
525– 674	2	2	2	1	7
675– 824		2	1		3
825– 974	1	1			2
975–1124				2	2
1125–1274	1				1
1275–1924				3	3

*The winters of 1938–39 and 1943–44 were mild and the other two were moderate.
†Direct distance between fall and spring covey location.

sample for computing movement for this season of the year. The difference between the percentage of banded birds on the study area in July and the following November indicates that an additional 17 per cent of the adult quail left the area in the summer and were replaced by unbanded birds from the surrounding area.

Buss *et al.* (1947) reported on the movement of 115 birds observed in Dunn County during the late spring of 1947. The percentage of banded birds decreased from 81 in March to 47 by June. This is a decline of 42 per cent. The Prairie du Sac population showed a movement of quail off the area of 66 per cent during the same period. The larger size of the Dunn county area accounts for much of this difference.

The second method for obtaining information on spring movement involved observing individually color-banded birds (Table 31). The movement from April 8 to May 26 (0.6 miles) was about half of the average movement observed betwen May 27 and June 23 (1.3 miles). The same degree of total spring movement was also indicated in the change in ratio of banded birds (Table 30).

TABLE 30

Movement of Quail Based on Observations of Banded Birds at Prairie du Sac, 1947

Month	Number Observed: Banded Males	Banded Females	Unbanded Males	Unbanded Females	Per Cent Banded
March	49	36	2	1	97
April	7	6	1	2	81
May	22	8	14	7	59
June	11	0	19	3	33
July	2	1	4	1	37
Total	91	51	40	14	—
November	5		20		20*

*This figure equals 21 per cent of the banded quail on the area in March. Thus 21 per cent remained on the area and 79 per cent moved off.

Of the 19 banded birds moving over 1 mile up to June, 23 had an east component of movement, and 5 a west component (Fig. 14). This difference is not statistically significant from the expected ratio for random movement. Likewise, a test of direction of the observed against the expected movements on a quadrant basis gave a nonsignificant value of Chi-square (3.003; 7.815 required at the 5 per cent level). In these analyses no allowance was made for the Wisconsin River which borders the area on the west restricting movement and also precluding observations on movement in this direction. Thus direction was nonoriented and unrelated to cover types; quail were observed throughout the area and appeared almost as often in areas devoid of cover as they did in sites having good winter range. Most of the observed birds were males but there was no sex differential in the distance moved.

A comparison of spring-to-summer quail movement at the two study areas, Prairie du Sac and Dunn County, showed

TABLE 31

Distance Moved by Quail Between Their Winter Range and Spring Observation Points at Prairie du Sac, 1947–48*

Distance Moved From Banding Site (Miles)	Observed April 8–May 26 Number	Per Cent	Observed May 27–June 23 Number	Per Cent
Less than 0.25	8	29	2	8
0.26–0.50	8	29	4	15
0.51–0.75	3	11	3	11
0.76–1.00	3	11	4	15
1.01–1.25	2	7	3	11
1.26–1.50	1	3	1	4
1.51–1.75	2	7	2	8
1.76–2.25	1	—	1	4
2.26–2.75	0	3	2	8
2.76–3.25	0	—	1	4
3.26–4.00	0	—	2	8
4.01–5.00	0	—	1	4
Total number	28		26	
Mean distance	0.6 mile		1.3 miles	
S. E.	0.1		0.2	

*249 quail in 27 coveys banded; 27 per cent survived to April.

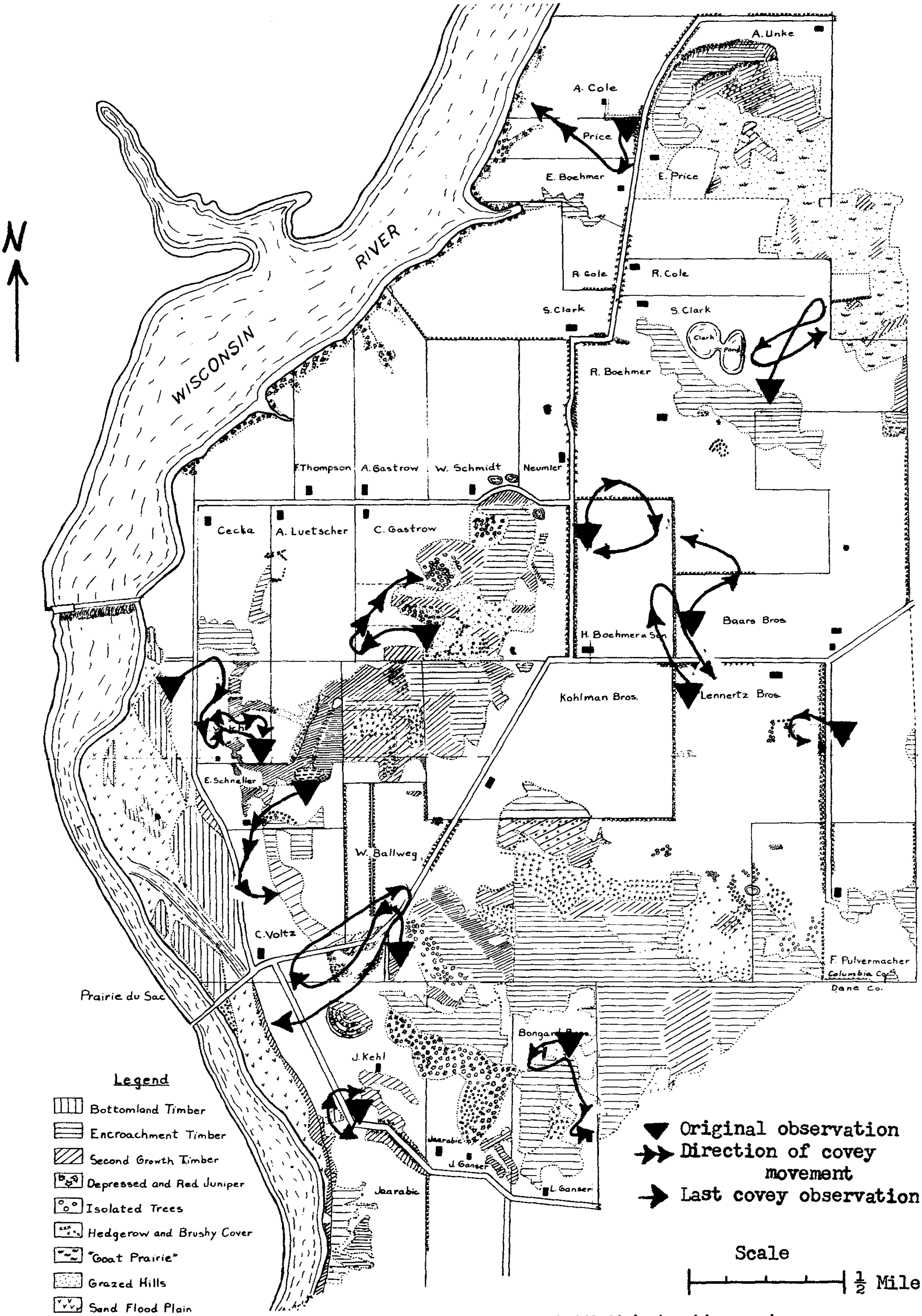


Figure 12. Quail covey movement at Prairie du Sac in the winter of 1943–44 showing minimum ranging.

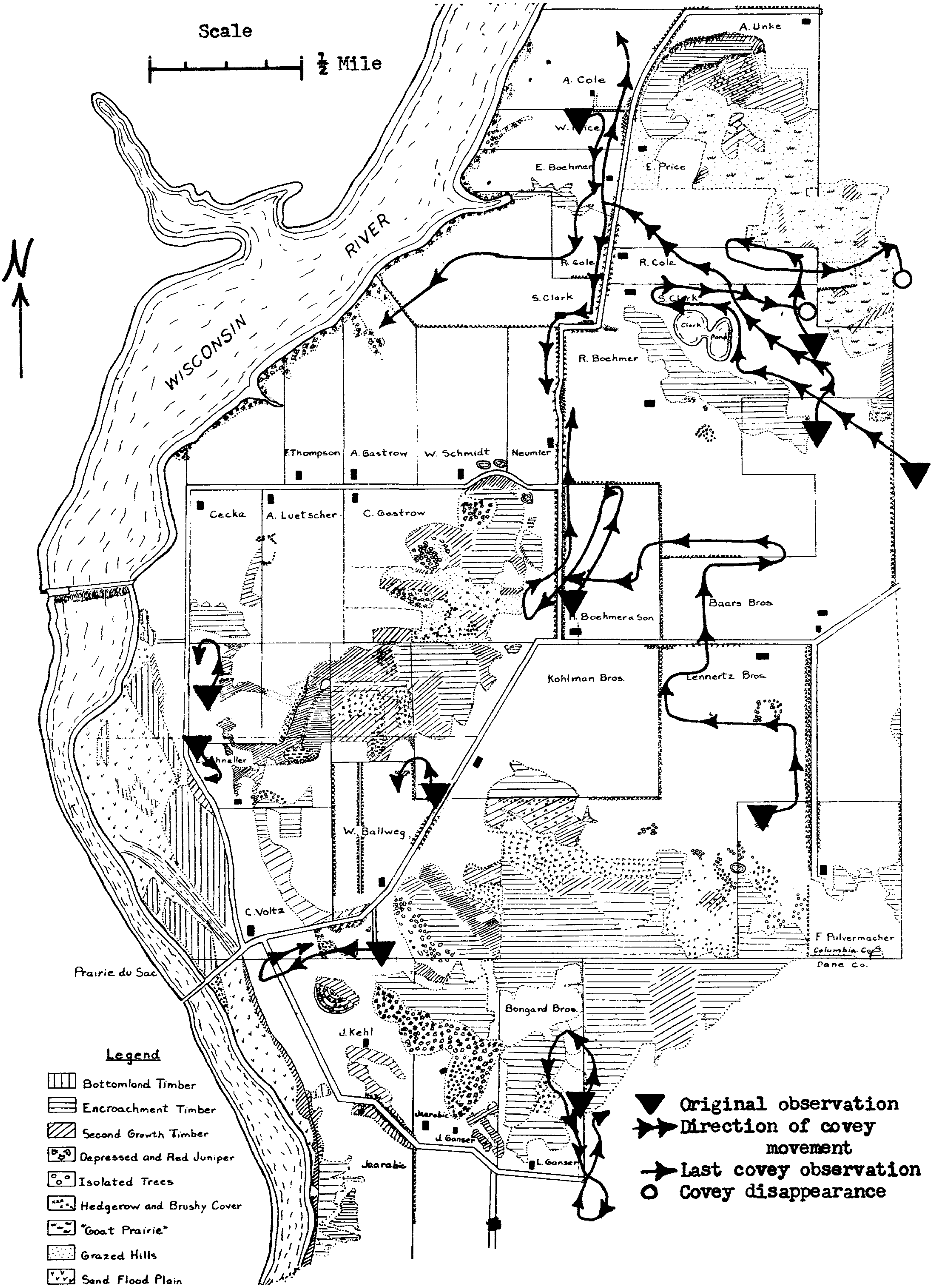


Figure 13. Quail covey movement at Prairie du Sac in the winter of 1946–47 showing maximum ranging.

that in both cases the average movement and the frequency distribution of distances moved are similar (Table 32). The similarity in the magnitude of movement is even more striking when we consider that the areas are different in geographical location, shape and bordering areas.

Although it was possible through the study on changes in percentage of banded birds on the Prairie du Sac area to obtain data on only the minimum distance moved, these data are important in interpreting population behavior and developing quail habitat-management programs for specific areas. It is as important to know how many birds leave an area as it is to know the actual distance resident birds move.

TABLE 32

Comparison of Spring-to-Summer Movement of Wisconsin Quail

Distance Moved (Miles)*	Prairie du Sac (1948) No.	Prairie du Sac (1948) Per Cent	Dunn County (1949) No.	Dunn County (1949) Per Cent
0.0–0.5	22	41	84	52
0.6–1.5	20	37	43	26
1.6–2.5	8	15	19	11
2.6–3.5	3	5	12	7
3.6–4.5	1	2	1	1
4.6–5.5	0	0	2	2
5.6–6.5	0	0	1	1
Total number	54		162	
Mean distance	1.0 mile		1.0 mile	
S. E.	0.1		0.1	

*Minimum distance moved based on observations of color-banded quail from April 16 to June 15 and includes some birds that had not completed their spring movement.

Winter to winter. Studies to determine winter-to-winter movement were based on only those birds that were retrapped on the study area, and tended to yield only minimum statistics (Tables 33, 34 and 35; and Fig. 14). Birds that moved beyond the study-area boundaries possibly traversed distances greater than those for which we obtained data but obviously are not included in our study. The limited Prairie du Sac observations show that the average movement between winters was 1.1 miles which is similar to the spring movements shown in Table 31. The latter observations, however, included both the banding area and adjacent lands extending up to 1 mile away from the closest point at which birds were trapped and released.

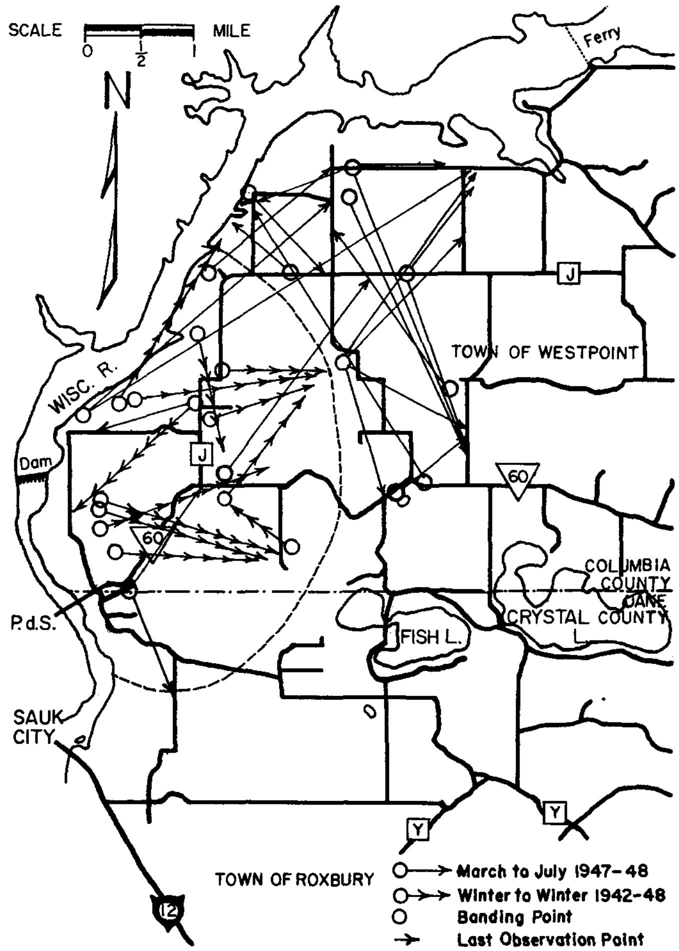


Figure 14. Quail movement from March to July and winter to winter at Prairie du Sac.

If winter-to-winter movement exceeded spring movement, the banding studies at the 9,900-acre Dunn County area which is much larger than Prairie du Sac should show these differences. Buss *et al.* (1947) reported some movements exceeding 3 miles for 1946–47 banding studies.

The average distance of 0.78 miles moved from winter to winter by all of the quail in the trapping sample, males and females (Table 33), was 20 per cent less than the spring observations indicated (Table 32). This difference is due in part to the inclusion of a greater percentage of females which moved less than males ($F = 12.2$; 7.17 is required at the

TABLE 33

Average Movements of Adult Quail Between Winters (Miles)

	Dunn County (1946–52) Males	Dunn County (1946–52) Females	Dunn County (1946–52) Total	Prairie du Sac (1942–48) Males	Prairie du Sac (1942–48) Females	Prairie du Sac (1942–48) Total	Both Areas Total
No. birds	55	28	105*	9	2	11	116
Mean distance	0.89	0.61	0.76			1.1	0.78
S. E.	0.11	0.03	0.08			0.2	0.08

*Includes 22 unsexed birds.

TABLE 34

Distribution of Movements of Adult Quail Between Winters*

	Miles							
	0–0.5	0.6–1.0	1.1–1.5	1.6–2.0	2.1–2.5	2.6–3.0	3.1–4.0	Total
Dunn County 1945-52								
Males	26	8	10	5	3	3	–	55
Females	19	4	1	2	2	–	–	28
Not sexed	13	7	—	1	–	–	1	22
Total including sex (?)	58	19	11	8	5	3	1	105
Prairie du Sac 1942-48								
Males and females	2	1	7	2	–	–	–	12

*If a bird repeated twice in the year of recapture, the point farthest from the original trapping was used as the move.

1 per cent point); spring observations included more males than females at Dunn County. It is also possible that some of the quail, which when last observed had moved distances that exceeded the spring average, continued afterward on a route that curved back toward their original banding site.

The fact that the movement for the one-third of the birds which exceeded 1 mile or more was distributed over a distance of 1–4 miles (Table 34) raises the question as to why "the long-distance movers" didn't settle down sooner. Possibly these birds didn't move farther in total distance between winters than birds trapped much closer to the original banding point, but their wanderings were in a straight line. This conjecture could only be tested by following many marked birds throughout the year, a procedure that was not practical and probably not possible.

At Dunn County 42 per cent of the adults trapped during three winters, 1948–51, consisted of birds that did not leave the area between winters. Half as many birds, 21 per cent, remained on the area between winters at Prairie du Sac, 1942–48. Since the Dunn County area is almost twice as large as the Prairie du Sac area, this accounts for the difference in egress from the study areas, as also was the case in spring movement. The 0.5-mile greater movement found at Prairie du Sac appears to be explainable by the circuitous pattern in which quail would have to move to remain on the area. This deduction is based on the observations made on spring movements which showed that few birds remained at or near their winter range. It is also sustained by a limited number of observations made on birds banded in one winter and retrapped two years later, which showed movement similar to that between winters (Table 35).

TABLE 35

Bobwhite Quail Movements Between Two or More Winters on the Dunn County Study Area, 1945–52

Miles Moved	Males	Females
0	1	1
1 1/2	1	
1 5/8	1	1
1 6/8	1	
1 7/8	1	

Even though the average distances moved were considerably different, the variation between distances moved by individual birds (Table 34) makes statistical tests for anything but great differences highly impractical.

Apparently Wisconsin quail move much greater distances than Missouri quail. Marsden and Baskett (1958) calculated that 16.6 per cent of the quail emigrated from a 2,240-acre area annually which is about 1/5 of the rate for quail in Prairie du Sac (4,500 acres).

Summary. Trapping and banding studies from 1942 to 1948 at Prairie du Sac and at Dunn County from 1947 to 1951 provided data on fall, spring and winter movement. The movement of quail between winter and mid-July averaged 1.3 miles. Changes in the percentage of banded birds showed that 79 per cent of the quail residing on the study area at Prairie du Sac (4,500 acres) left it between March and November and at the larger Dunn County area (10,000 acres) egress was 42 per cent of the population during a comparable period. The banding studies at Prairie du Sac also showed that 62 per cent of the birds left the area between March and July and an additional 17 between July and November.

Movement between winters is about 20 per cent less than *that for spring. This appears to be the result of quail* continuing to move until some begin to work back toward their original banding site between winters.

Average Annual Survival

Although numerous research projects have been conducted on the survival of bobwhite quail, these were based on either limited time-specific or dynamic life studies and were not expressed in survival series. Errington's reports generally covered winter survival, a calculated life equation (1933b), or productivity based on summer gain (1945). While Stoddard (1931) published information on what was essentially a survival series, for studies as early as 1925–26, this was presented expressly to show movement. Numerous reports, such as those by Stanford (1952), Murray and Frye (1957), Ripley (1957 and 1958) and Loveless (1958) referred to about an 80 per cent turnover based on age ratios.

Age ratios from winter-trapped birds and census data were used by Buss *et al.*, (1946) for two winters, 1945–46 and 1946–47, to calculate turnover. Marsden and Baskett (1958) calculated an 82 per cent annual mortality rate and a life expectancy of 8½ months after the first of October from recapture data on bobwhite quail.

The results of Wisconsin studies are presented in two sections. Studies by the late Aldo Leopold represent what is to our knowledge the first attempt to get data for calculating a survival series. Because of his pioneering efforts and also because his findings were never published but were turned over to us to include in this report, they are presented in considerable detail. This section is followed by our own studies which provide an opportunity to evaluate some of the shortcomings of time-specific or dynamic survival studies on banded birds described by Hickey (1952). Our studies were based on intensive surveys from fall to spring and in early summer, together with sex and age ratios, banding and movement data.

Early Wisconsin studies. Aldo Leopold initiated studies on Wisconsin bobwhite in 1927. Although the lack of a technique for aging birds handicapped these early studies, they nevertheless were the origin of a long series of subsequent survival and mortality investigations.

Two study areas were selected in the vicinity of Madison. The first, University Marsh farms, was primarily an agricultural area bounded by the city, Lake Mendota and farm land. The second, University Arboretum, was primarily a wild area bounded by farm lands and Lake Wingra. The results of these studies which Leopold expressed in "survival series," together with the names of the personnel conducting them, are shown in Table 36. Despite limitations such as lack of data on spring censuses and spring-to-fall movement, some basic information on quail survival was acquired.

Leopold assumed that since only a fraction of the quail was trapped on the area during most years, a proportionate number of banded birds each year should be in the segment of the untrapped population. Therefore, he corrected the return series (survival series) accordingly (Table 37). No attempt was made to add a correction factor for the quail that moved off the area.

The second-year returns of 2.2 per cent on the University Marsh and 0.3 per cent on the University Arboretum, and no further returns in subsequent years, not only indicated a low survival but also the fact that if quail did survive to the third year and left the area, they did not move back into it in subsequent years.

The relatively high number of returns for the small University Marsh Farms area (640 acres) which is almost surrounded by city and lake suggests restricted quail movement. The Arboretum (1,000 acres) is also small but since the area is bordered on three sides by areas into which quail could readily move, the relatively low return suggests a high rate of egress.

Leopold (1944) speculated that some unknown factor prevented a lower or higher percentage return of banded adults. This conjecture was based on the recognition that quail hatch a clutch of about 14 young. If all young survived, the percentage of adults in the population would be 12. If some young failed to survive, the percentage of adults would increase unless there were an equal rate of mortality among juveniles and adults which "is impossible".

Generally the rate of returns for all years (Tables 36 and 37), with the exception of the quail trapped in the winter of 1930–31 and retrapped in 1931–32, is consistent with expectations based on movement studies. The return of 19 quail

TABLE 36

Banding Returns from Early Wisconsin Bobwhite Population Studies

Banding Site and Bander	Winter	No. Banded	Fall Pop.	Per Cent Trapped	Returns in the Area*	Recoveries Elsewhere
University Marsh farms, 640 acres, Dane County						
H. G. Anderson et al.	1927–28	17	?	?	17 — 1 — 1 — 0 — 0	x
H. G. Anderson et al.	1928–29	17	100?	17%	17 — 1 — 0 — 0	x
Gundlach & Errington	1929–30	20	83	24%	20 — 1 — 0	x
Anderson, Stanek, Halpin	1930–31	125	about 126	100%	125 — 19 — ?	1 (2 mi.)
H. G. Anderson	1931–32	(96)†	about 115	100%		
	Total	179		Total	179 — 22 — 1 — 0	
				Per cent	100 — 12.3 — 0.5 — 0	
University Arboretum, 1,000 acres, Dane County						
Anderson & Wood	1936–37	14	70?	20%	14 — 1 — 1 — 0 — 0 — 0 — 0	
T. N. Sperry	1937–38	32	131	25%	32 — 2 — 0 — 0 — 0 — 0	
Sperry & Feeney	1938–39	141	about 143	100%	141 — 3 — 0 — 0 — 0	1 (10 mi.)
Sperry & Feeney	1939–40	81	170	48%	81 — 1 — 0 — 0	
T. N. Sperry	1940–41	64	65	99%	64 — 3 — 0	
John Catenhusen	1941–42	8	34	23%	8 — 1	1 (5 mi.)
G. Halazon & C. Kabat	1942–43	(10)†	20	100%		
	Total	340		Total	340 — 11 — 1	
				Per cent	100 — 3.2 — 0.3 — 0	

*Each number in the series represents the returns for all birds trapped on the area in a previous year except those in the first column which are the original catches.

†Not included in the totals.

TABLE 37

Corrected Banding Returns From Early Wisconsin Bobwhite Population Studies

Winter	Corrected Survival Series
University Marsh	
1927–28	17 — 6 — 4 — 0 — 0
1928–29	17 — 4 — 0 — 0
1929–30	20 — 1 — 0
1930–31	125 — 19
Total	179 — 30 — 4 — 0
Per cent	100 — 16.8 — 2.2 — 0
University Arboretum	
1936–37	14 — 4 — 1 — 0 — 0 — 0 — 0
1937–38	32 — 2 — 0 — 0 — 0 — 0
1938–39	141 — 6 — 0 — 0 — 0
1939–40	81 — 1 — 0 — 0
1940–41	64 — 9 — 0
1941–42	8 — 1
1942–43	10*
Total	340 — 23 — 1 — 0
Per cent	100 — 6.8 — 0.3

*Not included in totals.

in this series suggests either a very high survival or no movement. Errington (1933) reported that the population on this area was relatively high, about 1 bird per 6 acres.

Prairie du Sac studies. The early Wisconsin survival studies indicated that year-to-year losses exceeded 80 per cent. Through our population censuses we determined that the average winter loss from 1929 to 1951 was 50 per cent and through whistling counts we estimated that spring-to-summer losses averaged 17 per cent. In this section we will present the results of banding studies together with censuses aimed primarily at getting more precise information on seasonal losses, particularly spring to fall.

Our first objective was to determine whether year-to-year returns on banded quail would reveal the magnitude of seasonal losses. Also since our movement studies (Table 30), indicating that 79 per cent of the adults alive in mid-April left the area by mid-November, were based on just one year of direct information, the banding studies together with the census results provided an opportunity to evaluate the estimates previously obtained on movement. Furthermore, accurate spring-to-fall values on movement are required to calculate survival for this period, because as will be shown below the adults on the area each fall were present primarily as the result of ingress. Therefore, we were working with adults from two different populations. However, if ingress and egress of adults are in balance, fall age ratios can be used to calculate seasonal losses.

First, to determine the average April 1 to November 15 losses, it is necessary to obtain the number of adults present in the fall population and then divide this value by the number of early spring survivors. Since it is impossible to trap entire fall populations because heavy mortality occurs during the trapping period, it is necessary to calculate the total number of adults surviving in fall. This was done by multiplying the fall population by the percentage of adults in the trapped sample. The results show that there were 212 adults in the fall populations from 1942 to 1948 and that an estimated 42 per cent of the spring population survived to fall during 1943–47 (Table 38). But since only 22 per cent of these adults were on the area the previous spring, the balance had to have moved into the area.

The return of 22 per cent banded adults is similar to the results of our studies on spring-to-fall movement, which showed that 21 per cent of the adults remained on the area from spring to fall, and thus substantiates the field observations reported in Table 30.

To cross-check the validity of estimates of 42 per cent adults surviving from spring to fall and 21 per cent adults remaining on the area, we used these values together with winter age ratios and census figures to calculate the expected number of banded returns on adults and compared these values with the actual returns. The calculated average returns on adults banded in previous winters showed a very close agreement with the actual returns (totals for columns (5) and (6) in Table 39). Therefore, we concluded that this correlation substantiated the reliability of using average age ratios together with population censuses to calculate the adult segment of the fall population, which in turn can be used to calculate spring-to-fall survival.

The results of applying these factors to all of the census data obtained from 1929 to 1951 show that the average April 1 to November 15 mortality for this period was 69 per cent (Table 40).

The average mortality values shown in Table 40 will be used in all subsequent analyses of population dynamics for Wisconsin quail. Important points to note regarding the losses are as follows. Expressing the mortality as a percentage of the mid-November population, 50 per cent die from November 15 to April 1 and 35 per cent from April 1 to November 15. However, the April 1 to November 15 mortality when expressed as a percentage of the birds alive on April 1 is 69 per cent, exceeding the mortality rate for the winter period and indicating the importance of mortality in this season of the year on population levels.

The over-all biological importance of mortality and survival values in population behavior and the management of quail will be discussed later. But, it is important to highlight here some of the cause-and-effect relationships of certain extreme variations in population characteristics.

With the exception of the winter of 1945–46, the adult age ratios and the number of returns deviated only a few per cent from the average for 1942–48 (Table 38). Unfortunately our samples for the winter of 1945–46 were extremely small, limiting any importance that we might give to this deviation from the average adult age ratios and number of returns. If the age ratios and relatively high returns for the winter of 1945–46 happened to be true characteristics of the population behavior

TABLE 38

Annual Quail Population Losses and Returns on Banded Adults (Based on Trapping Studies at Prairie du Sac, 1942–48)

Winter	Fall Pop.	Spring Pop.	Trapped in Winter			Banded Survivors in Spring				Estimated Adults in Fall Pop.
			No.	Per Cent[1]	Per Cent Adults	No. Adults Banded	No. Re-turns[3]	Total No.	Per Cent[5]	
1942–43	353	75	55	16	13.3	7		53	71	47
1943–44	217	124	75	35	16.0	12	1	69	56	35
1944–45	246	95	47	19	10.6	5	1	43	45	26
1945–46	153	65	23	14	21.7	5	3	19	29	33
1946–47	194	87	99	52	17.2	17	0	84	97	33
1947–48	215	57	116	54	17.7	(9)[2]	5	53	(93)[2]	38
Total	1,378	503	415			46	10	321		212[6]
Average		35%[1]		30%			22%[4]		60%	42%[7]

[1]Per cent of the fall population.
[2]Not included in the totals for this column because this was the last year of trapping and no further returns were obtained on these trapped birds.
[3]Total adults trapped that were banded in previous winters.
[4]Per cent of banded adults trapped in previous winters.
[5]Per cent of the spring population.
[6]Estimated number of total adults surviving, both on and off the study area, from the previous spring's population (per cent of adults trapped in winter x fall population).
[7]Estimated per cent of adults surviving from spring to fall (212 divided by the spring population).

for this year, a combination of factors would have to be involved. These are abnormal movements of adults in spring, low adult mortality, and low productivity. The probability that all three of these conditions prevailed at the same time seems remote. Also there did not appear to be a density relationship since the rate of summer gain and spring density were both relatively low. Lacking evidence which would indicate that some factor or combination of factors operated to make the 1945–46 population characteristics different from other winters, we deduced that sampling error and possibly unbalanced movement were involved.

The other extreme deviations that seem worthy of comment which concern both high or low April 1 to November 15 losses (Table 40) can be explained as follows. Obviously the "0" losses shown for 1929 and 1937 are impossible. Unbalanced movement, high adult survival, and high productivity would be logical factors affecting these populations as will be explained in the sections on density relationships. The very high losses for years having high spring densities appear to be density related. High losses for years in the period 1948–51 appear to be related to habitat changes and other factors which offset density effects.

The November 15 to November 15 survival series for the period 1942–48 based on all of our data and extrapolation was 100–14–1–0 (Table 50). This is considerably lower than the estimates for Wisconsin pheasants reported by Leopold *et al.* (1943) and Buss (1946) who reported survival series of 100–30–9–1.8–0 and 100–26–9–4–0 respectively on the same refuge for different years. However, the pheasant survival series is from a winter-to-winter sample which varied in the dates in winter when birds were trapped.

Apparently the annual survival of Wisconsin quail is very

TABLE 39

Comparison of Calculated Return of Spring Survivors in Fall With Actual Returns From Trapping

Year	(1) Banded Survivors in Spring	(2) Per Cent Surviving From Spring to Fall*	(3) Est. Banded Spring Survivors in Fall (Total) (1) x (2)	(4) Est. Spring Survivors in Fall (On Area) (3) x 21%†	(5) Est. Spring Survivors Trapped‡	(6) Actual Winter Returns From Previous Spring's Survivors
1943	53	50	27	6	2	1
1944	69	21	15	3	1	1
1945	43	35	15	3	1	3
1946	19	51	10	2	1	0
1947	84	44	37	7	4	5
Total	268		107		9	10

*From Table 40.
†Per cent of birds remaining on area.
‡(4) x per cent of the fall population trapped.

TABLE 40

Annual Quail Population Changes, 1929–51 at Prairie du Sac

Year	Previous Fall Pop. (Nov. 15)	Spring Pop. April 1	Winter Loss No.	Winter Loss %	Nov. 15 Pop. Total	Nov. 15 Pop. No. of Adults*	April 1 to Nov. 15 Adult Losses No.†	April 1 to Nov. 15 Adult Losses Per Cent of Spring (April 1)	April 1 to Nov. 15 Adult Losses Per Cent of Previous Fall Pop.
1929	—	22	—	—	121	19	3	—	—
1930	121	112	9	7	257	40	72	64	60
1931	257	236	21	8	400	62	174	74	68
1932	400	290	110	28	406	63	227	78	57
1933	406	339	67	17	433	67	272	80	67
1934	433	288	145	33	411	63	225	78	52
1935	411	196	215	52	416	64	132	67	32
1936	416	65	351	84	140	22	43	66	10
1937	140	25	115	82	158	24	1	4	0
1938	158	39	119	75	148	23	16	41	10
1939	148	97	51	34	318	49	48	49	32
1940	318	133	185	58	288	44	89	67	28
1941	288	142	146	51	264	41	101	71	35
1942	264	122	142	54	353	47	75	61	28
1943	353	70	283	80	217	35	35	50	10
1944	217	124	93	43	246	26	98	79	45
1945	246	95	151	61	153	33	62	65	25
1946	153	65	88	58	191	33	32	49	21
1947	191	87	104	54	215	38	49	56	39
1948	215	57	158	73	109	17	40	70	19
1949	109	47	62	57	141	22	25	53	23
1950	141	87	54	38	163	25	62	71	44
1951	163	60	103	63	107	16	44	73	27
Avg.‡	252	126	126	50	252	39	87	69	35

*Estimated by multiplying the total fall population by the average per cent of adults (15.4, Table 21) found in the 1942–47 population except for the period 1942–47 where the actual per cent of adults is used.
†Number of adults in "fall population" subtracted from the "spring population".
‡Excludes 1929. Percentages are computed from the averages.

similar to that found in Georgia quail. Stoddard (1931) did not make survival studies as such, but his banding operations on the Forshala plantation showed 135 returns out of 1,031 quail banded in the spring of 1925 and 1926. In terms of a survival series occurring between one nesting season and the succeeding one, this would be expressed: 1,031–98–29–8. These data indicate that 13 per cent of the quail lived at least one year. On another study area Stoddard reported returns of 379–56–6–3, for a survival of 17 per cent. The intensity of trapping and losses between seasons, area populations, and other controlling factors were unknown.

Since the percentage of adults in a population provides an estimate of the average annual survival, as was indicated in the Prairie du Sac data, this information can be used to make general comparisons of year-to-year losses in many other states (Table 20). These data indicate that annual adult survival in Wisconsin is also similar to that in many other areas. However, precise comparisons can't be made using age ratios alone; population censuses are also required, because the age ratio in a rising population could be similar to one in a falling population but adult survival could be different in both.

The practicality of using the average percentage of adults in the trapped sample to compute the total adults in the fall population for all of the years from 1929 to 1951, except during the period 1942–48, is indicated from the following example. The average age ratios for fall collections in Wisconsin, which were statistically significant (Table 19), varied from 8 per cent to 23 per cent adults. These extremes in the percentage of adults were similar to the Prairie du Sac age ratios. Thus these data together with all of the other sources of information on the study area indicate that the Prairie du Sac age ratio data provided a reliable index of year-to-year losses. By using the mean percentage of 15.4 adults (Table 21) in calculating spring-to-fall losses for any one year from 1929 to 1951, the extreme errors which could be expected are plus or minus 6 per cent. We do not believe that such an error would distort the results obtained through the use of an average age ratio of 15.4 per cent in evaluating population behavior to the extent that the biological implication would be lost.

Of considerable importance in the mechanism that controls annual mortality is the relationship between winter (November 15 to March 31) and spring-to-fall (April 1 to November 14) losses (Fig. 15). The array indicates that when winter losses are high, spring-to-fall losses are low (r equals —.512; .423 required at the 5 per cent level). The 8 out of the 22 years in which the correlations deviated considerably from the average indicated that other factors affected favorably or unfavorably the impact of high winter losses on quail populations in some years. Generally the factor of adverse weather that caused heavy winter mortality created a spring population that had a higher survival rate from spring to fall than a population sustaining low winter losses.

Probably the most important relationship between seasonal changes is that of spring (April 1) populations and spring-

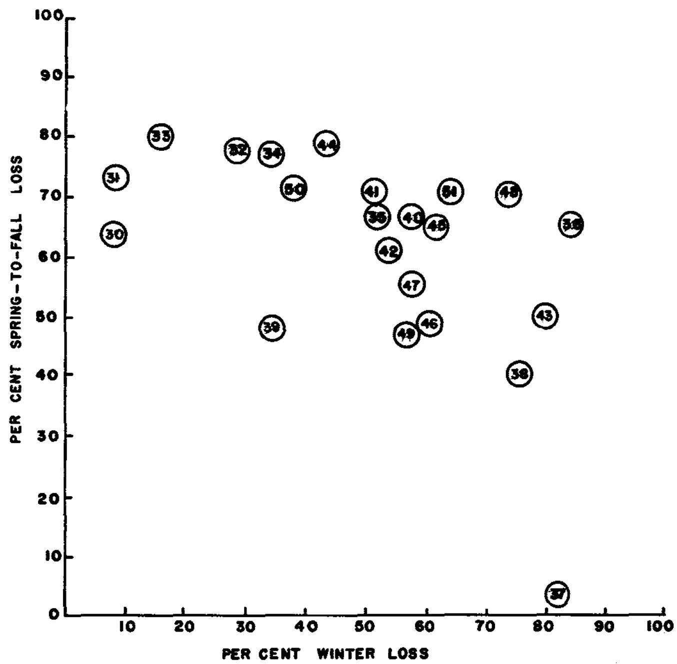


Figure 15. The relationship between winter (November 15–March 31) and subsequent spring-to-fall (April 1–November 14) losses in adult quail at Prairie du Sac from 1930 to 1950.

to-fall (April 1 to November 14) losses, shown in Figure 16. The array of co-ordinates which is positive shows a highly significant correlation (r equals .762 at the 1 per cent level using the logarithm of the spring population), clearly demonstrating that spring-to-fall mortality of adults was directly proportional to spring density.

Only the years 1929 and 1937 showed extreme deviations but even these two years depicted the same positive relationships as the other years. The very small spring-to-fall losses for these two years in which the spring population reached its lowest levels were probably the result of a combination of unbalanced egress, low summer mortality and high productivity.

While correlation between high winter losses and corresponding low spring densities and summer losses indicates a direct relationship, the occasional deviations indicate that under certain environmental conditions the relationship can be complex. These deviations and their possible causes will be discussed later in the section on fluctuations.

Density Relationships

The effect of seasonal densities of Wisconsin bobwhite quail on survival or reproductive gains are primarily reported in the discussion section together with data from other authors. These density relationships are based on studies of the natural population. With the exception of one year in which we deliberately reduced the Dunn County population, we did not have any opportunities to manipulate quail densities to simulate controlled studies.

Since we could not critically evaluate the impact of quail density on biological response, we conducted studies on penned pheasants where conditions could be controlled. Because we frequently relied on these pheasant studies to interpret our observations on natural quail populations, we elected to include them in this report rather than in a separate publication.

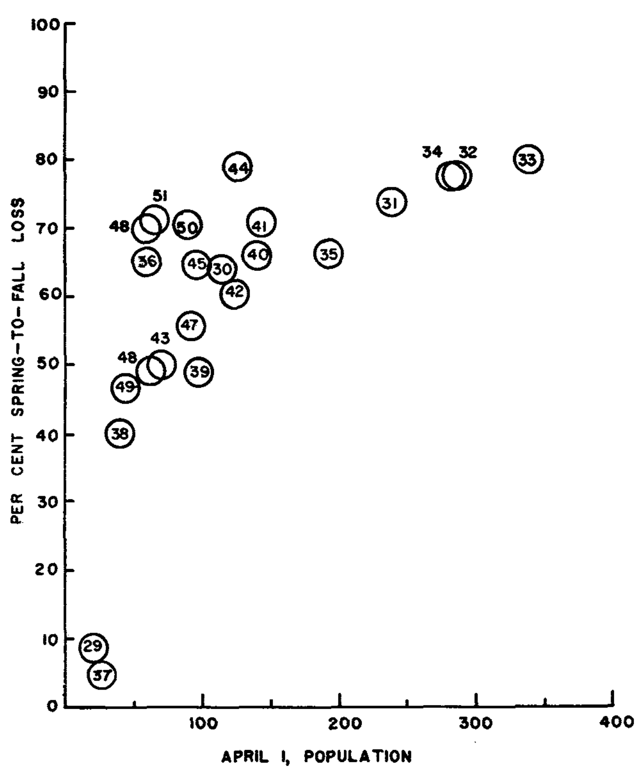
The results of the pheasant density studies together with age-ratio relationships are highlighted below for reader orientation and completely reported in Appendix B.

The results of Study I, designed to determine whether density clearly affects mating behavior, showed the following trend in the amount of fighting among cocks as the number of the birds in a 25- x 75-foot pen was increased: first, fighting became intense, then decreased sharply and finally ceased. But, the mating drive was not affected and the cocks continued to pursue hens at the same rate.

Under extremely high density in Study II (216 birds in 6 pens consisting of 18 hens and 18 cocks each for a density of 504 birds per acre) the hens laid approximately half of their eggs at random (not in nests) and frequently laid in and incubated each others' nests. This promiscuity was attributed to the extreme density and showed how this could greatly affect reproductive success.

One consequence of 2 or more hens laying in the same nest was observed in a supplemental study in which 10 hens and 1 cock were penned in a 25- x 100-foot enclosure. Despite the complete lack of cover and extreme density, most of the hens laid eggs in nests but only 1 hen possessed enough maternal drive to attempt to hatch a brood. The nest that was incubated contained 58 eggs, laid by at least 5 different hens, and 4 different-aged embryos. As soon as the first egg hatched, the incubating hen abandoned the nest.

Figure 16. The relationship between spring (April 1) quail population density and spring-to-fall (April 1–November 14) losses of adults at Prairie du Sac, 1929–50.



In follow-up studies designed to measure the impact of density-related behavior on reproductive rates (Study III), pheasants were penned at the rate of 1 cock to 5 hens (30 birds per acre). They dropped 53 per cent less eggs, laid 42 per cent more in nests, hatched their first young 8 days earlier and completed hatching their chicks 22 days earlier than did birds penned at the rate of 1 cock to 15 hens (90 birds per acre). However, the number of successful nests produced by both groups was the same. The detrimental effect of density in this case was the extra stress imposed by the effort involved in prolonged laying and incubating and late hatching of chicks. Under high densities strife among cocks was so great that in one case a dominant cock killed 2 other cocks. We have observed a few badly beaten cock pheasants and quail in wild habitat but never witnessed a killing that resulted from mating season strife. It is doubtful whether mortality from this cause alone could be a significant factor, but it nevertheless is another potential source of loss.

The effect of cocks on reproduction under conditions of heavy density was clearly demonstrated when the experiment described above was repeated the next year but in this case 3 cocks were found by trial and error that would tolerate each other. Thus the only difference between the penning arrangements was that we were comparing the reproductive performance of pheasant densities composed of 1 cock to 5 hens and 3 cocks to 15 hens. The effect of density on egg laying and nest formation was similar in both years. However, the number of successful nests hatched per hen was reduced from 0.9 to 0.3 in the pen containing 3 cocks. Also the date of hatching was later by one month and the number of chicks hatched per nest was reduced to one-half.

Since the spring and summer age ratios of breeding populations vary from year to year, Study IV was initiated to determine whether there was any difference in reproduction of young (1-year-old) and old (2-year-old) breeders. The results of this study showed that old birds were superior in all phases of reproduction and successfully hatched 40 per cent more clutches than young breeders.

Summary

The average hatching date from 1944 to 1960 was July 18, with broods hatching from June to October. July 13 was the median hatching date.

Fall population samples contained 61 per cent adult males and 51 per cent juvenile males. Adults averaged 16.1 per cent in state-wide fall samples and 15.7 and 15.4 at the Dunn County and Prairie du Sac Study area, respectively, in winter samples.

In the state-wide, fall population samples, the young-per-adult and young-per-adult-hen ratios were 5.4 and 13.3 respectively and in the winter-trapping samples on both of the study areas they were 5.4 and 14.4.

The average size of 254 coveys from November 1–15 was 17.0 and by the end of March the coveys had shrunk to 7.5 (1935–51). The correlation between covey size and summer gain and covey size and fall populations was not significant. The size of fall coveys appears to be an inherent characteristic of the species rather than a factor dependent upon other population characteristics.

There was no significant correlation between the ratio of males to females and young to adults in the birds that formed coveys; neither was there a correlation between the age of broods that composed coveys. The average number of broods composing coveys in November was 2.4.

Quail weights for juveniles and adults reached an annual peak in January and then declined to April. Based on these and other studies, there appears to be a correlation between weight changes in females and the time of egg laying and hatching. This relationship is similar to that in pheasants. The difference between weights of juvenile and adult males and females in winter months and between winters was not significant.

The movement of quail in winter averaged $\frac{1}{4}$ mile with a range of 150 yards to 1 mile. From spring to fall, 79 per cent of the Prairie du Sac area quail population left the area (4,500 acres) with 60 per cent of this movement occurring before early July. On the larger Dunn County area (10,000 acres) egress was 42 per cent of the population during a comparable period.

Spring dispersal was random and averaged 1.3 miles. The interwinter movement is 20 per cent less than the spring-to-fall movement. This difference in movement appears to be the result of quail continuing to move until some of them begin to turn back toward their winter range. The interwinter movement ranged from 1–4 miles.

Early studies based on winter band returns alone indicated an annual disappearance rate of 88–97 per cent. The annual mortality rate computed from a combination of banding returns, censuses and movement averaged 85 per cent (survival series = 100–14–1–0). The total annual mortality was subdivided into ecological seasons as follows: 50 per cent from November 15 to March 31 and 69 per cent from April 1 to November 14 with $\frac{2}{3}$ of this loss occurring between July 1 and September 15. High winter losses were generally followed by low spring densities and summer losses. The loss rate of adults in summer was correlated positively with spring density.

Pheasants were used in pen experiments to determine whether an increase in density affected reproduction. When density was increased threefold the number of clutches successfully hatched by the experimental hens decreased from 0.9 to 0.3 per hen. Some of the specific behaviorisms of the pheasants in the pen experiments such as promiscuous nesting were also observed in wild quail. These studies, together with other population behavior relationships to be reported later, indicated that potentially density changes can affect quail in the same way as they did the experimental pheasants.

Pen studies were also conducted to determine whether there was any difference in the reproductive performance between young and adult pheasants. Adult birds were superior in all reproductive phases compared to young birds.

Habitat Studies

The general habitat requirements of quail were revealed by their distribution in both the primary and secondary agricultural lands of the state, areas encompassing all soil types. In early history, prior to settlement in 1850, quail were reported present according to Schorger (1944) in all areas of the state except the solidly forested regions (Fig. 3). And although quail were reported as being occasionally abundant prior to settlement, it was not until 10–20 per cent of the land was in agriculture that quail began to be frequently reported as abundant in his report. The fantastically high densities reached in almost all portions of the occupied range from 1845 to 1855 showed that both food and cover supplies were ample.

A survey of the distribution of quail in Wisconsin in 1949 (Fig. 4) showed that this species occupied the identical range, except for the southeast, in which they were found a century earlier. During the 100 years elapsing between these periods, great changes took place in both wild and domestically produced vegetation. Although the density changed drastically between the mid-1800's and 1900's, wherever quail are found in Wisconsin there is no evidence to indicate malnutrition exists now. The thousands of quail we and other investigators have either observed, or examined at least outwardly, were vigorous, full-weight birds except in severe winters when food supplies were buried by snow.

When we consider that the bobwhite quail lived abundantly in the 1800's in Wisconsin on the flat central sandy areas, in the unglaciated hills of the southwest and west, and on the clay and peat soil of the southeastern part of the state, we have here a most remarkable bird. It is only in the southeastern quarter of Wisconsin that quail no longer exist. The reports of the dependency of bobwhite quail on shrubby growths for cover by Stoddard (1931), Leopold (1931), Errington and Hamerstrom (1936) and Schorger (1944), together with their distribution during the 1800's and 1900's provided us with an approach to studying current food and cover requirements and trends in availability as they relate to population behavior and game management practices. The obvious difference between the quail-less southeastern part of Wisconsin in the mid-1900's and the presently occupied range is in the amount of continuous shrubby cover (Thompson, 1951). Thus we proceeded to gather data through both literature review and field observations on changes in vegetation primarily used as quail cover. Food habit studies were made only incidentally to those on cover and through indirect approaches.

Food Requirements

The general food requirements of quail in Wisconsin and other states have been determined by several investigators including: Errington (1931), Errington and Hamerstrom (1936), Leopold (1931), Stoddard (1931), Martin (1935), Wright (1941), Baumgras (1943), Stollberg and Hine (1952), Larimer (1960) and Ellis (1961). These studies plus our own examinations show that corn, small grains, soybeans, and the larger weed seeds are the primary winter foods. Although the seeds of broad-leaved weeds and domestic crops are favored, quail eat a variety of seeds. Laessle and Frye (1956) found slough-grass *(Scleria muhlenbergii)* and wax myrtle (*Myrica* spp.) predominating in quail diets in Florida.

Some of the fruits of shrubs frequently eaten are wild grape (*Vitis* sp.), bittersweet (*Celastrus scandens*), and sumac (*Rhus* sp.). Mast crops and insects complete the main course. Fruits of shrubs are not a complete diet (Errington, 1931) and quail lose weight on these foods when eaten alone; they are "salad-type" foods. Some fruits may even be toxic to birds, such as *Rhus vernix* (Trainer and Kabat, 1961). With the exception of insects and green vegetation the same foods, when available, are eaten year round. Only snow and sleet cause extreme food shortages.

The great variety of seeds from commonly growing wild and cultivated plants eaten by quail allow it to exist in all but deep forested and wide-spread grassy areas. The heavy diet of seeds produced abundantly by weeds such as common ragweed (*Ambrosia artemisiifolia*), foxtail (*Setaria* sp.), smartweed and wild buckwheats (*Polygonum* sp.), and domestic crops indicate the adaptability of quail to live in cultivated land areas.

We did not conduct studies to determine the availability of seed on the ground, but a number of such studies have been carried out. In Missouri Korschgen (1958) analyzed soil samples for the type and amount of the seed present. He made the deduction that quail were able to find and utilize 10 per cent of the seed present, and also that on the average 15 g. of seed were eaten daily. Korschgen concluded that southern Missouri range could have supported 1 quail per 3 acres in a drouth year when seed supplies were at a minimum.

Leedy (1939) in Ohio, and Dalke (1935) and Baumgras (1943) in Michigan reported finding a much higher amount of seed on the ground than was found by Korschgen. Direct comparisons of the Missouri, Ohio and Michigan results with Wisconsin are not practical, but there is little reason to believe conditions would vary greatly in these four states. Errington and Hamerstrom (1936) concluded that "only under some emergency conditions or under those approximating the primitive, have we found survival delimited by the amount of food to be had during open winters". Also, the survival and condition of quail (see section on weights) indicate that the weed and domestic crop seed supply in Wisconsin fields was sufficient to support considerably higher populations of quail in mild winters than were found throughout our period of study. In addition, Wisconsin with its great dairy industry carries on the practice of spreading barnyard manure which is high in bird-food value throughout the winter on almost every farm in the state. Only in periods of deep snow does this practice fail to be performed with regularity.

The more important question is the trend of land use in regard to future food supplies; it will be discussed later.

Cover Requirements

The cover requirements of quail are well known. "They must have effective brush cover within access of wherever they may have to feed," and "Bobwhites seem to care little if a winter refuge thicket is made up of raspberry canes, plum brush, or something else, as long as it serves their needs" (Errington and Hamerstrom, 1936). Roosting cover may be herbaceous or brushy.

Errington *et al.* (1936) listed and described some of the most prevalent woody shrub or vine species used by quail for cover in the Prairie du Sac area. These include willow (*Salix* spp.), dogwood (*Cornus* spp.), raspberry (*Rubus* spp.), grapevine (*Vitis* spp.), haw (*Crataegus*), plum (*Prunus*), creeping juniper (*Juniperus communis depressa*) and elderberry (*Sambucus canadensis*).

In our studies the composition and quality of roosting cover was determined by the sites that individual coveys used as winter range. While almost any clump of woody or herbaceous vegetation was sporadically used by quail in winter, it was only those sites that contained ¼ mile or more of hedgerows at least 6 feet in width that repeatedly contained a covey.

In Wisconsin where most of the occupied quail range is located in farmed areas, primary concealment cover has for the last 50 or more years been located in hedgerows along fences, roads, streams and woodland margins. Also sprinkled throughout the Prairie du Sac study area on the hillsides and on the bank of the Wisconsin River are thickets (temporary cover) that are used by quail occasionally. With few exceptions the hillsides are grazed but the ravines and many scattered odd areas on the slopes have thickets of hazel (*Corylus rostrata*), raspberry, prickly ash (*Zanthoxylum americanum*), grape tangles and creeping juniper composing about 90 per cent of the prevailing cover. These hillside coverts vary in size from about 10 square feet in diameter to more than an acre.

The bank of the Wisconsin River in the north half of the area is about 25 per cent covered with brushy spots. The temporary cover on the hillsides and river bank, expressed in terms of a hedgerow, composes a strip approximately 6 feet in width and 2¾ miles long (Fig. 1).

The practice of grazing on the hillside has almost eliminated food plants, making these cover types usable only for emergency roosting. Quail are not adverse to remaining in wooded areas if feed sources such as tick trefoil (*Meibomia* spp.) are abundant (Leopold, 1931 and Stoddard, 1931). However, quail researchers agree that quail prefer open fields with shrubby growths whether in hedgerows or scattered in clumps.

The winter ranges of coveys at Prairie du Sac from 1936 to 1951 are shown in Figure 17. Errington *et al.* (1936) pointed out that when the quail population on the 4,500-acre Prairie du Sac area reached around 400 birds, covey ranges overlapped. However, from 1936 to 1951 the quail population exceeded 300 birds only in the winter of 1942–43. During this period it was possible to define areas that were usually occupied by only one covey in any one winter. A total of 24 separate covey ranges were defined. During the period 1936–51 these covey ranges were occupied 173 times; there were only 5 times in which more than 1 covey was found in the same covey range.

Under the intensive farming practices of Wisconsin there are few thickets of cover remaining interspersed in the form of clumps in fields. An occasional farm may have a brushy ravine or odd corner such as a rock outcrop, gravel pit or woodland edge that provides the predominant cover for an individual covey range. At Prairie du Sac there were 4 covey ranges of this type. The remaining 20 covey ranges contained hedgerows along fences and roads as the primary cover. However, even the 4 covey ranges cited above contained hedgrows that were used more often than the thickets. For about ten years, from 1941 to 1951, one covey range contained a 2-acre pine planting that provided solid cover while the branches remained lush at the ground level.

When Errington began his studies at Prairie du Sac there were 18.45 miles of hedgerow cover in the area. By 1950 this was reduced to 10.32 miles. The amount of hedgerow cover, its use and its proximity to food patches, which will be elaborated in the next section, indicate clearly the importance of this habitat feature to Wisconsin quail. Hedgerow cover located along streams, which are absent at Prairie du Sac, and rank vegetation along marsh edges, provided valuable cover in some areas.

Land-use and Quail Population Trends

Study area changes (1937–60)

Food supply. From 1937 to 1947 there were no detectable major changes in land use that would affect all types of food supplies. From the mid-1940's to 1960, however, the amount of corn left standing or in shocks (Table 41) as well as waste grain and weed seeds decreased significantly as a result of improvements in culture and harvesting equipment. The impact on quail cannot be considered as severe in most winters, for in moderate winters when the amount of snow remaining on the ground was very limited, these same fields still provided a good supply of feed in the form of waste corn and weed seeds.

In the past 30 years, decline in waste grain and weed seeds was offset by increased spreading of manure throughout the winter and greater amounts of waste corn in fields resulting from machine harvesting. However, since corn pickers are being constantly improved to reduce wastage, the previous gains to birds from this method of harvesting over hand picking is being lost.

The nutritional value of the seed available to quail was not studied. Wright (1941) analyzed the chemical composition of quail crop contents containing foods similar to those eaten by Wisconsin quail and found that they had a high nutritive value. Nestler (1946) suggested that there might be a short-

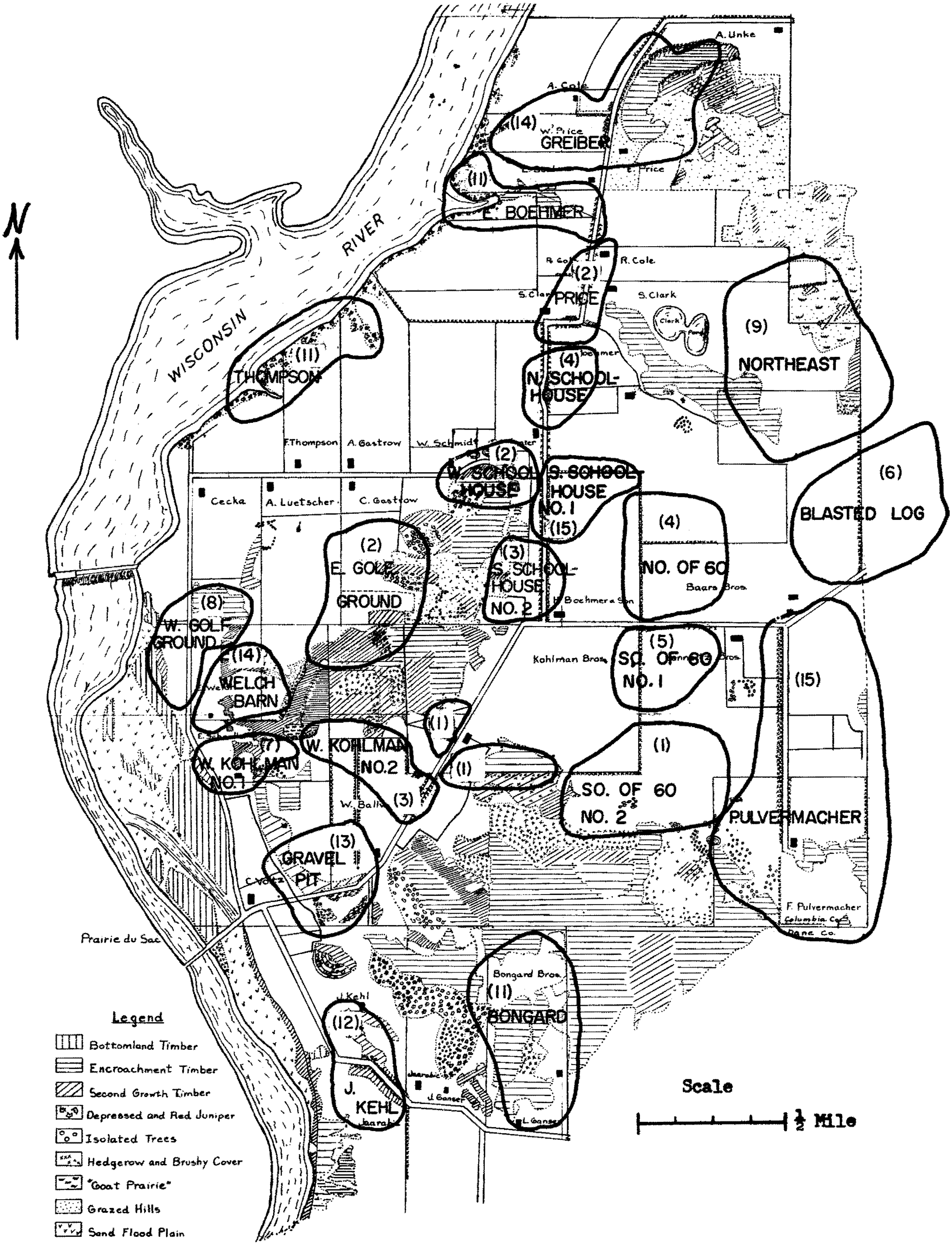


Figure 17. Winter ranges of individual quail coveys and the number of years they were occupied from 1935 to 1951 at Prairie du Sac

age of vitamin A in wild bird diets. Thompson and Bauman (1950) found no detectable vitamin A deficiencies in either quail or pheasants during 1946–47 in Wisconsin. Wild pheasants showed higher vitamin A storage levels than did game farm birds. The amounts of vitamin A stored were the same in winter as in fall. Schultz (1959) sampled 128 Ohio quail from two counties in two winters, 1946–48, and found no detectable "avitaminosis A". These studies indicated that if there are vitamin A shortages the condition is not significant or at least not conspicuous.

It is possible that in more arid areas such as Texas vitamin A shortages may occur (Lehmann, 1953). However, these shortages seemed to be correlated with lack of seed and mast crops especially in winter.

While there should have been ample weed and crop seed available to feed far more birds than were found on the study area during 1951–58, it was in this period that quail showed their greatest decline. Thus we have to conclude that although the trend in land use is for decreasing food supplies in the future, this condition was not a major factor in the quail population levels from 1937 to 1958. Also while the numbers of Prairie du Sac quail were declining, the general state population showed a significant increase in many other areas.

TABLE 41

Fields of Shocked Corn Remaining in Winter at Prairie du Sac

Year	Number of Fields	
	Fall	Winter
1942–43	25	15
1943–44	20	13
1947–48	8	5
1950–51	16	13
1957–58	*	6
1958–59	*	5†

*No data obtained.
†Only small parts of 5 fields remained.

Cover. While a number of changes in cover quality and quantity occurred on the area, as described previously, the outstanding difference between the 1930's and 1950's was in the amount of hedgerows. The number of hedgerows, their location and the period when they were removed from fences or roadsides is shown in Figure 18. Although hedgerow cover that was lost in any one covey range (Fig. 17) varied in quality, quail were found roosting in it during every winter in which a covey was present up to the year when it was removed. A few sites gained cover but these are too small to consider separately; they are accounted for in hedgerow tabulations.

The amount of cover lost during various time intervals and the total roadside and fencerow losses are shown in Table 42. The direct correlation between the downward trend of the quail population and hedgerow decline clearly shows the impact of cover loss and the lowered effectiveness of residual cover apparently to attract and hold quail (Table 43). For the first 20 years of the Prairie du Sac studies (1931–50), the quail population averaged 23 birds per mile of hedgerow. Weather conditions from 1931 to 1950 included all combinations of mild and severe winters. The stability of the relationship of quail per mile of hedgerow provides us with as reliable a habitat requirement factor as there is for most other wildlife species. This relationship we shall henceforth in this report refer to as the *quail:hedgerow-mile index.*

TABLE 42

Prairie du Sac Hedgerow Cover Losses

Period	Miles of Hedgerow				
	Present				
	Road-sides	Fence-rows	Total	Amount Re-moved	Cum. change (%)
Before 1935	9.12	9.33	18.45		
1936–40			16.94	1.51	8
1941–45			13.39	3.55	27
1946–50			10.22	3.17	45
1951–56			8.22	2.00	55
1957–58			7.12	1.10	61
1959–60	1.73	5.39	7.12	0	61
Total lost	7.39	3.94		11.33	
Per cent lost	81	42		61	

The rapid decline in the quail population after 1950 shows a breaking point in the area's capacity to sustain birds. From 1950 to 1955 the quail:hedgerow-mile index declined to 13 and from 1955 to 1958 to 3, approximating a 50 and 85 per cent decrease respectively in the area quail population. These declines occurred with only the additional loss of 2 and 1 miles of hedge or 11 and 5 per cent respectively of the original 18.45 miles of hedgerow.

The miles of hedgerow in an area become more meaningful to quail management when expressed in terms of acres of the area (Table 43). As long as the ratio of the acres of the area to 1 mile of hedgerow was 450 or less, the quail:hedgerow-mile index remained at an average of 23 (1931–50). But when the amount of hedgerows decreased only 20 per cent more leaving 1 mile of hedgerow to each 550 acres of land the quail population was reduced 50 per cent. The relationship of miles of hedgerow to acres of land henceforth will be referred to in this report as the *acres:hedgerow-mile index.* This index can be compared in importance to the acres of grassland required for prairie chicken (Hamerstrom, Mattson and Hamerstrom, 1957).

The relationship between the number of quail and the miles of hedgerow varied between 19 and 26 from 1931 to 1950. This variation is related directly to weather conditions and mortality in winter. Sleet storms in the winter of 1936–37 and 1937–38, following the murderous winter of 1935–36 when populations were reduced to an extreme low, prevented a rapid recovery to another high level between 1936 and 1940.

TABLE 43

Prairie du Sac Hedgerow Cover and Quail Population Trends

Period	Density: Fall (Maximum)	Density: July 1 Index*	Miles of Hedgerows	Quail (Fall) Per Mile of Hedge	Acres Per Quail	Acres in Area Per Mile of Hedge†
1931–35	433		18.45	23	10	250
1936–40	318		16.94	19	14	300
1941–45	353		13.49	26	13	350
1946–50	215	57	10.32	21	21	450
1951–55	107	53	8.32	13	42	550
1956–58	(19)‡	17	7.12	3	240	650
1959–60	0	0	7.12	0	—	650

*Whistling Counts.
†Rounded to nearest 50-acre interval.
‡Data were available for only 1958.

In Table 44 we estimate what the quail population could have been in 1958 if all fencelines and roadsides contained a hedgerow at Prairie du Sac. Using the estimate of 23 quail per mile of hedge we obtain a figure of 1,050 birds or 4.3 acres per quail. From historical information on land-use trends in Columbia and Green Counties that is presented next, it appears that we can also estimate the existing quail population for the period 1846–70.

The estimates above are reliable only to the extent that quality of cover and other factors were similar in the mid-1800's to those of 1934–50. The complex changes in vegetation in this period, resulting from the White Man's disturbance of true and brush prairie for agricultural purposes and the reduction of fires all affected quail habitat. The right combination of these factors could have created conditions that permitted an even higher quail population to develop than our estimates indicated. On the other hand, density-limiting factors could have kept the population of the mid-1800's below our estimate.

Land-use data show that the number of farms in Wisconsin reached a plateau about 1870. Since we do not know the actual number of fields per farm between 1846 and 1929, we cannot accurately determine the miles of hedges along field fencelines. However, we do know the fields must have been much smaller and the number considerably greater during this early settlement period. Arbitrarily we assumed that there were at least three times as many fencelines or field edges bordered by shrubs in 1850–70 than from 1929 to 1958. Thus, we use "3" as a conversion factor for estimating the miles of hedgerow along fencelines in this early period. We also have obtained records to show that the miles of roads in the area remained quite similar from the early 1860's to the late 1950's. Assuming again that all fencelines and roadsides contained hedgerows, we obtained a total population of 2,150 or 2.1 acres per quail.

We know that about 900 acres of the area are composed of high wooded bluffs with a low quail value even in the ungrazed portions. This means that the estimated population of 2,150 birds would have to be concentrated on 3,600 (4,500 minus 900 acres of nonagricultural land) or 1 bird on each 1.7 acres, which is as high a density as reported in any quail study in other states by Leopold (1931).

If there is any error in the estimate of miles of hedgerow or openings and cleared fields surrounded by brushy edges for the period 1850–70, it would appear to be on the conservative side. As each settler cleared his land or plowed prairie sod, he created new fields. It is obvious that these had to be small and numerous since the natural tendency would be to "open" the easiest sites first (Curtis, 1959). This practice would result in a patchwork of fields. Actually the landscape would resemble more a network of thickets sprinkled in-between fields on a matrix of oak savannas or mesic forests.

Additional cover was created by brushy growth springing up wherever the cutting of trees to get lumber for dwellings and fences occurred or sweeping prairie fires were curtailed by settlers, resulting in a great amount of edge developing in the openings in woodlands.

County and State-wide Changes (1840–1958)

In the previous sections we have shown the correlation between cover and quail populations on the Prairie du Sac study area. Since our studies and those reported by Errington extend back only to 1929, we could only estimate the area's quail populations in early history through a process of extrapolation. However, Crop Reporting Service records (Ebling *et al.*, 1948) on agricultural statistics from 1850 to

TABLE 44

Estimates of Potential Quail Population (If all fencelines and roadsides had hedgerow cover)

	1958	1846–70
(1) Miles of fenceline	23.8	71.4*
(2) Miles of roadside	22.4	22.4
(3) Potential hedgerows	46.2	93.8
(4) Quail per mile of hedgerow (Avg. for 1931–50)	23	23
(5) Total quail on area, (3) x (4)	1,050	2,150
(6) Acres per quail, 4,500/(5)	4.3	2.1

*Obtained by multiplying amount of potential hedgerows in fencelines in 1958 by 3, which is an estimated factor representing the greater number of fencelines on farms in 1850–70.

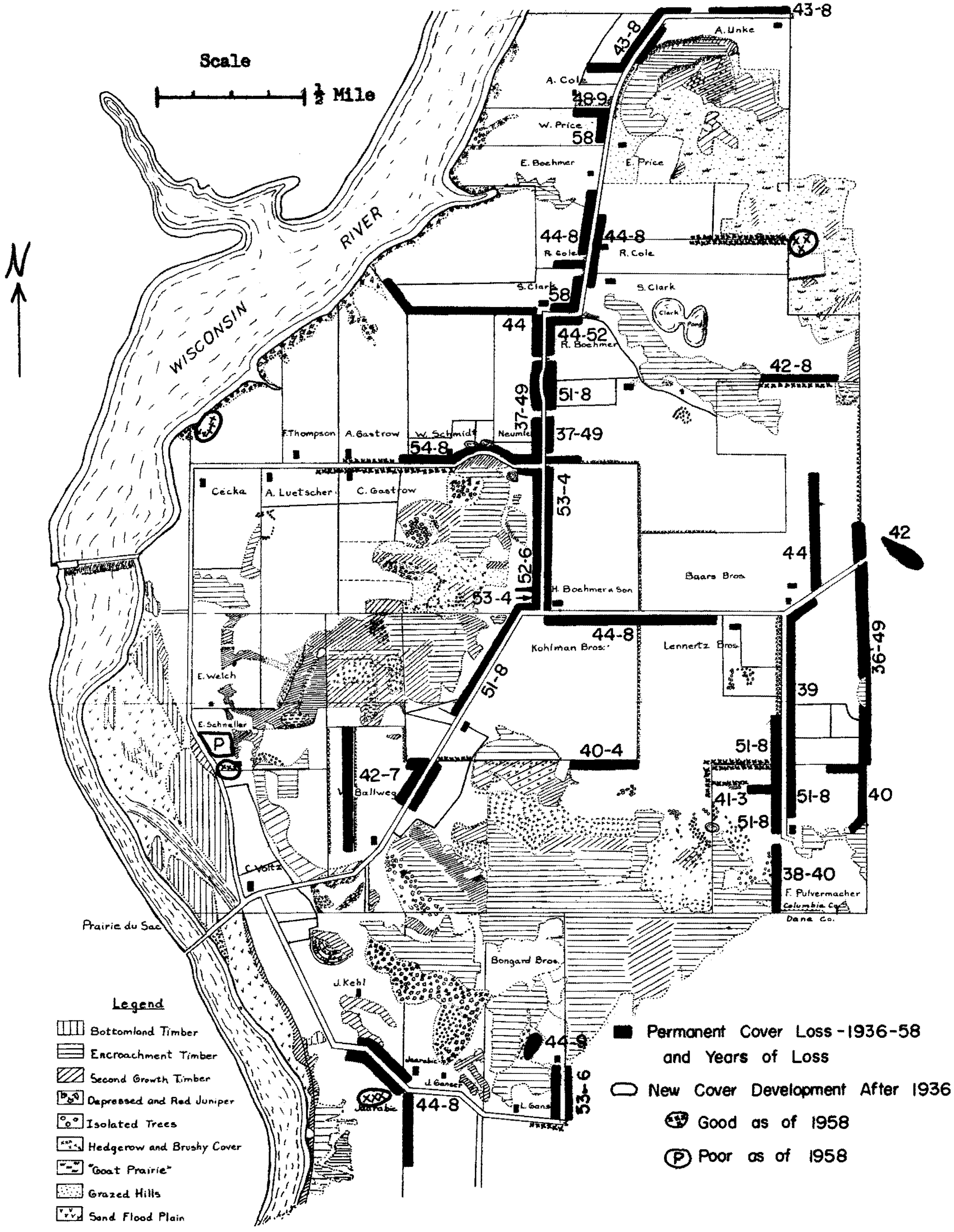
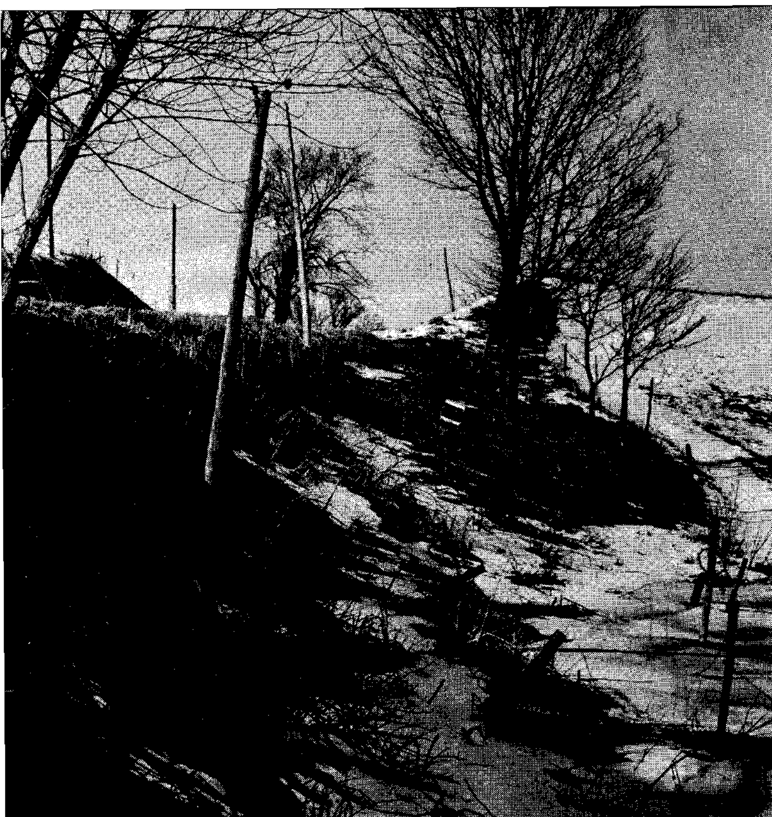


Figure 18. Roadside and fencerow cover changes on the Prairie du Sac area, 1936–58.



Roadside hedge removed from fill bank at Prairie du Sac where it had provided soil erosion protection, scenic value and excellent wildlife cover. Quail trap in background had previously been obscured by the dense shrubby vegetation.

1956 for the state and for Columbia County (Table 45) in which the study area is located may shed further light on past quail populations.

Farm development was almost zero in 1836. A territorial census at that time showed only 11,683 people. In 1840 there were 30,945; in the next decade settlement boomed and by 1848 the state population had reached 305,291. In 1850 there were only 20,177 farms in the entire state but by 1860 they had increased to 102,904.

The quail population increase which was reported by Leopold (1931), Schorger (1944) and others was directly correlated with the amazingly rapid development of farms from 1840 to 1870. By 1870 the acreage of cropland was within 15 per cent of its peak levels in 1910. This trend was strikingly reflected in the over five-fold increase in farms in Columbia County during this period (Table 45). The great amount of edge created by the rapidly increasing cropland acreage together with other changes presented ideal habitat for quail. The construction of rail fences also added greatly to the amount of hedgerow cover in early settlement.

The role of fire in pre- and post-settlement periods in creating or reducing the value of quail habitat is difficult to appraise. We don't believe pre-settlement fires which greatly contributed to the maintenance of the grassy prairies and oak savannas (Curtis, 1959) contributed equally to creating or destroying quail habitat. While food conditions might have been improved at least in mild winters, the amount of brushy edge which quail require appeared to be limited. The reduction of the prairie fires at the time of settlement reported by Curtis could have resulted in the development of brushy stands which would have improved quail habitat significantly.

The railroads which facilitated shipping of quail hunted for the market began to emerge in the 1850's and further contributed to the increase of edge and hedgerows. However, the miles of hedgerow cover created by railroads is insignificant compared to that created by field "breaking".

Of much greater importance than the railroads was the construction of roads. Two-thirds of the existing rural roads in Columbia County were constructed by 1861 (Table 46). The location and mileage of roads on the Prairie du Sac study area were the same in 1929–59 as they were in 1861. The amount of hedge cover along the railroad and road rights-of-way probably remained relatively unchanged until sometime shortly before 1900.

As the cropland acreage continued to increase, especially in the southeast and south central portions of the state, along with an increase of clean farming practices, more and more shrubby growth was apparently destroyed until by 1870 much of the great field edge cover so important to quail was gone.

Curtis (1959) described the changes in the prairie, oak opening, and oak forest of Jordan Township in Green County. In 1831, 22,540 acres or 98 per cent of the township were wooded (86 per cent oak opening and 12 per cent oak forest). The remainder was open prairie. By 1882 the wooded area was reduced to 33.6 per cent, which actually contained more trees than in 1831 because of the conversion from oak savanna to forest, and by 1902 the savanna lands were reduced to 10.2 per cent and the forested lands to 8.8 per cent. The 1861 map of Prairie du Sac showed more open land (Fig. 19) than did Jordan Township in Green County, but the development for farming obviously followed the same pattern.

While quail declined in many areas of Wisconsin in the late 1850's following several severe winters of that period (Schorger, 1944), they made some local recoveries, but by 1894 a significant decrease to a new low level was indicated by the closing of the Wisconsin hunting season in that year (Leopold, 1931). There is no evidence to indicate that the change in the acreages of various field crops were involved in the quail population decline. However, the increase in cattle and grazing of woodlands were obviously detrimental developments.

From this history it is apparent that in the period in which approximately one-third of the land was opened for farming, habitat was optimum for quail. From that point on the habitat deteriorated and quail decreased accordingly.

Although the removal of brushy hedgerows and scattered thickets through the intensification of agriculture and road building and maintenance was the major detrimental factor affecting quail habitat, the abandonment of farming in some submarginal areas beginning in the 1930's created another unfavorable trend.

The counties where field observations and studies have shown that quail and their habitat have been affected by farm abandonment include Green Lake, Marquette, Waushara and Columbia. There are also several other counties where the

TABLE 45

Columbia County Farm and Crop Acreage*

	1850	1870	1890	1910	1930	1945	1954
No. of farms	605	3,152	3,073	3,327	3,042	2,764	2,615
Farm acreage							
Avg.	154	134	147	141	146	162	166
Total	140,418	421,302	451,473	470,437	445,355	448,705	435,506
Corn	2,537	17,329	44,819	58,957	64,247	80,925	91,550
Oats	3,182	17,961	46,903	59,695	51,135	59,749	59,040
Barley	107	1,960	23,149	16,102	17,538	4,174	1,720
Rye	3	3,094	10,141	11,255	8,794	4,547	770
Wheat	14,601	130,804	21,447	2,042	2,367	1,208	2,020
Potatoes	479	1,888	3,876	7,098	4,116	1,678	550
Tobacco			504	3,521	1,986	563	270
Hay	9,438	30,898	58,745	57,768	63,142	58,379	51,810
Cattle (no.)	4,472	19,394	41,463	49,900	48,915	69,445	77,600
Woodlands pastured†					44,087	38,540	34,992
Other land pastured†					55,536	78,471	42,563
Woodland not pastured†					15,183	17,311	29,779

*Data from Crop Reporting Service reports.
†No data available before 1924. Data in "1930" column is for 1929.

habitat has been similarly affected but where the impact on quail numbers has not been studied. The rapidity with which this condition develops and the acuteness of the problem was observed in the 1,000-acre University of Wisconsin Arboretum in Dane County. In the 1930's and up to the early 1940's when parts of this area were farmed, the quail population reached a high of 170 birds. By 1950 farming on this area and on some bordering lands ceased, and simultaneously the quail population declined to near zero.

The results of the cover studies and the data on land-use changes do not add a new concept to quail management but they do for the first time provide a quantitative relationship between cover and quail populations. The importance of these relationships in practical land management designed to improve or at least sustain our present quail populations will be discussed in the following section.

Summary

Quail food supplies were ample throughout the year, except in severe winters. However, the development of more efficient harvesters of domestic crops and weed control methods may result in food shortages in the future.

In the occupied quail range in Wisconsin, changes in the miles of hedgerows and quail densities were directly correlated. At Prairie du Sac from 1931 to 1950 the hedgerow cover decreased from 18.45 to 10.32 miles (45 per cent) and quail densities were simultaneously reduced from 433 to 215 (50 per cent). During this period the ratio of acres of land to 1 mile of hedgerow in the study area *(acres:hedgerow-mile index)* changed from 250:1 to 450:1 but the ratio of quail to 1 mile of hedgerow *(quail:hedgerow-mile index)* remained at an average of about 23:1. These indices are recommended as criteria for evaluating and establishing quail habitat.

When the *acres:hedgerow-mile index* changed from 450:1 to 550:1 the *quail:hedgerow-mile index* declined to 13:1 and when the *acres:hedgerow-mile index* changed to 650:1 the quail population disappeared.

Based on the correlation of miles of hedgerows to quail density from 1931 to 1958, we estimated that there could have been 93.8 miles of hedgerow cover and 2,150 quail (2.1 acres per quail) on the Prairie du Sac area from 1846 to 1870.

The quail density on the Prairie du Sac area decreased from 1 quail to 10 acres in 1931–35 to 1:20 in 1946–50, 1:42 in

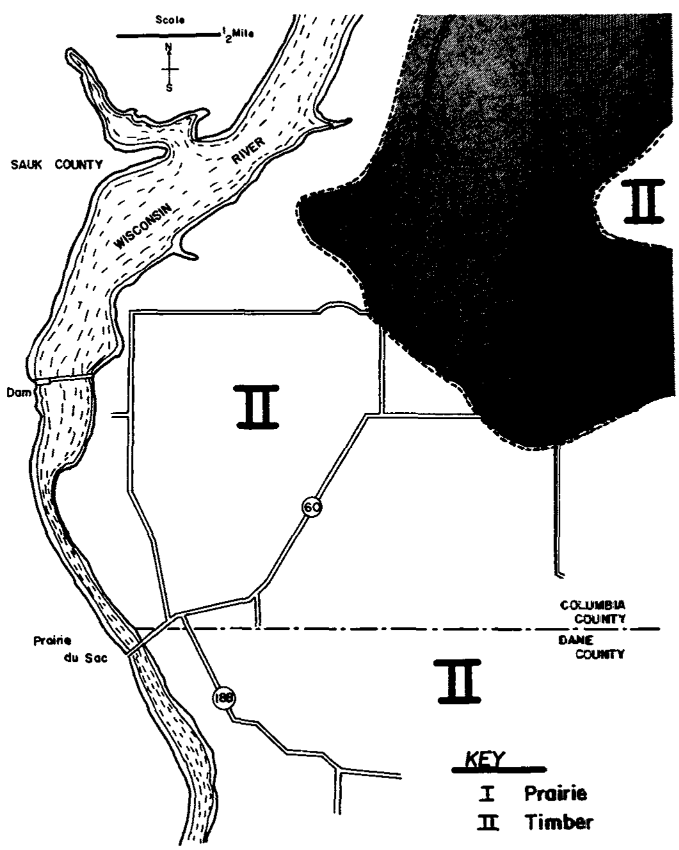


Figure 19. Prairie du Sac area in 1861.

1956–58 and "0" quail in 1959. State-wide, we estimated that in 1958 the density of quail was 1 bird to 20 acres in the better range and as a result of the severe winter of 1958–59 the quail density declined to 1:40 acres.

Hedgerows along roads comprised 50 per cent of the available cover in the Prairie du Sac area from 1931 to 1935. From 1935 to 1960 the roadside hedgerows decreased 81 per cent. The location and miles of roads in 1861 and 1929 were identical. Columbia County, in which the Prairie du Sac area is primarily located, and other areas in the state showed similar reduction in miles of hedgerow as did Prairie du Sac up to about 1950. After 1950, hedgerow losses also occurred in these other areas but at a slower rate than at Prairie du Sac.

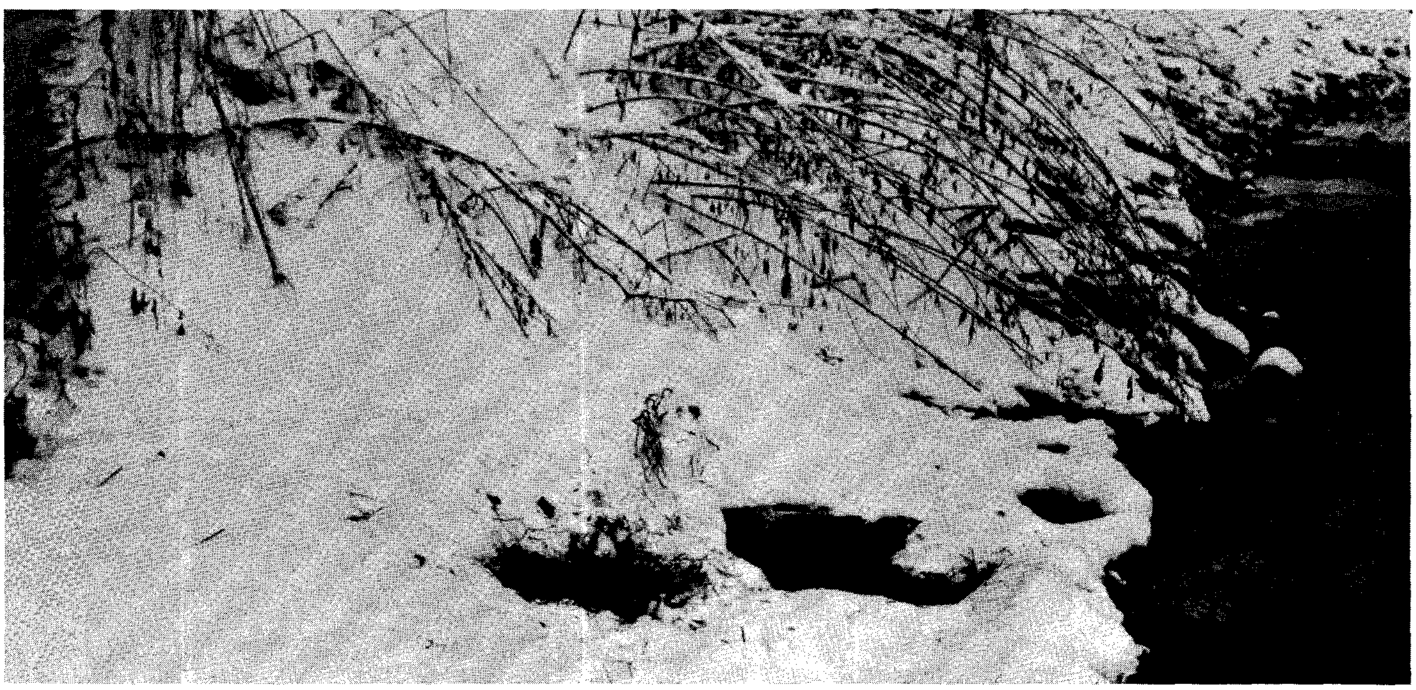
TABLE 46

Miles of Rural Roads in Columbia County, 1861–1958*

Year	Town Roads	County Trunks	State Trunks	Total Rural
1861†	—	—	—	978
1878	1,151	0	0	1,151
1926	1,000	121	228	1,349
1958	815	343	221	1,379

*Wm. F. Steuber, Wis. Highway Comm., in litt. January 5, 1959.
†From an Atlas of Wisconsin dated 1861.

When snows are deep, even some good hedgerows get buried. This is one reason why quail need an abundance of cover.



DISCUSSION: POPULATION CHANGES

Population changes are classified in this discussion as long-term trends, seasonal losses (within years) and short-term fluctuations (between years). This approach was based on the nature of the data we obtained and the information needed to manage a wildlife species.

Long-term changes reveal general habitat requirements and long-range management needs. Information on seasonal losses and short-term fluctuations is required not only for setting hunting seasons, but also for conducting habitat management programs which must be adjusted on the basis of population responses to various land-use practices.

Rarely is it possible to continue population studies on any wildlife species for even a 10-year period. It is usually even more difficult to obtain historical records that permit a tracing of the factors that controlled the population size of any wildlife species. In Wisconsin, however, bobwhite quail were studied intensively from 1929 to 1962, and historical information (Leopold, 1931 and Schorger, 1944) was also available.

The data on *seasonal losses* are based on intensive studies conducted from 1942 to 1948 at Prairie du Sac and at Dunn County from 1947 to 1951. The studies on *fluctuations* which concern changes between years, both losses and gains whether cyclic or irregular, began with Errington's investigations in 1929 and our own in 1942. The relationships between factors involved in the changes will be emphasized.

Long-term Trends

Distribution

The history of quail in Wisconsin from 1834 to 1960 clearly shows that the year-round climate has been the general controlling factor in state-wide distribution. The unoccupied Wisconsin quail range during this time has remained the same except for the addition of counties in the southeast and east central part of the state from which quail disappeared about 1900 (Fig. 3). In the north and north central counties the growing seasons are short, limiting the development of both wild and domestic seed-producing plants required by the bobwhite for food.

Within the occupied quail zone soil types vary from sand to heavy silt loams. Generally quail can be found on all soil types where agricultural land use predominates. For example, some areas in Green Lake and Marquette Counties which have sandy soils have produced as many quail as areas having loess soils in the southwest counties. Periodically during periods when mild winters prevail, quail have become relatively abundant in parts of counties such as Adams, Jackson and Marquette even though the ratio of wild to cultivated land is much higher than in the southwest counties.

Generally quail were most abundant when agriculture began to develop and spread in Wisconsin (mid-1850's). At this time they were distributed in great numbers across the entire southern half of Wisconsin. Here all types of soil and terrain were productive of quail. The southwestern counties (Driftless Area) are very hilly with flat valleys. The south central counties which contain both recently glaciated and unglaciated areas grade from very hilly land on the west to flat prairie soils on the east. Counties in the southeast quarter of the state feature relatively flat terrain with all types of soils separated by a ridge of glacial moraine.

Continentally, bobwhite quail, *Colinus virginianus* and its subspecies, occupies nearly all soil types from Wisconsin to Guatemala and from the Atlantic to the Great Plain states and Washington, Oregon and Idaho, where they became established after introduction (Aldrich and Duvall, 1955). Stoddard concluded from his studies that bobwhites thrive throughout the Piedmont and Coastal Plain regions regardless of geological differences, when their requirements in the form of food supply and sheltering vegetation are met, and do not occur on any formation unless these essentials exist. Therefore, we do not feel it is necessary to discuss in detail the geological character of their habitat.

Predators of all types have been and still are distributed throughout the Wisconsin quail range. At present the southwestern counties are the source of the highest quail populations extending over the largest solid range and also contain the heaviest fox density of the state. At the Prairie du Sac study area, quail populations fluctuated with no significant regard for either a falling or rising of fox, hawk, owl, weasel or skunk populations (Tables 8 and 12). Losses were occasionally observed but these occurred at low levels of predator populations as well as high.

Although adverse winter weather may have had a tremendous impact on long-term quail population trends prior to 1900 (Schorger, 1944), we have observed since 1929 that the populations were able to rebound to previous levels within a 3-year period following a "killing" year. Based on the 1929–60 quail observations, it appeared that there were no grounds for fearing a complete loss of quail in any Wisconsin county because of severe winters.

In the occupied quail range, agricultural land use is currently the limiting factor on distribution. The disappearance of quail in the southeastern and east central part of Wisconsin is clearly related to the removal of brushy cover primarily in the form of hedgerows. The presently occupied quail range can be expected to shrink further unless agricultural and roadside maintenance programs are integrated with wildlife management practices in the future to preserve and improve existing habitat (see the Management section for more details on this point.) For example, quail losses were very heavy in the extremely adverse winters of 1959–60 and 1961–62 because of heavy loss of cover from 1937 to 1958.

Continentally, the trend in quail density and distribution relating to land-use changes has been similar to Wisconsin's history. The pattern of quail increases with settlement about 100 years ago and decreases thereafter with intensive agriculture has been described by Latham and Studholme (1952) in Pennsylvania, Clarke (1954) in Ontario, and Brown (1956) in New York. Similar but less detailed appraisals in several other states were reported by Stanford (1952) in Missouri, Murray and Frye (1957) in Florida, and Ripley (1957 and 1958) in Massachusetts. Generally the impact of land-use changes was similar. Usually food and cover shortages developed as agricultural practices were greatly intensified. In the northeastern states such as Massachusetts (Ripley, 1957) farm abandonment subsequently became a factor in the quail decline.

Relative Density

Wisconsin quail populations have fluctuated from their highest known level in the period 1846–54 to their lowest level in 1962. However, the trend over this period has been generally downward. At their peak level, quail appeared to be well distributed over at least the southern one-half of Wisconsin. At all other times, with the exception of years immediately following a severe winter, some areas showed relatively high populations and others quite low. For example, quail were reported relatively abundant in the period 1865–75 in southern Wisconsin, but scarce at Madison and disappearing along Lake Michigan (Table 5).

Direct quantitative comparisons of population levels from 1834 to 1929 with those of more recent years are not possible, for we would have had to obtain data of the type obtained at Prairie du Sac in the years following 1929. However, it was possible to make some general comparisons using the Prairie du Sac studies which were of sufficient quality to estimate relative population levels at various periods.

Our best estimate of the average 1846–70 fall and winter densities at Prairie du Sac was 1 quail per 2 acres (Table 44). The highest density of quail found during the intensive studies was 1 quail per 10.4 acres in the early 1930's, a decrease of 80 per cent. The area population for 1946–50 showed a density of 1 quail per 20.9 acres for a total decline of 90 per cent. This latter estimate also represents average quail density for the entire occupied range in Wisconsin from 1954 to 1958. Quail declined again to less than 1 bird per 40 acres in 1959, and were virtually absent from 1960 to 1962.

Our 1846–54 estimate may seem low compared to the densities described by Schorger (1944). A rough comparison can be made by considering the number of quail that could be shot by a hunter out of various levels of population densities (Table 47). The potential hunting bag of quail for the periods 1940–59 and 1931–35 are based on actual hunting experience in areas having populations approximating those shown in the table. The potential bag for 1846–54 is an arithmetical projection from the other two periods. The potential kill for a population averaging 1 quail per 2 acres (all types of land are included here, both habitable and nonhabitable) parallels the kill in 1846–54 as reported by Schorger (1944)—"a good shot can bag 50–75 in a day" . . . "10 minute walk to flush a bevy" . . . "a new covey every five minutes."

TABLE 47

Potential Daily Bag of Quail by One Hunter With a Good Dog at Various Population Levels

Period	Coveys Flushed in 6 Hours	Acres Per Quail	Potential Hunting Bag
1846–54*	30	2	50–100
1931–35†	6	10.4	10–20
1940–59†	3	20.9	5–10

*Based on estimates shown in Table 44.
†Actual observations.

Since many spots within the quail range were probably not occupied in the mid-1850's, a population averaging 1 quail per 2 acres distributed over a large area may actually be greater than the densities of 0.3, 1.0 and 1.8 acres per quail cited by Leopold (1931) and Stoddard (1931) on selected areas in the north central and southeastern states respectively.

It is doubtful that quail could have been much more abundant than an average of 1 quail per acre over an area as large as a county when consideration is given to the various factors that limit density, including intolerance. The prevalence of very favorable habitat and occurrence of a series of mild winters such as reported by Schorger (1944), however, could result in local concentrations periodically exceeding a quail per acre.

The market hunting records (tons of quail shipped by railroad) also offered evidence of high populations for 1846–54.

In summary, quail populations have declined steadily, with occasional upswings, from 1854 to 1962. At the Prairie du Sac study area the quail population showed five declines and upswings (Table 8). The last cataclysmic decline occurred in the winter of 1958–59 climaxing a downward trend since 1942–43, and reduced the population to nearly zero. In many areas in the state the population increased generally from 1951 to 1958, the result of the longest series of mild winters in the last 30 years. The favorable winter weather that occurred during this same period could not compensate for the loss of quail habitat due to the hedgerow removal that took place simultaneously.

Primary Factors

Many factors affect population levels of birds. These factors may be favorable or detrimental and may vary in degree and effect. The only factors to which we could ascribe long-term trends of quail populations were those of land-use practices.

For purposes of discussing these factors the period from 1846 to 1960 was divided into three eras: 1846–70, 1871–1928 and 1929–1960. Our information for 1846–70, based on the reports of Leopold (1931) and Schorger (1944) is generally adequate, since the changes in land use and quail populations were conspicuous. From 1871 to 1928, even though some information was again provided by Leopold and Schorger, knowledge is generally lacking. However, intensive studies have given us relatively complete knowledge on what changes transpired in quail populations and land use from 1929 to 1960 and also have provided information that could be used to interpret the changes that occurred from 1871 to 1930.

The degree to which various habitat factors operated to create the spectacular increase of quail following settlement and early expansion of agriculture in the mid-1850's cannot precisely be determined. Deductions based on the intensive studies conducted between 1929 and 1960 in Wisconsin and in other states strongly indicate that extremely favorable habitat was created by rapid settlement, the cessation of prairie fires and the ensuing expansion of agriculture and road building. The prime requirement of quail habitat, the brushy hedgerows and thickets adjacent to or scattered among numerous openings, should have been met across all of southern Wisconsin.

Simultaneously food supplies must have remained in abundance or even increased in proportion to the added cover. The long-term trend in types of quail food was a shift from native species growing on uncultivated soils to domestic crops and the seeds of weed species growing in cultivated fields (Curtis, 1959). One type of area where food supplies declined was in the woodlands. Native plant species such as wild legumes growing in ungrazed woods that formerly provided some quail food were practically eliminated by domestic livestock (Leopold, 1931); such areas became gradually quail-less except when used for occasional roosting.

It is very doubtful that native flora in the uncultivated prairies, oak openings and oak forests produced much quail food that would be available in winter except in years when bare-ground conditions prevailed (Schorger, 1944 and Curtis, 1959). In at least one case, however, a wild plant species probably did make a significant quail food contribution. Schorger (1944) reported that historical records showed quail populations declined rapidly in Sheboygan County after 1868 following the elimination of a wild bean crop through settlement.

The creation of openings, growth of brush thickets, production of ample food together with a series of mild winters produced the optimum conditions required to achieve the great populations of quail that developed from 1846 to 1870.

Intensive studies from 1929 to 1960 showed the degree to which the decline in miles of hedgerows and number of quail was correlated on the Prairie du Sac area. These studies together with historical records also provided the basis for concluding that, while the number and type of plant species changed greatly between the mid-1850's and the period 1929–60, food supplies remained ample.

To get a better understanding of the population changes that occurred from 1870 to 1929, we estimated the amount of hedgerows on the Prairie du Sac area in the mid-1850's and then correlated the rate of decline of cover and quail numbers. Our estimates indicated that there could have been about 93.8 miles of hedgerows along fences and roads on the Prairie du Sac area within the period 1846–70 (Table 44). By subtracting from this the amount of hedgerow cover on the study area in the period 1931–35, 18.45 miles, we obtained a gross loss figure of 75.3 miles. Thus, the average loss between the periods of 1846–70 and 1931–35 is estimated at 1.3 per cent of the original or 1.2 miles per year. Based on our *quail: hedgerow-mile* index this is a reduction of about 1,732 quail or 25 birds per year.

However, from our analysis of land-use changes we deduced that by 1880 about 50 per cent of the estimated 71.4 miles of hedgerows along fencelines disappeared due to an increase in the size of crop fields (Table 45), leaving about 35.8 miles (Table 48). Added to this was the cover, 22.4 miles, that was estimated to have developed along roads which were constructed in this period (Table 44). Thus the gain in hedgerows along roads offset the loss of field hedgerows from about 1860 to 1870.

It is possible that there might have been some periods from about 1860 to 1928 in which cover losses temporarily accelerated that are not detectable from land-use records. If there were, this might explain the reason why the quail hunting season was closed about 1895. If this were not the case, however, and cover-loss rates were constant, then we would have to conclude that in the period around 1895 there were 50 per cent more quail than when the hunting season was opened again in 1932.

It is probable that hedgerow losses along roadsides were more rapid from 1930 to 1960 than from 1900 to 1930 since the procedure of annually "chopping-out" brush in rights-of-way along secondary roads began only about 30 years ago. This process was accelerated when high-speed equipment and shrub-destroying herbicides were developed for rapidly and permanently destroying hedgerows along roadsides. Prior to this time hand-cutting operations and low-capacity mowing machines resulted only in temporary cover removal. However, even these slower operations where frequently repeated were able to suppress the regrowth of cover.

TABLE 48

Loss Rates in Miles of Hedgerow at the Prairie du Sac Study Area

Periods	Miles of Hedgerow Present: Along Fences	Roadsides	Total	Annual Loss Rates Between Periods/ (Miles)‡
1846–54*	71.4	——	71.4	
1860–80*	35.8	22.4	58.2	0.7
1931–35†	9.3	9.1	18.4	0.6
1956–58†	5.4	1.7	7.1	0.5

*Estimates.
†Actual.
‡These values were obtained by dividing the total cover loss occurring between periods by the total number of years elapsing between the mid-points of each period.

While cover losses have not been generally as drastic in most parts of the rest of the occupied quail range in Wisconsin as at Prairie du Sac, some similar observations were made in several Wisconsin areas. The Dunn County area began to show the effects of cover loss after 1940 but the history of hedgerow removal was not intensively studied.

In a Green Lake County transect (Table 6) a drastic reduction was observed in hedgerow cover and in the number of whistling birds between 1955 and 1958. This reduction occurred on that part of the transect which was adjacent to a complete road-rebuilding job, resulting in all of the hedgerow cover being removed. Since this transect was on the very edge of the easternmost range occupied by quail in this area, any loss of habitat would be expected to have had a severe effect on the population.

Observations on the Waushara, Columbia-Sauk-Adams and Marquette transects (Fig. 5) showed that although the total numbers of whistling birds remained relatively high from 1955 to 1958, they decreased significantly at some stops in the best agricultural sites. On each transect, generally, the more marginal farm areas were contributing the highest whistling counts whereas the best farming sites had a low population of quail.

On the other hand, in the above counties and also in Green Lake there were areas in which the number of abandoned farms increased to the point where quail populations declined perceptibly. In the first 10–20 years after the trend in farm abandonment began, quail habitat improved. An abandoned farm which rapidly becomes a plot of weeds and shrubs, particularly if surrounded by intensively farmed areas, almost as rapidly develops into a wildlife oasis. However, when the number of abandoned farms increases to the point that parts of whole townships are affected, the value of such areas for farm game, particularly quail, decreases. On the abandoned farms, weedy fallow fields favorable for farm game such as quail and pheasants soon give way to grasses, then shrubs, and subsequently trees. This succession results in a near foodless, semi-forest type of area. This trend in land use is similar to that reported in parts of Massachusetts by Ripley (1957 and 1958).

Generally the impact of farm abandonment on quail is just beginning in this area of about 600 square miles located approximately between Wautoma and Poynette which still contains some of the better quail range in the state. The rate of farm abandonment in this area can be expected to increase considerably in the next 10 years since most of the area is submarginal for agriculture. Many of the fields on these abandoned farms are being planted to coniferous trees, speeding up the deterioration of farm game habitat. In Waushara County alone 2,803,935 trees were distributed for planting in 1959. The future of quail in these areas will depend on the possibility of developing a practical food-patch system. If this land-use change affected quail alone, consideration of a farm game management program would not appear to be justifiable. Unfortunately, cottontail rabbits and pheasants will also be unfavorably affected.

Secondary Factors

A number of other factors can influence long-term trends, but they are not basically responsible for a permanent increase or decrease. A brief discussion of the impact of these factors is presented in the following sections.

Hunting. From 1846 to about 1870 many tons of quail were reported taken by market hunters. The shipments from Beloit in 1854–55 constituted about 55,000 quail (Schorger, 1944). Harvests of this magnitude, which were occurring at a time when cover conditions were deteriorating due to intensification of agriculture (Table 45) and adverse winters were occurring simultaneously, could obviously have had a profound effect on long-term trends. Following this era of heavy market hunting, quail never recovered to their previous high levels. Thus at least in some areas market hunting appeared to accelerate the decline of Wisconsin quail populations.

Sport hunting was reported as negligible in the nineteenth century, and the highest estimated kill of quail by sport hunters in an area of 30 counties reached 50,000 in 1957 (Table 10). The limited importance of the sport hunting kill is indicated in the following comparisons with annual losses from all causes.

The average number of quail dying from all causes in any quail population exceeds 80 per cent each year (Table 50). Considering seven of the southwest counties containing the best quail range in the state, we have an area of 3,447,680 acres with an estimated over-all density of 1 quail per 30 acres in 1957. This area, which would have about 115,000 birds, would sustain an annual loss of about 92,000 under a mortality rate of 80 per cent. Thus it is apparent that a Southwest District kill of 19,000 would be a small part of the annual losses in the state quail population. Furthermore the estimated kill (Appendix C) rose from a reported 551 in 1932 to 52,054 in 1957 and, while the Wisconsin quail population fluctuated in this period, it showed a generally increasing trend with the greatest gains observed when the kill was the highest. This indicates little or no detrimental effect of sport hunting on quail numbers.

Winter weather. The relationship of winter weather to long-term trends depends on the interval under consideration. Schorger (1944) deduced that a series of mild winters from 1849 to 1853 contributed directly to the great increase of quail observed in that period, while a series of severe winters from 1853 to 1857 was correlated with a great decline of quail. The Prairie du Sac studies from 1929 to 1951 showed that in five winters characterized by having 3 or more inches of snow on the ground for 3 or more months, mortality ranged from 70 to 84 per cent, whereas in winters having snow on the ground for 1½ to 2 months the mortality ranged from 51 to 61 per cent. All of the years which showed heavy mortality had the severe snow or sleet conditions (Fig. 8 and Table 11). Thus we can safely conclude that any time a series of severe winters occurred in this region quail populations declined drastically.

The question then is whether or not there is a relation between some determinable and regularly re-occurring series of either mild or adverse winters and long-term trends in the quail population.

Schorger (1944) classified the winters from 1840 to 1900 on the basis of a range of conditions from "exceptionally mild" to "very severe". There were 21 years in which the winters were severe or very severe. Ten of these winters occurred within one year of each other, 6 within 2, 4 within 5, and 2 within 6 years.

Our Prairie du Sac studies provided a more precise measurement of the effect of severe winters on quail populations. These correlations form a series of peaks which superficially indicate cyclic trends (Fig. 20). However, a close examination of the length of the intervals between the peaks shows that they occur very irregularly and are related to the years of winter severity and not to time intervals, forming a series of the random oscillations described by Cole (1951). The interval in years between the six peaks in which losses exceeded 70 per cent ranged from 1 to 6.

The relationship between severe winters and high mortality at Prairie du Sac is similar to that reported for the state by Schorger (1944). The number of individual severe winters occurring in each decade of the periods 1840–1900 (Schorger's report) and 1929–59 ranged from 2 to 7.

The influence of other species. Our observations on other wildlife species were primarily restricted to the Prairie du Sac study area. The number of all species that might affect the bobwhite quail were estimated early each winter from 1929 to 1951 and are shown in part in Table 12. During this period ruffed grouse, pheasants, skunks and red fox increased

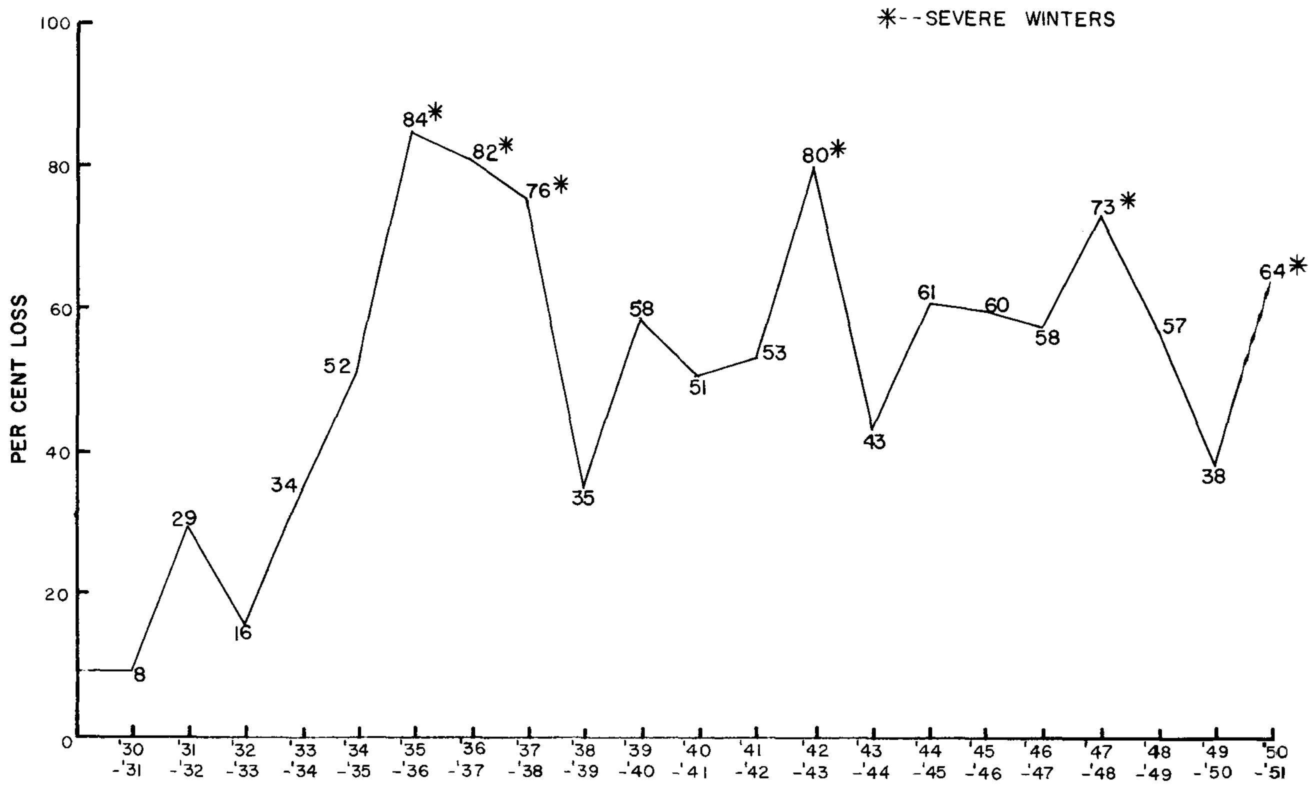


Figure 20. Annual winter loss (%) at Prairie du Sac showing the effects of severe winters, 1929–51.

steadily from the early 1930's to the 1940's then leveled off or decreased moderately.

There was no evidence of either long- or short-term effects of any of these species on quail. While we did not intensively study either the predators or competitors for habitat such as pheasants, our observations did not uncover any significant trends that might have resulted from the joint occupation of the area by quail and other species.

Errington (1945) speculated that the increase of pheasants or a combination of pheasants and ruffed grouse might have a depressing effect on quail populations. Our observations showed that both pheasants and quail frequently occupied the same coverts with no apparent conflict at least from the standpoint of quail density and survival.

The red fox population on the Prairie du Sac study area followed the same trend as was recorded state-wide. However, the quail-red fox populations trends here were different. For example, in 1958 both red foxes and bobwhite quail increased significantly in the state but at Prairie du Sac quail continued to decline.

Diseases. We failed to find evidence which indicated a specific need for disease studies. Field personnel of the Wisconsin Conservation Department routinely submit for autopsy any weak or dead wildlife specimens they find when the cause for the mortality or debility is unknown.

From 1938 to 1942 a total of 25 wild quail were autopsied (Hine, 1956). Seventeen of these showed some involvement with ulcerative enteritis, a common disease in game farm quail (Durant and Doll, 1941 and Kirkpatrick *et al.*, 1950). In 1950, 25 well-nourished quail trapped in Dunn County were autopsied. The usual incidence of parasites (Stoddard, 1931) was found, but no fatal disease-producing organisms were detected.

In other studies quail have been found to be susceptible to many parasites and diseases common to domestic fowl and other wild gallinaceous species, but mortality from these causes were considered negligible at all seasons (Stoddard, 1931 and Parmalee, 1952).

In 1957 we detected another instance of ulcerative enteritis in birds trapped in Waushara County for transplantation purposes. Sixty-seven quail were trapped and held for three weeks in a brooder house previously used for pheasants. In 1958 another covey was trapped in the same area, and one of the quail which otherwise appeared thrifty showed old intestinal scars presumably caused by ulcerative enteritis. The quail that died of this disease in 1957 during shipment or shortly after they arrived at the release point appeared to have become infected while in the holding pens or possibly had carried the disease without development of clinical symptoms until time of confinement.

Summary

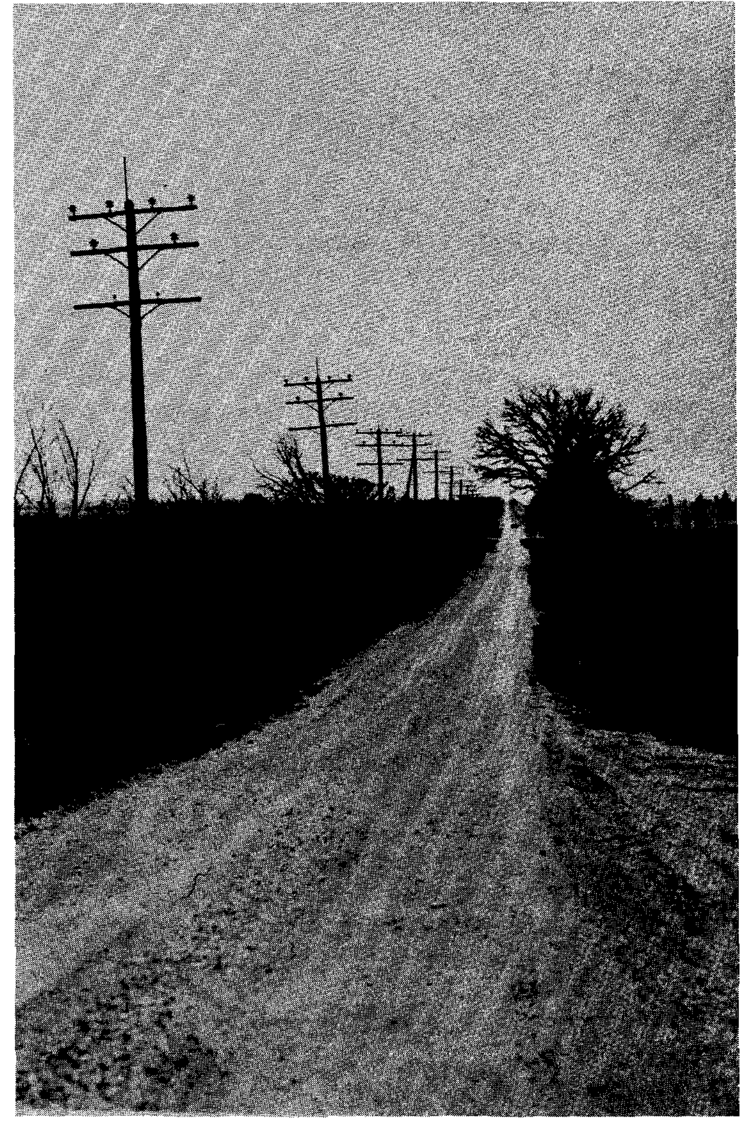
The same factors affect the long-term trend and the distribution of quail. Throughout the years from 1846 to 1960 adverse winters which occurred irregularly resulted in drastic reductions of quail populations but these effects were always temporary. Loss of hedgerow cover was directly correlated with the shrinkage of the occupied quail range from the mid-1850's to the early 1900's, and indirectly with quail disappearing in the southeast quarter of the state about 1900.

Quail populations on the Prairie du Sac study area are estimated at 1 bird per 2 acres in the mid-1800's, and were censused at 1 bird per 10.4 acres in the early 1930's and 1 bird per 20.9 acres from 1946 to 1950. The study area population collapsed in the late 1950's and in several other scattered areas, but state-wide it fluctuated around 1 bird per 20 acres in the better quail range. In 1958 following an extremely adverse winter, the fall quail population dropped to less than 1 bird per 40 acres and declined further in the winter of 1961–62.

Optimum range was created state-wide by settlement which featured a curtailment of fires, an expansion of agriculture and road building in the 1850's, and the simultaneous occurrence of mild winters which permitted a rapid response of quail to the improved habitat. Further expansion of agriculture after 1860 and roadside debrushing later resulted in hedgerow loss.

Quail populations were directly correlated with the amount of hedgerow cover present. A trend in cover loss was estimated for the period 1846–1931 for Columbia County and determined for 1931–58 on the Prairie du Sac study area.

Market hunting probably resulted in drastic reductions of quail populations in a few areas. Sport hunting at best has had a negligible effect on quail populations. There was no evidence whatsoever that predators, other game species such as pheasants, or diseases had a long-term, detrimental effect on the quail population trend except possibly in a few local areas.



Seasonal Losses

Rather than discuss the ramifications of all the various findings in the order presented in the Results Section, we elected to use this material to develop a dynamic life table (Deevey, 1947 and Hickey, 1952) based on a theoretical population surviving for a period of 28 months. This is followed by a discussion of the major factors affecting population changes for each season.

In our studies at Prairie du Sac we were able to census the quail population at all seasons of the year except between July and October. However, the loss even during this period could be computed from the July and early fall censuses with the aid of data from sex and age ratios and band returns. Also while we were not able to obtain seasonal trend information annually on clutch sizes and mortality in young birds during summer and early fall, we were able to get some usable information for this purpose from the Dunn County study area in 1948.

Life Table and Turnover

The average seasonal changes in a Wisconsin quail population are shown in Table 49. We started the life table with July 15, which approximated the average hatching date for the state-wide population, rather than with the start of incubation since we did not have data for this period. Losses were not computed for each group of birds hatching at different weekly intervals since our brood loss study was based on averages representing all classes.

The loss rates for all seasons are based on actual measurements. The instantaneous mortality rates (i) are computed from these losses and are expressed on a 1-week basis for the period. Observations were begun when broods became visible in the field at ages varying from 1 to 4 weeks. Pierce (1951a) and Klimstra (1950a) reported that mortality was highest in quail during their first 2 weeks of life, averaging about 4 per cent per week. However, since the difference in mortality rates between our studies and those of Klimstra and Pierce is small and the periods of study overlap, we used about 2 per cent per week ($i = .020$) as the rate of weekly loss from hatching to 4 months of age.

No attempt was made to set confidence limits to the figures in the last column representing survival because of the diversity of the data going into the table. We do not believe that any sampling errors in these values would change their reliability as far as their general biological importance is concerned. Similarly the loss rates are averages from data varying in quality and quantity. Knowledge of the November 15 to March 31 loss rate is nearly absolute, whereas our loss rates for July 15 to November 14 are based on data from one year and checked against other studies. Our computations suffice for a basic delineation of quail population mechanics, but it is recognized that some refinement could be achieved by additional data on juvenile losses in summer and adult losses in spring.

We wish to point out that when the instantaneous mortality rate (i) is applied in the estimation of quail mortality for any season, caution should be used to prevent overgeneralization. These rates were calculated from average seasonal losses. For example, the over-all average winter loss (November 15 to March 31) is 50 per cent. However, losses in the month of January greatly exceed those of any other winter month (Fig. 9.)

If population size and composition for any specific year are desired, adjustments should be made from information obtained in that year on winter weather conditions, fall age ratios and hatching dates. Usually this type of information can be readily obtained. For example, in Wisconsin, if adverse winter weather prevailed involving 2 to 3 months of unmelted snow on the ground, the loss rate for this period would be about 75 per cent instead of the average 50 per cent.

An adjustment has to be made also for calculating the fall population for any specific year if only the spring (April 1) population is known. As will be shown later the rate of summer gain and summer and fall loss is related to the spring density. The use of the average summer and fall loss statistic shown in Table 49 would result in either over- or underestimating the annual population.

Since the composition of our calculated population is based in part on age ratios, there should be an agreement with other data collected on sex and age ratio studies in this report. For example, in Table 49 the ratio of young to old quail in November (71 young and 11 adults) is 87:13 per cent young to adults. The collection of age data from hunting season bags showed 16 per cent adults, while winter results showed 15 at Prairie du Sac.

Based also on the computations in Table 49, our hypothetical population had 10 adult females on July 15 (37 per cent of 29) and 100 young for a ratio of 10:1. This, as would be expected, is a lower ratio than that obtained from brood data which showed an average of 13 young. However, the brood data excluded broodless hens. Therefore, the difference between the two ratios may provide a crude estimate of the number of adult females that failed to raise young. Apparently about 20 per cent of the adult hens alive in fall failed to produce a brood.

Additional survival series for quail from other studies are shown in Table 50. These series are on a year-interval basis, and are presented here for comparison with seasonal losses. To facilitate this comparison the instantaneous mortality rates (given for a weekly basis) are inserted for comparison with rates listed in Table 49. The higher turnover indicated by the Dunn County and Arboretum studies than by those at University Bay and Prairie du Sac may be due in part to sampling but is probably more related to movement. The Prairie du Sac survival values are based on corrections for egress of birds from the study area. The University Bay and Arboretum trapping results were not corrected for egress but were corrected for unbanded residue. The Bay results were, however, greatly affected by a high number of returns for one year, 1930–31, which showed 19 returns out of 125 birds trapped. We cannot account for the high returns of this one year. Generally the survival values and instantaneous mortality rates agree with the computations shown in Table 49, except that where no

TABLE 49

Dynamic Life Table for a Theoretical Wisconsin Quail Population From the Time of Hatching to Their Third Winter (Based on Prairie du Sac and Dunn County Studies)

Period	Age of Birds Lost (Months) (X)	Loss Rates	Instantaneous Mortality Rate (i) on 1-Week Basis (q_x)	Population Size: Before Loss* (l_x)	Birds Lost† (d_x)	Birds Surviving†
Average hatching date (July 18)		None		100	0	100
July 15–November 14	0–4	29%	0.020	100	29	71
November 15–March 31	5–8	50% of Nov. pop.	0.038	71	36	35
April 1–July 14	8–12	⊤ 17% of March pop.	0.012	35	6	29
		69%	0.037			
July 15–November 14	12–16	⊥ 63% of July pop.	0.058	29	18	11
November 15–March 31	16–20	50% of Nov. pop.	0.038	11	6	5
April 1–July 14	20–24	⊤ 17% of March pop.	0.012	5	1	4
		69%	0.037			
July 15–November 14	24–28	⊥ 63% of July pop.	0.058	4	3	1

*Applies to first date in Column 1.
†Applies to second date in Column 1.

TABLE 50

Wisconsin and Missouri Quail Survival Series (Winter to Winter) With Calculated Instantaneous Mortality Rates (*i*, weekly basis) Between Years

Area	Date	Survival Series					
		First Year	*i*	Second Year	*i*	Third Year	Fourth Year
Prairie du Sac*	1942–48	100	(.038)	14	(.05)	1	0
University Bay†	1927–32	100	(.034)	16.8	(.04)	2.2	0
University Arboretum†	1936–43	100	(.052)	6.8	(.06)	0.3	0
Dunn County (Buss 1948)†	1944–45	100	(.046)	9	(.06)	0.5	—
Missouri (Bennitt, 1951)‡	1939–48	100	(.033)	18	(.03)	3	<1

*Corrected for movement and untrapped residue.
†Corrected for untrapped residue only.
‡Based on calculations from age ratios.

correction was made for movement, the indicated mortality includes the egress loss.

The relatively high adult loss rate from April to November of 69 per cent of the April population or 63 per cent of the July adult population presents for the first time to our knowledge information on adult mortality in this period of the year, based on many years of censuses and banding. Previously, Buss *et al.* (1947) deduced that adult losses occurred primarily in spring and that those adults surviving to summer were highly successful in hatching and rearing broods, 13 young raised per brood. And Errington (1933) speculated that adult losses were negligible from March to November but that juvenile losses were high. Buss and Errington made their deductions from actual data on some population characteristics but lacked year-round observations. In a more complete three-year study, but one in which sample size was limited, Pierce (1951a) reported a summer loss of 54 per cent banded adults.

To our knowledge the only other investigation in which a bobwhite population was described on a year-round basis was that of Marsden and Baskett (1958) who reported an annual mortality rate of 82 per cent derived from age ratios from recaptured birds. This 82 per cent annual mortality is slightly lower than the 85 per cent for Wisconsin. Their extinction curve calculated from this same recapture data gave an annual value of 98.6 on their 2,240-acre area in Missouri. The difference in the two annual rates, 16.6 per cent, is ascribed to egress from the area. The extinction series shows the greatest loss rates in the months of November through January, June through July and the following September through December, but these authors did not explain whether the greater losses in these periods were due to increased egress or mortality. Their estimates are contrastingly different from our calculations for seasonal changes and we can find no explanation for the occurrence of the higher loss rates in the periods they reported.

It appears almost impossible to make any direct comparisons in the seasonal losses of bobwhite quail and other species, nor is it within the scope of this report to do this. However, some generalizations are warranted, and will be made only in connection with Wisconsin gallinaceous species.

No seasonal loss studies comparable to those for quail have been made on Wisconsin gallinaceous species other than on pheasants. One study is in progress and data are unavailable at present except for winter losses. Gates (1962) estimated losses of 40 and 25–30 per cent for pheasants for the winters of 1958–59 and 1961–62 respectively in the best pheasant range in Wisconsin. Wagner (1957) evaluated pheasant losses and concluded that summer losses were higher than winter.

Losses for other Wisconsin species can be only inferred from fall and winter age ratios and other limited data. Various studies showed the percentage of immature birds for the following species: Hungarian partridge, 77 (Hickey and McCabe, 1953); sharp-tailed grouse, 61 (F. N. Hamerstrom, Wis. Conservation Dept., in litt., July 1962); ruffed grouse, 80 (Dorney and Kabat, 1960); and pheasants, 72 (Kozlik and Kabat, 1949). Since game farm pheasants are liberated in all areas of the state except Milwaukee County, we are citing the percentage of immature pheasants for only this area.

In summary, the age ratios for Wisconsin pheasants, ruffed grouse and Hungarian partridge suggest a slightly lower annual mortality than that of quail. The prairie grouse age ratios indicate an annual mortality that is about 15 per cent lower than quail.

We have not attempted to make comparisons between seasonal losses in Wisconsin gallinaceous species and those in other areas because of the great disparity between species and environmental conditions in other areas. For example, Jenkins (1961) reported spring-to-autumn losses of Hungarian partridge in England ranging from 3 to 13 per cent.

The shrinkage of a quail population beginning with a fall

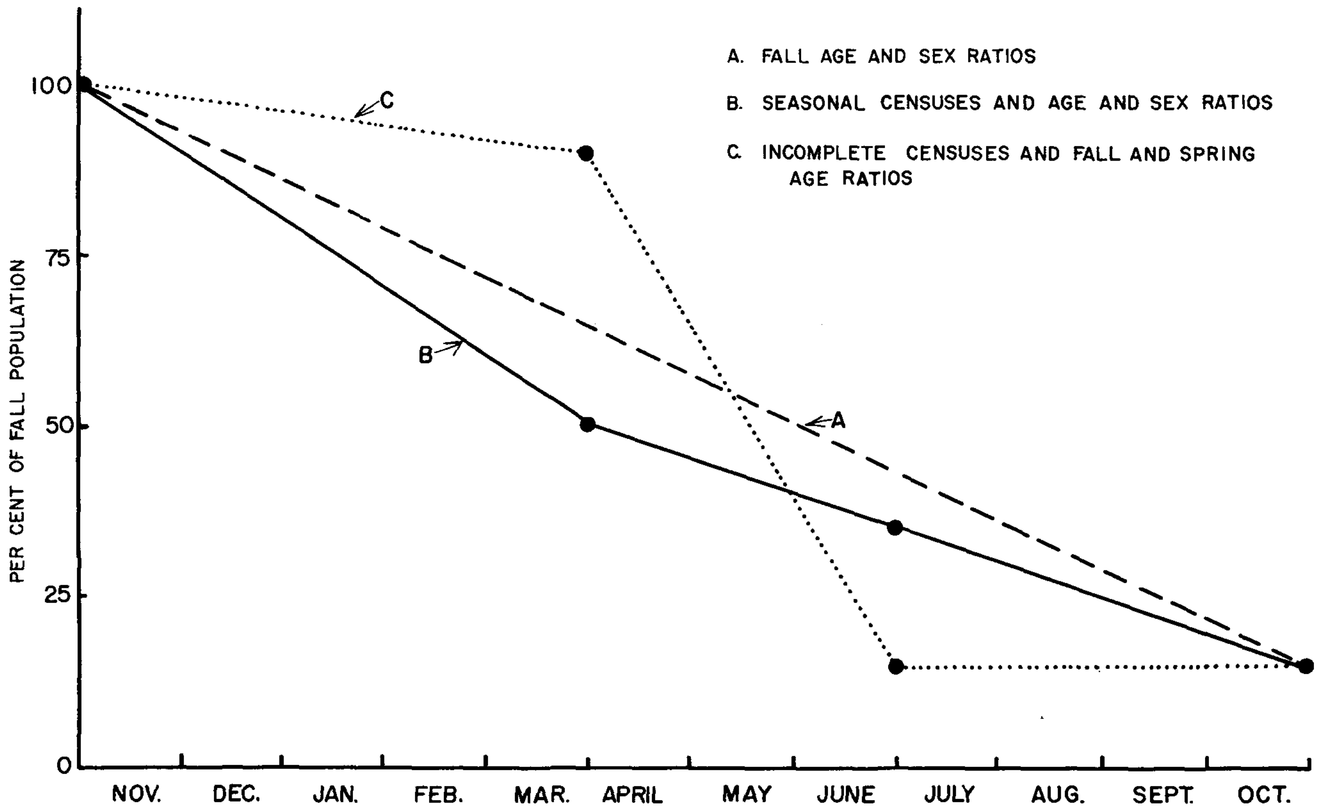


Figure 21. Shrinkage rates of a quail population based on different types of data.

population and based on varying quantities of data is diagramatically presented in Figure 21. These projections indicate the importance of obtaining complete seasonal data for interpreting population dynamics.

Major Factors Associated with Seasonal Losses

Winter (November 15 to March 31)

The average winter loss of 50 per cent based on 22 years of data was representative of a normal Wisconsin winter characterized by having 1–2 months in which the amount of unmelted snow exceeded 3 inches (Figs. 8 and 9, Tables 11 and 40). Losses less than or exceeding 50 per cent were directly correlated with snow conditions. Errington (1945) classified winter mortality clearly attributable to weather conditions as *emergency losses*. He also reported that there were a number of periods in certain winters where relatively heavy mortality occurred that was not associated with weather conditions. He classified these as *nonemergency* losses and related them to some unknown factors. In our intensive studies from 1942 to 1951 and extensive observations from 1951 to 1958 we were unable to find winters in which heavy losses were not directly correlated with weather conditions (nonemergency losses) (Table 11). Further, a detailed review of the winter mortality for each one of the years in the period 1937–51 (Fig. 8) led us to conclude that these losses were also due primarily to emergency conditions with two possible minor exceptions: those for 1943–44 and 1948–49 which will be discussed in the section on fluctuations.

On the Prairie du Sac area we found a number of coveys with relatively immature quail which succumbed totally or at least in part with the advent of the first spell of adverse winter weather (Fig. 8.) Such losses could only be detected when fall censuses were made early enough to determine that some coveys contained late-hatched young. Information on the statewide collection of quail showed that an average of 9 per cent hatched after September 1. (Table 16). The average early winter mortality resulting from late-hatched birds was 10 per cent (Fig. 9.)

The size of the fall population showed no correlation with the magnitude of winter loss rates that followed (Table 40). Small fall populations as well as large ones showed mortality rates consistent with the severity of winter. The significance of this will be explained in detail in the sections on fluctuations and management.

Spring to Summer (April 1 to July 14)

The average loss for adult quail in this period was 17 per cent (Table 49). We did not make any studies of the causes of this mortality except indirect ones on reproductive stress.

A number of causes reported in other studies obviously contribute to the mortality in this period, but with two exceptions they overlap the summer and fall season and these, together with our stress studies, will be discussed in the section immediately following this one and under fluctuations.

Two sources of spring mortality that do not overlap the summer period are cooler weather during early nesting and increased vulnerability to predation resulting when quail leave familiar habitat and enter unknown surroundings during spring movement. Adults nesting in May contribute one-third of the production of young (Table 16). During May, temperatures are lower than in June, and thus both embryos and hatching chicks would be expected to be influenced by this factor more in spring than in summer. This deduction is based on studies of other avian species conducted under controlled conditions. MacMullan and Eberhardt (1953), for example, found that while pheasant embryos in eggs, particularly in the early stages of incubation, withstood chilling quite well, no young chicks exposed to temperatures of 45° F. for 3 hours survived. While this factor might be directly responsible for fluctuations in young birds, the only impact on adults would be the stress of additional nesting efforts.

Since most birds, particularly males, move into unfamiliar surroundings during spring movement, they could be more vulnerable to predators during their whistling activities. However, we can assume that this loss is less significant than the loss of nesting birds to predation.

Summer and Fall (July 15 to November 14)

During this season a high mortality occurred among both adults and newly hatched young. The high nesting loss reported for such species as pheasants does not appear to be a significant mortality factor for quail. Rather, the primary factor influencing late summer and fall quail loss appears to be the physiological stress of reproduction.

We have determined a crude rate of loss for young birds and the month of occurrence but not the cause. Quantitative data on numbers or percentage of young birds dying in summer after they have left the nest are completely lacking. The types of factors that cause mortality are frequently mentioned in the literature, but only a few actual cases resulting from any one of these has been described. The causes of young bird mortality include: predation, particularly on newly hatched birds; diseases and parasites; lack of food and water in more arid states (Lehmann, 1953a); unfavorable weather conditions, and accidents, especially those due to farm machinery. These may be minor factors since none of the many field studies on quail mortality have reported conspicuous large-scale losses of young birds in late spring or summer. Nest losses were frequently cited (Stoddard, 1931; Errington, 1933b; Lehmann, 1946; Klimstra, 1950a; and Stanford, 1952) but here only eggs or newly-hatched chicks were reported destroyed.

Quantitative information on the major causes of adult mortality in spring and summer is almost as sparse as for young birds. While nest destruction is high, mortality to adults at the nest site during this period seems limited. Lehmann (1946), Stoddard (1931) and Errington (1933b) reported the following rates of nest destruction by natural predators: 51 per cent of 189 nests, 37 per cent of 602 nests and 16 per cent of 59 nests, respectively. In his studies Lehmann found 14 adults and Errington 1 out of 69 hens killed during nesting, but Stoddard reported that among mammalian predators only cats killed nesting adults and further concluded that sooner or later all pairs hatched young.

Loss of adult quail hens during nesting could be an important factor in spring and summer mortality if this species nested in hayfields with the same frequency as pheasants and Hungarian partridge. Gates (1960 and 1961) reported a minimum mortality of the spring breeding population due to hay mowing of 18.7 in 1959 and 27.5 and 15.6 per cent in 1960 on two different study areas. Only these two recent Wisconsin studies are cited because of the difference in hayfield phenology and mortality rates which are increasing as the machinery used becomes more destructive and the hay-mowing dates are advanced. While the destruction of pheasant nests in Wisconsin hayfields has always been high (Leopold, 1937 and Buss, 1948), mortality of hens during haying operations was lower in the past.

Hungarian partridge seemed to suffer the same fate in hayfields in the past as pheasants. McCabe and Hawkins (1946) reported that of 435 nests found 68 per cent failed to produce young, and that hay mowing was responsible for 53 per cent of the failures. They concluded that hay mowing was a major factor in holding down Hun populations in Wisconsin. However, hatching dates extended from May 21 to August 24 with a peak in late June. While past hay-mowing dates may have coincided with Hun nesting phenology, present haying operations are occurring earlier.

Studies of the use of different cover types for nesting by quail in Wisconsin are limited to those of Errington (1933b), who found 14 out of 69 nests in hayfields. Of these, 11 were destroyed during haying, but no adult mortality was reported. Klimstra (1950a) in Iowa reported on the distribution of 46 nests and failed to find a single nest in hayfields. Predators destroyed 58 per cent of nests but no adult mortality was cited. The Iowa findings are not strictly comparable to Wisconsin because the percentage of lands in hayfields is lower there.

It appears that adult quail have a much lower mortality during nesting than pheasants and Hungarian partridge, especially in hayfields, since quail nest over a longer period of time and have a hatching peak in mid-July which falls between hay-mowing periods. Furthermore, during the summer many types of vegetative cover are abundant for nesting and are preferred by quail, especially bluegrass both in Iowa and Wisconsin.

Therefore, although the percentage of adults killed during nesting could be significant, it apparently does not constitute a major segment of spring-to-fall mortality. This becomes all the more true when one considers that it usually is the hen that is destroyed during nesting, but that our data indicate a high loss of both sexes in summer. Interestingly, the advancement of hay cutting dates is becoming critical in pheasant survival but favorable to quail and probably Hungarian partridge which hatch later and over a longer period of time.

We did not study the cause of mortality in adult quail under controlled conditions, but we did conduct a pen study on the pheasant, a better experimental bird, to get an insight on the possible effect of reproduction efforts as a stress factor which directly or indirectly contributed to the high loss rate prevailing between mid-July and September.

The pheasant pen studies were based on the premise that weight changes reflect physical and physiological conditions. Then, since reproduction efforts or certain environmental conditions characteristic of seasonal changes are stresses that weaken species such as pheasant and quail, possibly they can be quantitatively evaluated by measuring weight changes. The results of these studies (Kabat *et al.*, 1950) showed that the weights of adult pheasants are lowest in summer and highest in late winter. Weight decreases were directly correlated with the number of eggs laid and with the stage of the primary wing-feather molt. The correlation between eggs laid and weight loss may be complex. Greeley (1962) in a study of calcium deficiency in hen pheasants did not find a relationship between weight loss and egg production.

Although there are some differences in the weight losses of quail and pheasants, both showed trends that indicated an increased physiological weakness in summer. Quail reached a weight peak in January, declined from February to April and then hens began to gain weight in May (Tables 27 and 28 and other authors). While we did not conduct a year-round study on the factors involved in the quail weight cycle, we believe that the reason their weights were proportionately lower in March and April than those of pheasants is related to the later onset of reproductive activity. Pheasants showed a weight gain during this period that was associated with an increase in fatty tissue. Studies of inherent weight cycles in pheasants by Breitenbach and Meyer (1959) showed that the amount of fatty tissue increases in late winter even when the birds are under the regime of a maintenance diet.

Other laboratory-type studies (Kabat *et al.*, 1956 and Greeley, 1953) showed that when pheasants were subjected to a starvation regime at all seasons of the year, they succumbed most rapidly in summer and their stress adaptation mechanisms were also at a low ebb in summer. Breitenbach *et al.* (1959) observed that hen pheasants which incubate a clutch and brood young have seriously depleted their energy stores and therefore are highly vulnerable to other stress factors.

Wagner (1957) tested the concept of the physiological weakness of pheasants in summer by analyzing available population data and concluded that summer losses were also high in wild pheasants under natural conditions.

Physiological studies in bobwhite quail have been limited to specific studies on the response of gonads in pen-reared birds to light treatments and the effect of simulated gunshot injuries on reproduction (Baldini *et al.*, 1952, Kirkpatrick *et al.*, 1952 and Kirkpatrick, 1959). However, their reproductive behavior, weight loss trend, molting pattern and population behavior indicate they are physiologically similar to pheasants. Therefore, the above explanation should apply to summer mortality in quail as well as in pheasants.

Short-term Fluctuations (Between Years)

The average population changes between seasons presented in the preceding section provide a general picture of the population status from season to season throughout the year. Great variation was observed in the size of seasonal populations and losses between years. The extreme differences in seasonal levels expressed as percentages of the highest levels for each season were as follows: early winter, 75, spring, 93, and early summer, 67. Fluctuations in losses were also high. Here we shall present an evaluation of the magnitude of the fluctuations for all seasons and their causes.

Losses

Winter

Winter population losses (November 15 to March 31) at the Prairie du Sac study area have ranged from 8 to 84 per cent and fluctuated at irregular intervals from 1929 to 1951 (Fig. 20). These data show that the interval between the peak losses was 7 and 5 years and between the lowest losses it was 6 and 5 years. Also there was a great amount of variation in the magnitude of losses for the interim years between peaks and troughs. The magnitude and irregularity of winter quail losses in other states was described in the Results under the section on Losses.

As was indicated earlier in this report (Table 11) and in other studies, the highest losses were all directly correlated with the months of unmelted snow. In two cases moderately high losses occurred in average or mild winters, 1943–44 and 1948–49 (43 and 57 per cent respectively). Possibly these two winter losses reflected a delayed impact of the previous winters, 1942–43 and 1947–48, which were very severe. Additional evidence on the possibility that severe winters may affect the subsequent population is shown in the state-wide transects (Table 6) which revealed a greater decline in the spring quail populations of 1952 and 1960 than would be expected since these periods followed two mild winters. However, these mild winters had been preceded by severe winters which may have stressed the birds sufficiently to create a physiological weakness which was transmitted to their progeny resulting in a higher winter mortality than was expected in the next two generations. A similar trend in the over-all state quail population was shown by the questionnaires sent to farmers by the Federal-State Crop Reporting Service. Nagra and Meyer (pers. communication) also obtained some evidence for a possible delayed effect of adverse winters in pheasants. They found the occurrence of a low stress resistance in second-generation progeny of adult hen pheasants which were artificially "cold-stressed." Further studies are being made by these investigators.

While winter losses are primarily associated with adverse weather, some additional though minor factors may contribute to the irregular fluctuations. Accidents, domestic animal depredations occurring when coveys feed in or roost near farm yards, and wild predators can occasionally occur in combination in some winters to create measurable losses, but we did not find any cases where these factors comprised more than a small percentage of the total mortality.

Infrequently the total winter mortality can be significantly influenced by late hatching (after September 1). About 10 per cent of the quail in Wisconsin hatch after September 1 (Table 16). The October to late December mortality of these juveniles from 1944 to 1948, as previously described in the section on "Hatching Dates", was almost 100 per cent. Data obtained in 1947 from a state-wide sample of hunter-killed birds suggest that the early winter loss of quail could have been as high as 19 per cent in this year. This estimate is based on the fact that the fall sample contained 19 per cent late-hatched birds but a winter-trapped sample showed no late-hatched birds.

No evidence of quail weakened by disease was found in the birds we trapped or observed during the entire Prairie du Sac study. However, it is possible that diseases might have operated as predisposing factors that weakened some quail, increasing the mortality rate in periods of additional stress such as those invoked by adverse winter weather. The finding of some ulcerative enteritis involvement described previously in quail trapped in another Wisconsin area suggests this possibility.

Each winter one or more of the coveys on the study area moved from a covert located in a site having adequate winter food to one having inferior habitat where the mortality rate was high. We do not know the cause of this movement. There was no apparent evidence of predator pressure, human molestation or shortage of food and cover. Usually the reverse was true; birds moved from inferior range to better habitat. There was no evidence of mass movements at any season of the year such as reported by Leopold (1931), although in some winters some coveys moved about three times as far from their fall coverts as did the more sedentary birds which ranged less than 440 yards. In the year 1946–47 for example, 4 of 10 coveys moved farther than average (Fig. 13). We consider this behavior as somewhat abnormal, but since the number of quail dying from these coveys was only moderately higher than from the coveys that remained in their fall coverts, the total winter mortality was not significantly affected.

Probably the strongest evidence we obtained to support our conclusion that both the peak and low winter population levels and the winter losses occurred irregularly lies in the fact that none of the population characteristics presented in our section on results indicated any pattern of relationship with the winter population changes. There were no indicated cyclic trends in the correlations between: the percentage of winter loss and summer gain (Fig. 15), covey composition and size, weights, movement and mortality. It is possible but not probable that winter population levels and changes might show cyclic trends if winter mortality caused by adverse weather were not such an important controlling factor.

Spring to Summer

Although almost half of the immature quail are added annually to the population in this period, we will discuss only adult losses in this section. Variation in mortality rates of young birds will be discussed in the following section since the peak of hatch is after mid-July.

Our information on adult losses from spring to summer (April 1 to July 14) is based on 6 years of data, from 1946 to 1951. The losses of adults ranged from 5 to 29 per cent (Table 13). Because we used two slightly different methods in getting the data from 1946 to 1948 and from 1949 to 1951 and because this is a relatively short period of study, we do not believe these data are sufficient to show any significant pattern of loss trends. We also believe that fluctuations in losses in this period should be proportional but of a lower magnitude to those occurring in the balance of the summer and early fall for which we have considerable data.

The major factor in spring-to-fall losses appears to be reproductive stresses that are related to density with their greatest impact on adult losses occurring after mid-July. Since these stress factors begin in late spring and continue to fall, we will discuss them under the section on summer-to-fall losses.

Spring losses from predation on birds moving into unknown areas after covey breakup and early nesting attempts would be expected to fluctuate. We would expect predation on pre-nesting hens and males to vary with their vulnerability and the abundance of predators and to be correlated with density. Birds engaged in mating season strife due to higher densities would be more exposed to predators. An abundance of nesting birds might also result in a higher numerical loss to predators, but not necessarily percentage-wise.

Seasons in which abnormally cool weather prevails might or might not have an increased effect on adult mortality during nesting. If cool weather results indirectly in renesting, such birds might be more exposed to predators. On the other hand late-nesting birds might escape the early flights of migrating avian predators.

In summary, lack of quantitative data leaves the question of fluctuations in spring adult mortality open to speculation. However, we showed (Fig. 16) that spring-to-fall losses of adults appeared to be density-related, since a highly significant correlation exists.

Summer and Fall

Although adult losses during summer and fall (July 15 to November 14) continued until an average of 63 per cent of the mid-July population was gone, these were compensated for by reproduction so that the total population actually increased. Errington (1945) classified the difference between the spring and fall population, which he expressed in a percentage, as *summer gain*. It would seem that summer gain would thus be the number of young produced and surviving to fall expressed as a percentage of the adults alive in spring. At the time of his studies information on adult losses in summer was not available. Actually summer gain is a term used by Errington to col-

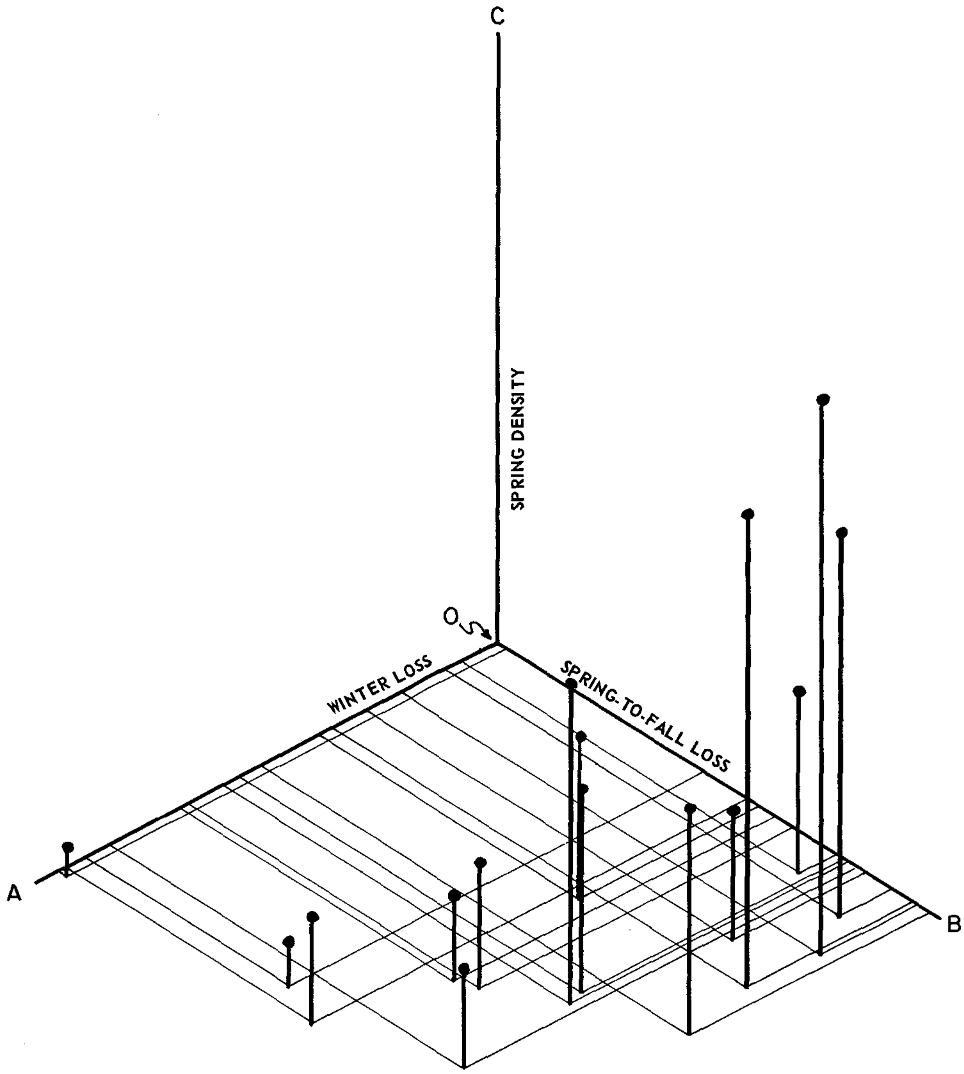


Figure 22. A three-dimensional representation of the relation between winter loss, the following spring density and summer loss for quail at Prairie du Sac, 1930–51. (Each pin represents one unit of relationships. To simplify the drawing, values which fell close together on the graph were averaged. Thus relationships for 11 of the 22 years were reduced to four pins.

The axes all commence at zero at the center point of origin with increasing values outward. Axis A is the percentage of winter loss, C the numerical value of spring density, and B the percentage of adult summer loss. The base of each pin is the ordinate for the per cent of both winter and summer loss. The length of the pin represents the spring density.)

lectively encompass all of the density changes that occurred in the period between April and November. In this section we will only consider adult losses. The contributions of adults and young to summer gain and other population relationships will be discussed later.

Adults. Spring-to-fall losses of adults fluctuated irregularly from near zero to 80 per cent of the spring population (Table 40). If the abnormally low losses for the years 1929 and 1937 are excluded, the range is from 40 to 80 per cent, with a mean of 66. In either case the variation is great.

The cause of this fluctuation is related to both winter losses and spring density which in turn are interrelated. We have previously shown that winter losses and spring density are inversely correlated and that spring density is directly correlated with spring-to-fall losses (with two exceptions which will be discussed later). This three-dimensional relationship is shown in Figure 22. Both winter losses and spring densities fluctuated irregularly. How these density-dependent factors affected spring-to-fall losses is our next question.

In the section on seasonal losses we have shown that the major factor in spring-to-fall losses appeared to be reproductive stress. Therefore, any factor or combinations of factors that would increase reproduction stresses (intensity of egg-laying and length of the periods of laying, incubation and rearing of young) would proportionately reduce the hens' resistance to direct causes of mortality such as diseases and predation. The physiological stress factors that increase mortality rates in cocks have not been studied. Possibly stresses related to prolonged and strenuous mating activities may be sufficiently exhausting to increase the vulnerability of males to direct mortality factors in this period. In both males and females a prolonged breeding season would delay the period of the recuperation to full strength beyond the season when environmental conditions such as food availability and weather are optimum for this process (Kabat *et al.*, 1950, Stokes, 1954 and Breitenbach and Meyer, 1959).

The obvious factors that could affect the reproduction phases are weather, diseases, predation, unfavorable habitat (this is also related to weather) and spring density. Since only spring density has shown a direct and highly significant correlation with summer losses, we have concentrated our studies on this factor through pheasant density studies on penned birds. Only the pertinent results of these studies together with related field observations on quail that might affect spring-to-fall mortality are presented here. These studies are completely reported in Appendix B.

It is important first to point out some basic differences between pheasants and quail before discussing the studies. The pheasant is polygamous and the quail monogamous. Bobwhite males often incubate clutches and brood chicks (Stoddard, 1931), while pheasant males do this only on rare occasions. Despite these differences, if population density affects breeding in gallinaceous birds, basic responses to this factor should be detectable in controlled experiments regardless of the species studied.

The pheasant studies showed that moderately high density stimulated intense fighting among cocks, but under very high density fighting decreased. The fighting response of cocks was very sensitive to density changes but their mating drive was unaffected.

Hen productivity and cock behavior was studied at two levels of density. Under the higher density hens laid more eggs at random, had a higher total egg production, started more nests and hatched fewer young and at later dates. Also cock fighting was so intense that dominant cocks at times killed inferior cocks. This over-all behavioral response to density resulted in prolonged breeding efforts constituting an increased physiological stress on the birds.

However, even under the most unfavorable habitat and density, some hens produced young. Dump nests (nests containing eggs laid by two or more hens) frequently were incubated, but the eggs had uneven-aged embryos and the hen sometimes abandoned the nest as soon as the first eggs hatched.

Although direct comparisons of the behavior of birds under high density conditions in pens cannot be made with wild pheasants and quail, field observations on these species have shown that similar breeding reactions have occurred in the wild (Stokes, 1954 and Stoddard, 1931). During our observations on movement and whistling activities we also noticed a great amount of antagonism between males, as did Stoddard (1931).

These studies strongly suggest that density through its impact on reproduction affects spring-to-fall losses. However, even though this relationship seems clear, it is important to analyze two other possible relationships that might modify density effects; these are delayed effect of adverse winters and a differential in the productivity of young and adult birds.

Summer-to-fall losses of adults fluctuated widely between years. The inverse relationship of winter losses and density-related summer and fall losses is clear with two exceptions. A severe winter would be expected to invoke a stress on the surviving adults and this theoretically could be reflected in the mortality rates of the adults and possibly their first generation progeny. However, the summer and fall losses following winters of high losses did not reflect the effect of stress in the first year.

Possibly there is a physiological response in quail that compensates during the summer and fall for any detrimental effects of a previous severe winter on the summer survival of the adults and their progeny (Errington, 1956). This may simply come about through elimination of inferior birds in adverse winters, leaving superior birds which have a high survival and reproductive rate. This reaction is then followed by relatively low production and survival occurring in the second generation following severe winters. This could result from the presence of a weakness in the offspring transmitted from the survivors of the preceding winter, which, although surviving, could not give their offspring full vigor. Such a complex combination of environmental and physiological relationships could delay the adverse effect of a severe winter on survival and reproduction, as may have been the case in 1950–51 and 1958–59 (Tables 6 and 7).

The pen studies on pheasants indicated that hens 2 years old and older were superior to 1-year-olds in most phases of reproduction. Superiority in the year-to-year survival of adults has also been reported in wild pheasants by Buss (1946) and McCabe (1949) and in ruffed grouse males by Palmer (1956), Bump (1947), Edminster (1947), Dorney and Kabat (1960) and Hale and Dorney (1963). Reproductive stress could be one of the factors involved in the superior survival of adult birds. Since older adults appear to be highly successful breeders, they should have a shorter breeding season and a lower reproductive stress than younger adults and presumably a lower summer mortality rate. Thus in years when spring density is moderately high and the adult carryover is also proportionately high, summer losses of adults could be lower than average.

This evidence from the field and from the pen studies, while speculative, suggests mechanisms that would modify spring density effects on summer losses of adults.

It would be difficult to detect fluctuations in the losses of adults occurring in any one time interval resulting from stress relationships within the period from mid-July to mid-November by field observations alone. The prolonged hatching period of quail indicates that if the mortality rate resulting from physiological stress for any one month of this period fluctuates more than for another, the magnitude of variation will be small. Ideally, field studies should be combined with physiological examinations of collected specimens. However, since this was not done in our study the only insight we can get at this time on the magnitude of fluctuations in mortality of adults occurring between July and November will have to come through extrapolation from the available data on censuses and age and sex ratios. The first step in this process is to determine what portion of the total 63 per cent summer and fall (July 15 to November 14) mortality of adults occurred in the first and second halves of this period.

Our fall samples of age and sex data and the information from such studies as Marsden and Baskett (1958) showed that there was little or no differential mortality in age classes from mid-September to the following spring. We also calculated an 18 per cent mortality rate for young birds from mid-September to mid-November (2 per cent per week, Table 49). Thus we deduced that since the adult mortality rate for this period appeared to be the same as that for young birds, 18 per cent of adults surviving from summer also died between mid-September and mid-November. Use of this value (18 per cent) together with information in Table 49, suggests that four-fifths of the mortality from mid-July to mid-November occurred before mid-September.

Further evidence to support the deduction that the adult mortality rate from spring to fall is highest between mid-July and September is shown in the following analogy. Fifteen per cent of the quail in the fall population are adults, of which 40 per cent are females. Therefore, for each living adult hen on the area in fall there are 14 juveniles. If each of these adult hens were equally responsible for producing the juveniles in the fall population, each would have to hatch and rear without any mortality all 14 juveniles. Since this is highly improbable even with adult males rearing some broods, a considerable number of adult females must die after they hatch their young.

While all adults had a high summer mortality rate, the female losses averaged about 33 per cent higher than the males. This is shown by sex ratio studies reported by numerous authors and by our own studies (Table 20) in which the males comprised about 60 per cent of the adult population. This difference could be accounted for in part by increased stress losses during the reproduction period. Losses during nesting from physical factors are significant and the effort involved in egg laying, incubation and brooding can be expected to be more stressful on hens than on cocks; thus a differential mortality of only 33 per cent is understandable. The above authors (Table 20) have also shown that this sex differential in adult mortality fluctuates between years. This added mortality in the adult hen would occur in the period when the summer mortality was highest. Thus we can conclude that fluctuations did occur in the period from mid-July to mid-September. Whether the fluctuations in adult mortality also occurred in early fall is more difficult to determine. However, it is expected that birds which undergo greater breeding-season stress in certain years would also have higher mortality in the following fall as well as in the summer.

Young. We and apparently other investigators as well lacked the facilities for obtaining enough data on broods during a successive series of years to observe actual fluctuations in survival rates of young quail in summer and fall.

The only quantitative reports citing mortality rates of quail in the post-hatching period are those of Klimstra (1950a) in Iowa, Pierce (1951a) in Mississippi and our own (Table 14).

The results of studies on the mortality rate and related population dynamics of immature birds of other species in summer are conflicting, but tend to indicate that considerable fluctuations do occur. Stokes (1954) on Pelee Island and Shick (1952) in Michigan, both in three-year studies, reported variations in the mortality rate of young pheasants of 7 per cent from hatching to October, and 26 per cent from hatching to September, respectively. And Gates (1960 and 1961) in Wisconsin reported a minimum summer mortality for two successive years of 32 and 29 per cent.

Additional evidence of geographical variation in mortality rates of young birds is found in Stokes (1954), who compared rates for pheasants cited by four different investigators. These rates covering juvenile mortality between 1 and 9 weeks of age were: 37 per cent in Iowa (Baskett, 1947), 44 per cent in Iowa (Errington and Hamerstrom, 1937), 12 per cent in Pennsylvania (Randall, 1940) and 22 per cent in South Dakota (Smith, 1950).

In studies on ruffed grouse, fluctuations in population levels have been attributed to variations in young-bird mortality in summer by Bump (1947:571–572) and to a lesser extent by Dorney and Kabat (1960) in Wisconsin. Siivonen (1952) reported that brood losses of tetraonids were highest in the years when populations were lowest. However, the reverse was true in the Wisconsin ruffed grouse study. Lack (1954b), Southern (1959) and Dorney and Kabat (1960) found evidence of young-bird mortality rates being linked to density. Late-hatched broods of the alpine swift, blackbird and great tit were observed to have higher mortality rates than those hatched early (Lack, 1956). However, Haugen and Speake (1957) and Reid and Goodrum (1960) reported that years characterized by late hatches of quail showed very high fall populations, indicating that at least in some years the mortality rate in summer of late-hatched birds is not excessive.

One source of variation observed in loss rate of juvenile birds is the degree of maturity attained by fall. From 1944 to 1948 we observed seven coveys of quail composed of juveniles which hatched after September 1. These juveniles suffered almost a 100 per cent loss between mid-October and late December as compared to about a 60 per cent loss of young in coveys composed of earlier-hatched birds.

Stokes (1954) observed a similar differential of loss rate in Pelee Island pheasants. He also reported that late-hatched pheasants weighed less at a given age than those hatched earlier. Juvenile quail whose hatching dates departed widely from the average hatching dates also tended to be lighter in weight at any given age (Thompson and Kabat, unpubl. ms.). The variation in the maturity of young arising from year-to-year differences in hatching phenology, intensified by the lower weight gains of late hatching, could thus give rise to annual fluctuations in juvenile mortality.

Since our data on summer loss rates of juveniles were limited, we were unable to make direct comparisons with other population data. However, we could compare two characteristics of the juvenile component of the quail population with certain adult population characteristics. In the first of these, state-wide hatching dates (Table 16) were compared with early summer density of adults (Table 6). The correlation was not significant ($r = 0.291$, with 0.553 required at the 5 per cent level). We are unable to state whether there was no relationship in these two characteristics or whether some other factors obscured a relationship.

Next we compared the percentage of juveniles in the fall population with summer loss rate of adults (Fig. 23). Although a high value of r (0.653) was obtained, with all points

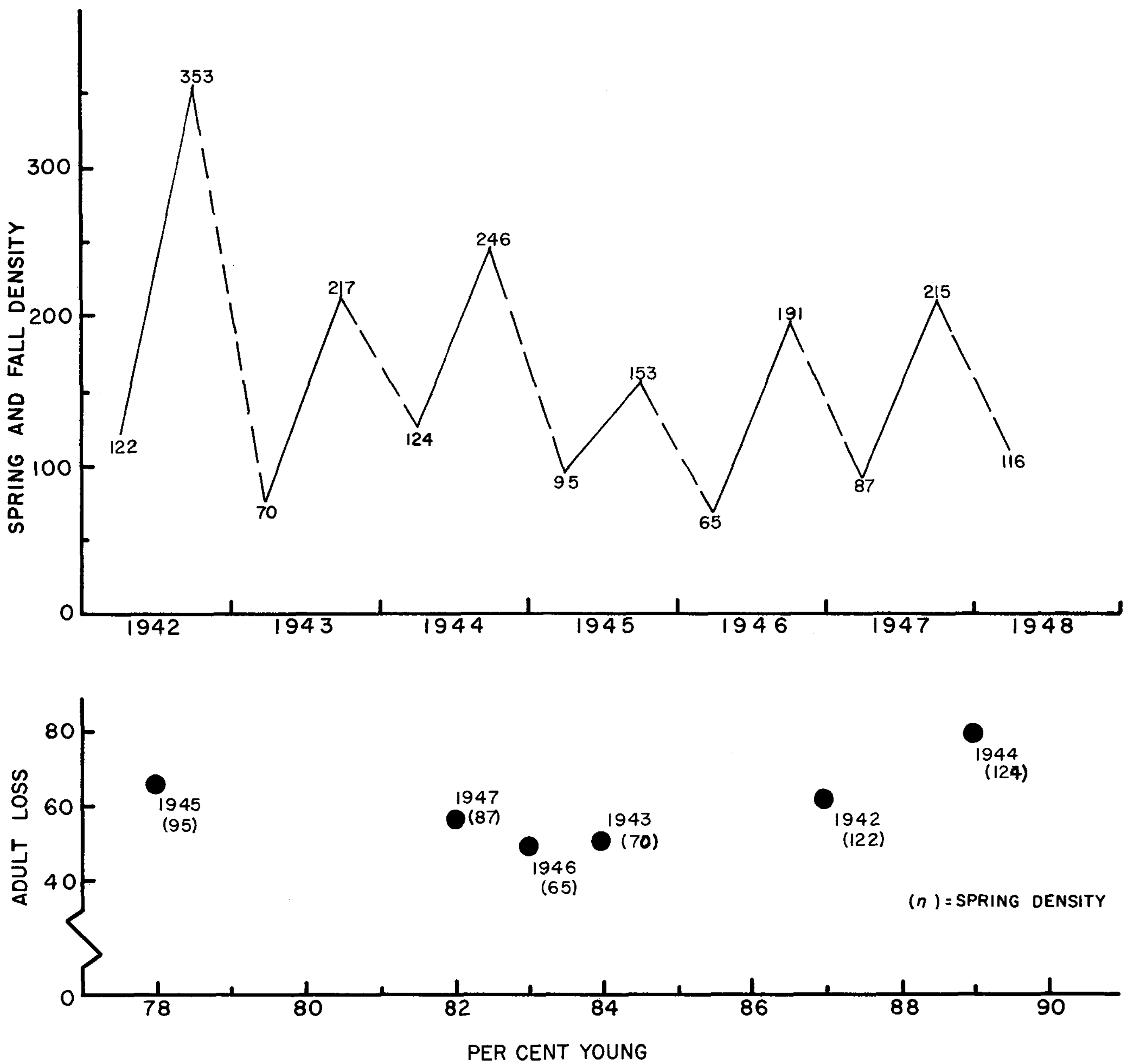


Figure 23. The spring and fall density, 1942–47, and the regression of the percentage of spring-to-fall loss of adults on the percentage of juveniles in the fall population (Prairie du Sac).

falling in line except 1947 (1945 omitted due to the small number of birds trapped), this was not a statistically significant value (0.878 required at 5 per cent level). This suggests that obtaining additional data might be worthwhile to further test this relationship.

If the positive correlation together with the positive summer gain is truly representative of quail populations, then a relatively high production and survival of young birds compensates for high adult spring-to-fall losses. This surmise is supported by the high percentage of young and the high rate of summer gain in 1942 and 1944.

Since spring density is so highly correlated with summer losses in adults, it is of interest to speculate on its relationship with summer mortality in juveniles. We have previously calculated that the adult loss between mid-July and mid-November is 63 per cent, of which 82 per cent occurs between mid-July and mid-September. Thus the density of adults is being significantly reduced during the time that young are being added to the over-all population, which further lessens the possible impact of adult densities on young-bird mortality. The loss of adults during this period also decreases the potential number of broods that could be hatched by any given spring population and this in turn reduces the opportunity for competition between broods. Further, since the summer loss of adults is density related, the breeding population level trends toward constancy from year to year .

The only evidence we had that disease might be a factor in the magnitude of spring-to-fall loss for quail was the finding of the intestinal enteritis involvement mentioned earlier.

Erickson *et al.* (1949) in Minnesota and Dorney and Kabat (1960) in northern Wisconsin found that the incidence of the blood protozoan, (*Leucocytozoon bonasae*) and nematodes (*Ascaridia*) increased directly with rising population levels of ruffed grouse. Adult pheasant hens which always show a low stress resistance in summer were found to be infested with bacteria (37%) of the *Salmonella* (paratyphoid) group in July but were free of bacterial diseases and blood parasites in winter (Kabat *et al.,* 1956). It is possible that a similar condition might exist in quail populations, but our studies were not designed to determine whether this factor was density related. Since quail are far more gregarious from fall to spring than ruffed grouse and pheasants, disease transmission should be simple and, while the potential disease organisms do not appear to affect winter mortality, they may decrease the resistance of adult quail in summer in proportion to the spring density. Also, weakened adults would be expected to produce inferior young.

Summer Gains and Relationships

As was the case with fall, spring and summer population levels and seasonal losses (Table 40 and Fig. 24), summer gains fluctuated irregularly. In Figure 25 we reproduced the regression of summer gains on spring density which includes data previously reported by Errington (1945 and 1957) and our own from 1943 to 1950.

The addition of our data on spring populations and summer gains for this eight-year period does not change the basic inverse relationship reported by Errington but the variation does increase. The inverse relationship is highly significant when analyzed either as a linear or nonlinear regression (Table 51). The central portion of the distribution appeared essentially linear but inclusion of extreme values produced a curvilinear conformation (Fig. 25). Inspection of the data suggested that logarithmic transformation would rectify the curvilinear regression, and this led to an F value of 37.8 as against the untransformed data which yielded 14.0.

At the lowest and highest spring population levels the summer gains fit the curvilinear regression very well. But, summer gains for the average spring population levels ranging from approximately 50 to 100 show considerable variation, 61 to 228 per cent. Similar density relationship and variation was found by Mosby and Overton (1950) in a five-year study during the period 1936–49 in Virginia. Kozicky and Hendrickson (1952), in their study on a quail population in Decatur County, Iowa, found that the regression of spring density and summer gain was not significantly correlated primarily because two years strongly deviated from the average. This variation indicates the degree to which the factors other than density operate at these spring population levels to offset in part or void the density effects at least for some years.

Several of the factors that could modify the direct effect of spring and summer density on summer gain have been discussed. These included: delayed effect of adverse winter weather, higher reproduction potential of adults (birds 2 or more years old), summer losses of adults (which, however, may be a cause and effect relationship), weather conditions during the hatching season and the relationship of hatching dates to survival. Further explanation on the role of density in suppressing summer gains is warranted.

First, some of the variation in summer gain for the average range of the spring population levels was probably due to chance sampling. Next it is apparent that since at average spring population levels the effect of increasing density is just beginning to be expressed, other factors such as weather conditions and disease could be more influential causes of mortality. The influences of summer weather conditions on density impact is difficult to determine, because of the great spread of time over which quail hatching occurs (May to October) and the inherent variation in annual climatic and other environmental conditions.

The peak of the behaviorisms of intolerance, cock fighting and harassment of hens by cocks would naturally occur at the highest spring density levels causing a maximum depressing effect on reproduction and adult survival. The manner in which density affects productivity has been observed and theorized in many reports. Kluijver (1951) speculated that quarrels may be a factor. Intraspecific conflict causes diffusion of males into suboptimal habitat (Collias, 1944 and Tinbergen, 1957). The number of territories is proportional to density, and there is an irreducible minimum territory size, which, when reached, precludes breeding by any additional birds (Kluijver and Tinbergen, 1953). Collias and Jahn (1959) studying a captive flock of Canada geese concluded that a loss of productivity was due to the birds resisting the crowded condition.

Density effects may be quite subtle. The presence of a large number of broods hatching simultaneously in a given area may cause some of the incubating hens to abandon their clutches. Linder and Agee (1963) found that in the presence of captive chicks, both in sight of them and in contact with them, wild hen pheasants did abandon their nests.

The rate at which these density behaviorisms potentially

TABLE 51

Statistical Analysis of the Regression of Summer Gain on the Spring Population of Prairie du Sac Quail, 1929–50

Method of Analysis	Regression Coefficient	Correlation Coefficient (r)	Regression Equation	F Value
Linear regression	—0.910	—0.641	$\dot{Y}=271.6—0.910\ X$	14.0†
Linear regression with logarithmic transformation	—0.804	—0.808	$\log \dot{Y}=3.75—0.814 \log X$	37.8†

†Values are beyond the 1 per cent level.

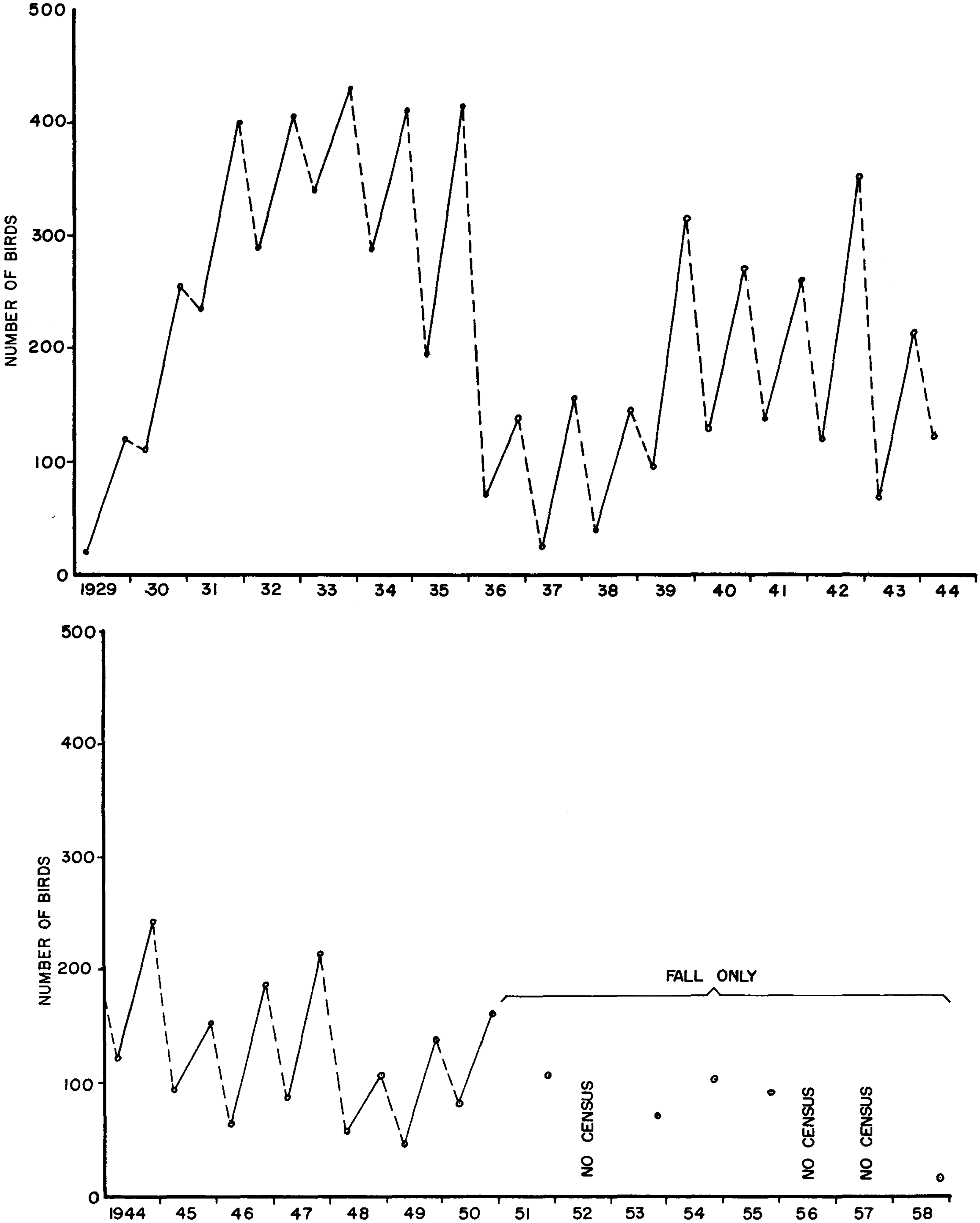


Figure 24. Fall and spring population censuses at the Prairie du Sac study area, 1929–58.

"build up" to affect both the mortality of adults in summer and the summer gain could also depend in part on the distribution of the birds and the accompanying environmental conditions. In some years all of the spring survivors on an area may be concentrated in one small part of it; under such conditions even a relatively low population could be subjected to high density conditions.

The amount and type of wind and rainy weather, and the longevity and intensity of periods of either high or low temperatures, which were observed to decrease male whistling activities, could modify straight density effects. Stempel (1960) observed that early whistling activity and high production were directly correlated. Thus it is expected that variation in summer gain would naturally prevail at the light-to-medium spring density levels of quail rather than be an exception.

Finally, the high reproductive gain that occurred at the relatively low spring levels in 1929, 1937 and to a lesser degree in 1938 at Prairie du Sac, may be reversed when populations are further decreased. The surviving birds may become so widely dispersed that the distance between them exceeds the range of spring movement since the natural tendency for quail in spring is to move at random from their wintering areas. To reproduce, quail must be able to find desirable mates during spring dispersal; thus the population must be high enough to provide this opportunity.

The Prairie du Sac study area observations that suggested these deductions are as follows: From 1957 to 1959, the spring population declined to about one-half of the relatively low 1929 and 1937 levels. Theoretically summer gains should have been very high, but the fall population for 1959 fell to 20 per cent of the 1929 and 1937 levels, and in 1960 it sank to zero. This indicated that the breeding potential failed to respond in the expected inverse density relationship. The spring population at these low levels was about 1 bird per 200 acres in contrast to the density of about 1 bird per 150 acres in 1929 and 1937. Further, there were more birds in the surrounding areas in the earlier years than in 1958 and 1959 providing a source of ingress. This prerequisite for facilitating breeding is an important consideration in making transplants of wild birds or liberations of game farm stock and illustrates the loss of reproduction potential at very low densities.

The quail transplantation experiments (Appendix D) support the hypothesis that breeding potential can collapse at very low densities. The disappearance of the birds in one area the first spring after release, and in the other within two to three years, suggests that as a result of spring dispersal the surviving birds failed to find acceptable mates and were unable to reproduce. These transplant populations which were very low in number should have scored a high summer gain but instead the reverse occurred.

Interrelationship of Factors Controlling Population Levels

Ideally the interrelationship between seasonal mortality, summer gain and fall populations should be analyzed on the basis of the number of young birds produced and the adults surviving in summer when the population is at the year's peak. Unfortunately such data are very difficult, if not impossible, to obtain. Therefore, the fall census and age and sex ratios which are relatively easy to obtain in November are used as the source of data for calculating summer gain and interpreting population mechanisms.

We have presented data showing that spring density was inversely correlated with winter losses, the percentage of spring-to-fall adult losses was directly related to spring density, and the percentage of young alive in fall tended to be directly correlated with the spring-to-fall loss of adults, although the latter correlation was not statistically significant. This interrelationship suggests that there may be a three-phase "built-in" mechanism in quail populations that makes them self-regulating. The operation of such a mechanism is illustrated in Table 52 for the Prairie du Sac area. It is important to note that the number of adults was very similar in all but one year while the number of young varied considerably. This indicates why adult density is not an important factor in the summer loss rate of young birds.

If the mechanism worked perfectly, the fall population would be relatively equal each year. However, we know that this was not the case because the fall population did not remain at a static level from year to year but varied considerably. Always there was an increase of quail during the sum-

TABLE 52

Population Changes Illustrating Quail Population Mechanics at Prairie du Sac

Year	Preceding Fall Pop.	Winter Loss (%)	Spring Density	Summer Loss of Adults (%)	Fall Population: Total Birds	Young: No.	Young: Per Cent	Adults: No.	Adults: Per Cent
1943	353	80	70	50	217	182	83.9	35	16
1944	217	43	124	79	246	220	89.1	26	10.6
1945	246	61	95	65	153	120	78.3	33	21.7
1946	153	58	65	49	191	158	82.8	33	17.2
1947	191	54	87	56	215	177	82.3	38	17.7
Avg.	232	62*	88	62*	204	171	84*	33	16*

*Computed.

mer at the Prairie du Sac area until their demise in 1958–59. The fluctuations in the fall population both at Prairie du Sac (Fig. 24) and state-wide (Table 6) were irregular and great. During the period of our 1929–51 studies (Table 40), the fall population fluctuated from a high of 433 to a low of 109, or a mean fluctuation of 172 per cent.

It should be pointed out that the high spring density of any one year only suppressed summer gain thus limiting the increase of the fall population over that existing in the previous spring. Fall populations always exceeded spring populations. Actually the correlation between spring and fall population was very high ($r = 0.898$) on the Prairie du Sac area. Kozicky and Hendrickson (1952) found a similar correlation on their study area in Iowa.

This density-related, self-adjustment mechanism was most effective when spring populations were either high or relatively low. At medium population levels other factors were apparently more influential than the density-related factors. This mechanism required about 3 years to bring low population levels to a peak under favorable conditions.

The direct relationship between the production of young birds and fluctuations in the fall population is very complex according to our studies. The proportion of young birds both on the Prairie du Sac area and in statewide fall populations was always relatively high and fluctuated considerably, 78 to 89 and 76 to 92 per cent respectively. Also there was a lack of correlation between the fall population levels and age ratios (Tables 6, 19 and 38). If the percentage of young in the fall population had been significantly correlated with the percentage of summer gain or spring density, this would have indicated a simple relationship. However, as shown in Figure 26 this was not the case at Prairie du Sac. Instead of the percentage of young birds in the fall population being directly correlated with summer gain, our data indicated a tendency for the percentage of young to be directly correlated with summer losses of adults (Fig. 23).

A study of the relationship of production and fall population levels on a larger area in Missouri showed results comparable to those we obtained in Wisconsin. Studies in 1939–51 by Bennitt (1951) led to the conclusion that there was an inverse relationship between the mid-July breeding population (call index) and the percentage of young in the fall population that was highly significant in Missouri quail. This correlation was contrary to our findings and indicated that either the population behavior and mechanics were actually different between the two states or that our results were

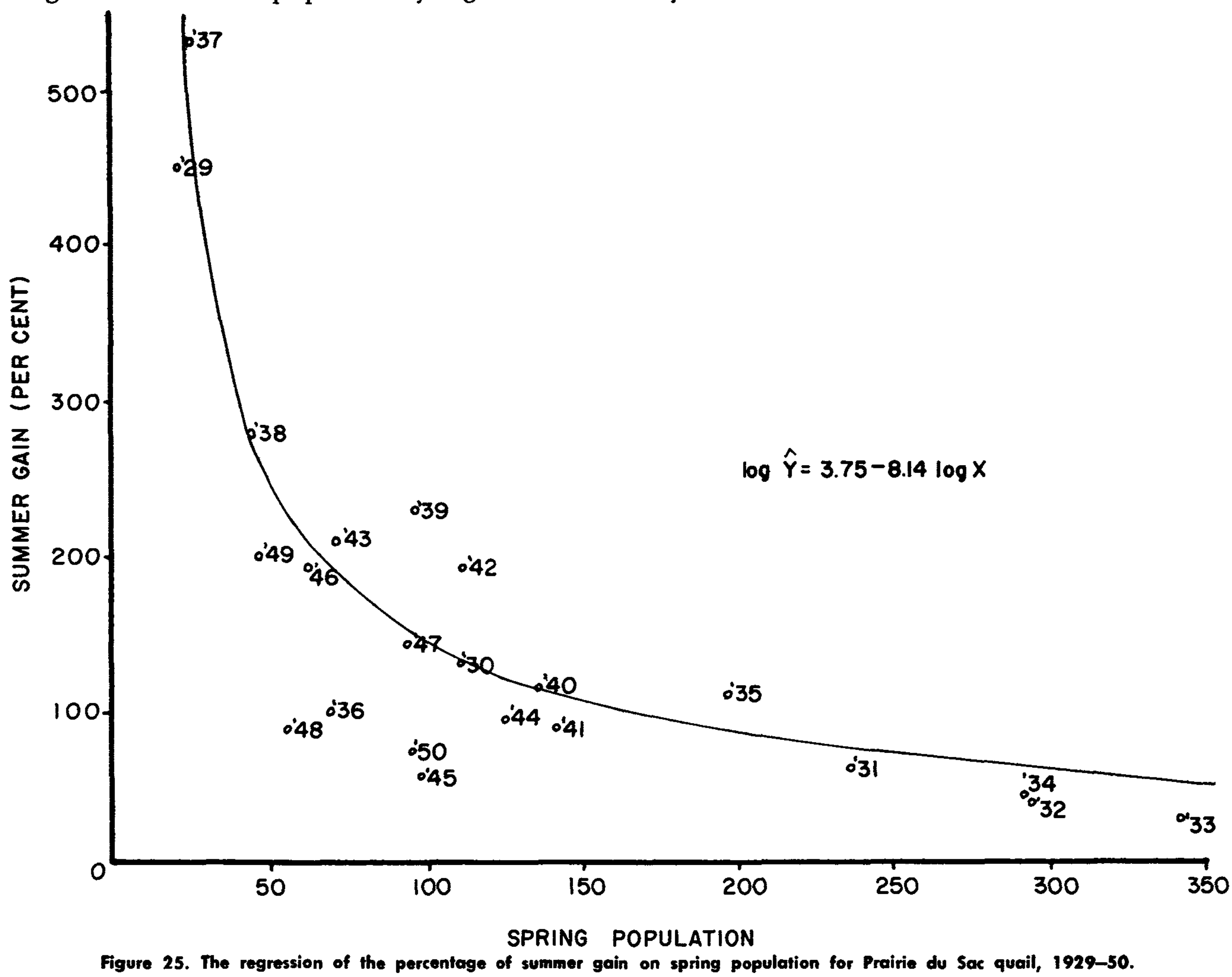


Figure 25. The regression of the percentage of summer gain on spring population for Prairie du Sac quail, 1929–50.

TABLE 53

*Missouri Quail Whistling Surveys (July) and Fall Age Ratios (November–December)**

Region	Call Index, Per Cent Young and Young Per Adult Hen						
	1950	1951	1952	1953	1954	1955	1960
Northwest	2.17	1.91 82 10.8	1.51 82 10.3	1.56 78 9.3	1.08 84 11.8	1.53 88 18.4	0.47 88 7.2
Northeast	2.38 80	2.35 81 8.8	1.70 82 9.0	2.09 80 9.1	2.12 82 11.4	2.74 87 15.4	1.19 88 14.4
Western Prairies	2.51	2.32 81 10.6	1.61 79 8.3	1.74 77 7.7	1.32 80 9.0	1.46 84 12.0	1.07 87 13.2
Western Ozark Border	2.86	2.93 75 8.6	1.87 74 8.0	1.21 74 6.2	0.96 78 8.8	1.41 86 13.8	2.1 89 13.6
N. & E. Ozark Border and Lowlands	1.83 80	1.91 73 6.8	1.81 76 5.4	1.68 78 7.9	1.20 82 11.0	1.59 87 16.4	1.44 82 9.4
Ozark Plateau	2.27	2.34 73 7.6	1.53 70 5.7	1.77 69 5.3	1.30 80 10.0	2.45 86 13.2	1.94 80 7.8
State Call Index	2.15 80	2.25 77 8.7	1.64 77 7.8	1.72 76 7.6	1.38 81 10.2	1.95 86 14.4	1.37 84 10.8

***Unpublished data supplied by Jack A. Stanford, Missouri Conservation Commission.**

spurious. However, additional studies of Missouri quail from 1951 to 1955 and 1960 (Table 53) substantiated the results obtained at Prairie du Sac. These data showed absolutely no correlation between the call index and fall age ratios. The years showing the highest and lowest call indexes had near identical percentages of young birds and young-to-adult hen ratios. There was no apparent difference in the density of the populations sampled for the years reported by Bennitt and Stanford.

The reason why fall age ratios frequently are not correlated with breeding population density may be the result of adult mortality in summer being density related, but young bird mortality seems to be related to other environmental factors which were previously discussed. However, the productive potential of adults, at times, can also be directly suppressed by unfavorable environmental factors. Lehmann (1946a), Stanford (1953a) and Stempel (1960) reported that in 1942, 1952 and 1953, and 1953 and 1955, respectively, adults hatched few young because of drouthy conditions.

Stempel also found in his Iowa study that in the two years in which production was low, the percentage of young was high in one and low in the other.

Since our detailed population data were obtained for the period 1942–47 at Prairie du Sac and 1945–51 at Dunn County, it is of interest to consider the projection of the relationship of adult mortality rates in summer and spring density relationships on the former area to the period from 1929 to 1942 when only census data were available. The spring population in the years for which we have sex and age ratio data (1942–48) ranged from 57 to 124. These population levels are numerically low for the study area when compared to those for the early 1930's. However, on the basis of a unit of available hedgerow cover, as was pointed out in the section on fluctuations in spring losses, the spring population of 124 for 1943 which was the highest in the years of our intensive study is comparable to the approximate 300 level of the early 1930's. Thus, since adult mortality rates were high in all the years intensively studied, it is logical to expect that this was also the case in every year during the period 1929–50 except possibly in 1929 and 1937. In these latter two years, the summer gain was so high that it could have occurred only as the result of very low adult mortality rates, high reproductive rates or more birds entering the area than leaving it.

Because all of our studies on the relationship of spring density to summer gain were based on natural events, we decided to determine the recovery rate of quail through an "inversity" reaction from a deliberate reduction of the winter population. In the winter of 1949–50, we removed 182 or 48 per cent of the quail from the Dunn County study area. The removal simulated a relatively large winter loss or a heavy hunter harvest over and above that which naturally occurred. Censuses of the fall population in 1950, the year following the removal, showed a density that was approximately one-third lower than that of the previous year. This is a moderate decrease compared to the number of birds removed together with the natural loss in the previous winter and does indicate

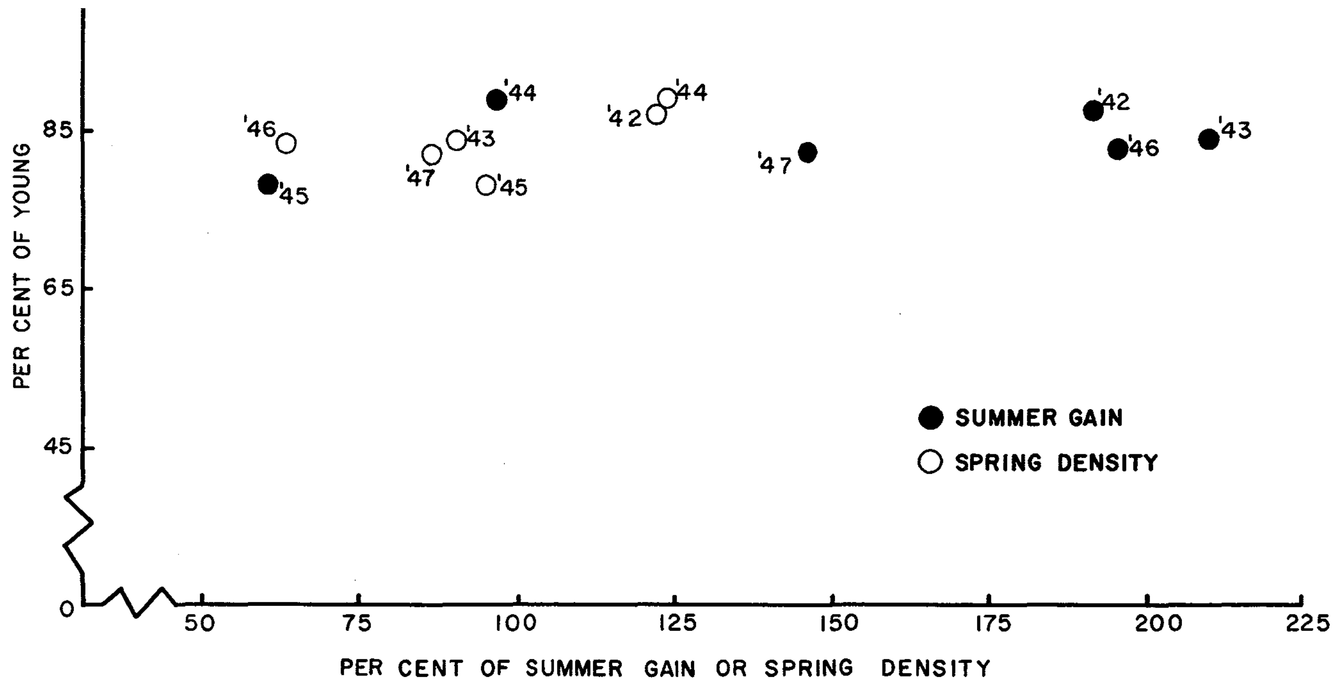


Figure 26. The relationship between the percentage of summer gain and spring density with the percentage of young (Prairie du Sac).

an "inversity response". On the other hand the age ratios for the following year showed 86 per cent young, a change of only 2 per cent between years which was not statistically significant. Thus while spring density and summer gain showed an inverse relationship, the percentage of young in the fall population and spring density again failed to show a detectable correlation. The relatively rapid fall population recovery at Dunn County substantiated the Prairie du Sac findings on density relationships.

General Fluctuations

In this section we will first briefly compare the status and fluctuations of quail with four other Wisconsin game species. We will then present some views from the literature on fluctuations in other wildlife species, and finally re-emphasize some of the points of the preceding discussion on the nature and basic causes of major fluctuations in the Wisconsin bobwhite quail population.

Fluctuations in the population levels of five Wisconsin game birds are expressed in a simplified manner in Table 54. There appears to be no synchrony of fluctuation between species, nor even similar direction of trends in abundance. This is not surprising when we consider some of the commonly known factors that affect the population levels of these species.

In 1931–35, quail and prairie grouse were at a peak level and the other three species were down. Pheasant and Hungarian partridge populations were just becoming established after being introduced into the state in the previous two decades. Quail habitat was at its best.

From 1931–35 to 1956–60 the habitat of all species except ruffed grouse was in a process of relatively rapid deterioration. The openings required by prairie grouse were rapidly closing from natural plant succession and tree planting, a situation which has now reached the stage where both species are maintained only because their habitat is being preserved through a special management program. Prairie grouse now exist in islands of specifically preserved habitat.

The quality of quail habitat in 1955–59, though not as critical as that of prairie grouse, reached a low. However, the new low in Wisconsin quail populations is due primarily to the severe winter of 1958–59. Actually if it had not been for this one winter, quail might have reached their highest population level since the 1941–50 levels because of a long series of mild winters that preceded the killing winter.

Drainage of wetlands which contain good nesting and roosting cover and earlier hay cutting has continued to reduce the quality of habitat for pheasants and Hungarian partridge. The institution of the Soil Bank, a program which resulted in the retiring of 733,082 acres of cropland in Wisconsin, compensated for some of the detrimental impacts of the drainage and earlier hay-cutting programs. In general the range of ruffed grouse in 1955–59, though not as good as in the earlier years, still appeared to be able to carry a large population of these birds.

In view of the dynamic nature of changes in the habitat of these species and the weather patterns that affect them in varying degrees, we would expect fluctuations to be irregular rather than periodic or synchronized. The occurrence of unfavorable weather either in winter or spring can counteract the impact of favorable habitat. Conversely, the impact of a relatively unfavorable habitat can be reversed or altered by favorable weather.

Throughout the preceding sections of this report we have presented data which have shown that quail are not cyclic in their population fluctuations. In some ways a statement of this type seems almost heretical considering the various views expressed on this subject in the literature. A few pertinent references illustrating these views, most of which were taken from "A Symposium on Cycles in Animal Populations" in *The Journal of Wildlife Management*, January 1954, follow.

After about two decades in which the populations of several wildlife species were reported as being cyclic, Palmgren (1949), Cole (1951 and 1954), and Lack (1954a) questioned the existence of synchronized fluctuations and, if they did exist, whether or not they could possibly be caused by any extrinsic factors. Palmgren appeared to be the first student of populations to propose that the reported cyclic trends were random fluctuations. Cole then showed mathematically that these cyclic trends could be random oscillations, serially correlated. Hickey (1954) re-examined some of the cyclic reports and concluded that only the lynx exhibited cyclic trends at the continental level and ruffed grouse on a local level.

Other investigators disagreed that such a simple explanation as Cole's random oscillations could account for the many observations on cyclic trends: Rowan (1954), Errington (1954), Moran (1954), Siivonen (1948, 1952, 1954 and 1957), Siivonen and Koskimies (1955) and MacLulich (1957). Both Moran and MacLulich believed that other factors such as birth and death rates, density and time have to be considered together with population levels to determine whether a population is cyclic.

Fortunately in our study we were able to obtain data on both population levels and population characteristics to utilize in determining whether bobwhite quail were cyclic. Neither population levels nor various characteristics showed any cyclic tendencies. Instead, fall population levels were directly correlated with spring density which in turn reflected winter losses caused by adverse weather. The impact of spring density modified by other factors was on the summer loss of adults.

How misinterpretations could result from lack of sufficient data is illustrated in Figure 24. Fall population levels from 1937 to 1950 reached a peak almost every third year. However, an examination of the entire series of years studied from 1929 to 1958 shows that, if anything, these were random oscillations, serially correlated.

If the irregular fluctuations in population levels and other characteristics occurred only at the Prairie du Sac study area, some concern might be in order in attempting to project the findings to the behavior of the state population. However, state-wide data on quail in Wisconsin (Tables 6 and 7) and in Missouri (Table 53 and Bennitt, 1951) show trends similar to those observed at Prairie du Sac. The agreement of intensive study results with information on the more general state-wide population fluctuations sustain the observations obtained on our study areas.

TABLE 54

Population Estimates of Five Wisconsin Game Birds Based on Their Rank in Hunting Season Harvest*

Period	Ruffed Grouse	Prairie Grouse†	Pheasant	Hungarian Partridge	Quail‡
1931–34	5	1	6	5	1
1935–39	6	3	5	3	3
1940–44	4	2	1	4	2
1945–49	3	–	4	6	4
1950–54	1	4	2	1	5
1955–59	2	5	3	2	6

*Obtained by averaging the kill for each interval (except for quail); 1 = highest, 2 = next highest, etc.
†Sharp-tailed grouse and prairie chicken combined.
‡Based on censuses.

It is possible that other species of wildlife such as the ruffed grouse at Cloquet (Marshall, 1954), which has shown some tendency for cyclic trends, cannot be compared to quail because quail are extremely sensitive to the climatic and habitat vicissitudes occurring in Wisconsin. On the other hand, Wisconsin ruffed grouse have not shown the same regularity as the Minnesota grouse, and spring population levels have fluctuated considerably less than fall populations (Dorney and Kabat, 1960).

If adverse winter weather were the factor that masked cyclic trends in quail, populations in more southern climates then might reveal such trends. Quail survival rates did appear to increase moderately with milder climate as indicated by the age ratios reported for Missouri and Florida by Bennitt (1951), Marsden *et al.* (1958) and Murray *et al.* (1957). These authors together with Stoddard (1931) did not report any cyclic tendencies in the quail populations they were studying in their states. However, Stanford (1960) in a popular article merely reported quail population peaks in 1939, 1949 and 1959 as evidence of a possible cyclic behavior but gave no further explanation.

This section can be logically closed with a brief re-emphasis on some major factors affecting population levels. The first concerns the relationship between spring and fall populations.

Since spring density and summer gain were inversely proportional, one might not expect that spring density and fall population levels would show a high correlation. Actually the reverse was true. There are several posible explanations for this relationship. The following seems to be most plausible.

Spring population levels have always been low enough to invoke high summer gains which raised the fall population level above that of spring. Apparently the reproductive capacity of this species is great enough to produce a population increase except in local cases of extremely low production and poor adult survival. This appeared to occur at Prairie du Sac from 1958–59 where habitat losses became so extreme that the population's adjustment mechanisms finally failed.

It is important to reiterate at this point of the discussion that while density relationships were involved in modifying population levels, the only factor that was observed to drastically reduce quail numbers in any one year was a very severe winter.

Another correlation, and as far as habitat management practices are concerned perhaps the most important in fall population relationships, was that between the area quail populations and the miles of hedgerow cover. Generally we expected that fall quail populations would be proportional to the spring density of adults and that year-to-year changes in the amount of hedgerow coverts would be reflected by increased winter losses. This expectation was based on the assumption that hedgerows were not required as cover except in winter. This was not the case. Fall quail populations showed a direct relationship to the amount of existing hedgerows. However, as hedgerow cover decreased, the summer gain no longer restored the fall population to the levels reached in years when this type of cover was more abundant.

The correlation of the number of coveys on the study area in early fall with hedgerow cover indicates that this type of habitat previously considered as winter cover is also required in late summer and early fall (Table 43). Quail coveys were found in summer and early fall in only those areas where hedgerow cover was adequate for winter protection (Figs. 17 and 18). The apparent dependence of quail in Wisconsin on hedgerow cover at all times of the year explains the rapid decrease in quail populations when habitat deteriorates and points to hedgerow cover as a long-term type of limiting factor on summer gains and "inversity response".

Summary

A dynamic life table based on average seasonal changes was developed from data obtained primarily from the Prairie du Sac and Dunn County study areas and secondarily from statewide populations. By obtaining data on the population for one or two seasons of the year it is possible within limits through the use of this table to estimate the population for any other season.

Average seasonal losses of adults expressed as a percentage of the birds dying from one season to the next were: 69 per cent from spring to fall (April 1 to November 14), 50 per cent from fall to spring (November 15 to March 31) and 17 per cent in spring (April 1 to July 14). The loss of young birds from the time of hatching to mid-fall was calculated to be 29 per cent.

The ranges in the percentage fluctuation in seasonal loss rates were: for winter to spring (November 15 to March 31), 8 to 84; spring to July (April 1 to July 14), 0 to 68; and spring to fall (April 1 to November 14), 4 to 80. The calendar intervals for which the losses are stated correspond approximately to natural periods in the bobwhite's life history.

Fluctuations in quail population levels and loss rates were irregular and great for all seasons. For example, at the Prairie du Sac area from 1929 to 1951, the variation in population levels expressed as the percentage change between the highest and lowest levels was 75 for early winter and 94 for spring. The early summer population level based on whistling counts showed a 100 per cent change.

Many factors were responsible for fluctuations in seasonal population levels and loss rates, but only a few were found to be dominant. The effect of these factors may be direct and simple, or complex and interrelated.

Winter losses were caused primarly by adverse weather and fluctuated directly with the number of months the ground remained covered with snow depths exceeding 3 inches. Losses ranged from as low as 4 per cent in winters having less than 1 month of snow cover to 80 per cent when there was a ground cover of snow lasting 3 months. Early winter losses which consisted primarily of late-hatched birds reached as high as 19 per cent (1947), but averaged 10 per cent.

While severe winters resulted in a lower spring density, they did not directly affect the survival of adults in the following summer. However, the population levels for the fall of the second year following the occurrence of severe winter losses in 1947–48 and 1950–51 were abnormally low, indicating the possibility of a delayed depressive effect.

Spring population levels fluctuated with winter losses, and summer population levels of adult quail fluctuated directly with spring densities.

No specific factors causing fluctuations in spring and early summer mortality were detected, but field observations on quail and controlled pen studies on pheasants indicated that the higher the breeding population density the more prolonged was mating-period activity, a condition which led to lower brood production in pheasants. Prolonged breeding constitutes an additional stress on birds that may not result in an increased rate of spring mortality, but may contribute to higher summer and fall losses later. This stress effect results specifically from an increase of fighting between males, harassment of hens by cocks, hens laying many eggs at random before laying them in nests and promiscuity in nesting behavior. The end result of this abnormal behavior is climaxed by later hatching, and the hatching of fewer and smaller clutches.

The positive correlation between fluctuations in summer losses of adults and the spring density indicated that the effect of prolonged breeding did result in higher summer and fall mortality rates.

The causes of fluctuation in the summer-to-fall losses of young appeared to be more complex than those for adults. There was no correlation between the percentage of young in the fall population with spring density and summer gain. Apparently young birds were more vulnerable to other environmental factors than to factors related to spring density. This is indicated by late- and early-hatched broods which were smaller and weighed less in fall than those produced at average dates. Late-hatched birds also had a very high mortality in fall compared to juveniles which hatched at average dates.

During all of the years of our intensive studies the population level in fall always exceeded that of the previous spring, suggesting a simple relationship. But the degree to which the fall population exceeded the previous spring density was not based on a simple relationship, because generally the percentage increase between spring and fall (summer gain) was inversely proportional to the spring density. Factors associated with high spring densities suppressed summer gain and those associated with low spring densities stimulated it; at medium spring population levels, however, other factors compensated for much of the density effect, resulting in marked deviations above and below the expected pattern. Further, when the spring population decreased to the very low level of about 1 quail per 200 acres, density effects appeared to be completely eliminated, and the following fall population level declined below that of the previous spring. This decline was attributed to the spring dispersal behavior of quail which were at such a low density level that there were too few birds present in any one site to permit an opportunity to breed. This appears to explain why very low density populations disappear and why the stocking of areas with small numbers of wild birds fails.

The interrelationship of winter losses, spring density, summer and fall loss of adults and summer gain composes a self-adjustment mechanism that controls quail population levels in conjunction with the influence of climatic and habitat factors. Apparently when spring density levels reach the height where intolerance between existing birds significantly affects breeding behavior, summer gains are suppressed and the fall population levels off. Conversely, when the spring population level is low due to heavy winter losses, density effects are removed and the full reproduction potential of quail is attained, resulting in a high summer gain and an increasing fall population. This is the reason why, under favorable environmental conditions, low populations can recover to high levels in a period of 3 to 4 years, and why high populations do not keep increasing to infinity. This interrelationship also shows why it is possible to harvest surplus birds without reducing the breeding population to the extent that populations will decline in successive years of hunting.

MANAGEMENT

While the primary purpose of this section is to highlight the basic findings of our entire study, it is designed to trace through all of the steps required to manage not only quail but certain other wildlife species as well. Management programs for any wildlife species are generally directed in two ways: toward the population and toward the habitat. Before proceeding with the more detailed portion of this section, it is necessary to consider some basic premises concerning the possibilities of, and the justifications for, managing quail in Wisconsin.

Wisconsin lands have provided a sufficient amount of cover and food to sustain a significant shootable population of quail. The question now is, can quail continue to survive under the current pressure of land use on the existing habitat? To answer this question we must first examine our knowledge of habitat requirements.

Studies of winter survival indicate that while food supplies are limited in severe winters, they are generally ample in mild and sufficient in average winters. Cover in the form of brushy hedgerows has been found to be directly correlated with quail density and therefore is considered as being the main limiting factor of quail habitat. It has been generally decreasing since the late 1800's. The rate of loss of hedgerow cover and the impact of this on quail up to 1936 could only be estimated. From 1936 up to the present date we were able to measure this habitat change and correlate it with a decline in the quail population on the Prairie du Sac study area.

From this correlation we are able to calculate a value for the miles of hedgerow required to sustain a quail covey under the habitat conditions prevailing at Prairie du Sac. This value together with a basic knowledge of quail population behavior provides information which shows how quail can be managed on a sustained basis. The problem remaining now is to develop the mechanics for preserving and increasing hedgerow cover in a practical program.

Justification for a Quail Management Program Based on Hedgerow Development

Consideration of the primary management program for quail, involving preserving and establishing hedgerows in agricultural areas, raises serious concern over its practical aspects. First of all we must evaluate just what could be accomplished if it were possible to conduct a successful hedgerow management program.

If we were able to preserve the remaining hedgerow cover at the 4,500-acre Prairie du Sac area and restore 50 per cent of the amount lost, which would be a reasonable goal, our best estimate of the fall quail population resulting from this effort would be 200 birds or about 1 bird per 20 acres. This means that the average farm of 150 acres in this area would have on it 1 covey containing about 17 birds in 1 out of 2 years. There would be very few farmers that could be expected to carry out the effort required to increase the amount of hedgerow on their farms for this type of reward alone.

Under existing conditions of land use, the maximum quail population that could be expected under even the most successful habitat restoration project in the best Wisconsin quail range would be 1 covey per year for each 150-acre farm.

Fortunately hedgerows provide other benefits than for quail alone. The question is, do the additional values outweigh the disadvantages to an extent that they can be realistically advocated as a form of land management?

Brushy hedgerows provide habitat for many forms of plants and animals including insects, rodents, game birds, mammals, and songbirds, as well as plant disease organisms, etc. Some forms of these are beneficial, others are harmful. They usually occupy the same hedgerow simultaneously. Often one or the other predominates depending on location, age, composition of the plant species of the hedgerow, and the use to which adjacent lands are put.

The brushy hedgerow therefore can be both desirable and undesirable, depending on the interest under consideration. In the following subsection we will discuss many of the pros and cons of hedgerows on rural lands. It is not our purpose to present a complete analysis or literature review of this subject since this was not the objective of our study. Rather we will present a list of the most important considerations relating to hedgerows and a few basic references concerning them.

Pheasants and Hungarian Partridge

The quantitative importance of hedgerows to these two upland game species has not yet been intensively studied. The primary limiting factor in the pheasant habitat of Wisconsin is permanent herbaceous nesting cover consisting of hay, abandoned weedy fields and wetlands (Buss, 1946 and Gates, 1960). While pheasants and Huns both use hedgerows for roosting and for nesting when they are available, the question of whether they are indispensable or not remains to be answered. At Prairie du Sac there are only a few small scattered marshes and generally little other herbaceous vegetation to provide winter cover. It is common knowledge that pheasants are present in local areas within their occupied range in winter only if some form of cover is available. A minimum of from 20 to 80 pheasants have been observed using hedgerows at Prairie du Sac at one time or another each winter from 1939 to 1950. Therefore, we must conclude that hedgerows are a necessary feature of pheasant habitat in this area. Although this pheasant habitat and the resulting populations in this area are classified as only fair, nevertheless pheasants do provide interest and incentive for some recreation by area residents.

Cottontail Rabbits

Probably the cottontail rabbit among all upland game species receives the greatest value from brushy hedgerows. While grassy and weedy fields are selected for nesting sites where a choice is available, shrubby hedgerows also frequently contain nests (Friley, 1955). This author also found that 70 to 80 per cent of the "forms" found on his study area were near escape cover which included brush. During the winter when the ground is covered with snow, brushy areas in uplands provide the only available escape cover other than burrows and piles of material such as rock and wood. Bruna (1952) found a density of 1 rabbit per acre in fall on the best Kentucky range characterized by abundant cover and permanent pasture. Smith (1950) in New York found 54 per cent of 279 winter rabbit dens located in hedgerows and brushy fencerows.

Unfortunately it is very difficult to express quantitatively the value of brushy cover to cottontail rabbits. In a half-mile-long roadside hedgerow at Prairie du Sac, from 1 to 8 rabbits or a maximum of 13 per acre were observed during several winters incidental to our quail studies. This is one example of the use of hedgerows by rabbits. Whether these rabbits were produced in the hedgerow or in adjacent fields is immaterial. The important point here is that this habitat feature was a necessary component of the range since it was the only winter cover available.

Breeding habitat requires a combination of nesting, feeding and escape cover. An 80-acre study area in Iowa (Linder and Hendrickson, 1956) having such a combination of cover produced about 1 rabbit per acre. This production figure was based on the number of rabbits that safely left the nests. Naturally the majority of these nestlings would die before the following winter when heavier cover was predominantly used.

The damage to orchards, gardens, truck and field crops caused by rabbits is a problem to be reckoned with in managing habitat for this species. In general the permission given to landowners in Wisconsin to hunt rabbits on their land at any time has provided a satisfactory means of dispensing with this difficulty when it arises.

Other Game Species

Ruffed grouse and their broods are commonly found in hedgerows when this cover type is located near woodlands. Edminster (1947) emphasized the importance of shrubby borders along woodlands adjacent to farm fields in habitat improvement for ruffed grouse. Hedgerows are used by squirrels and by deer to cross open farmlands; they also harbor woodchucks which create many holes for rabbits (Petrides, 1942). Hedgerow maintenance or development would be particularly valuable in southwestern Wisconsin, where deer and ruffed grouse are relatively abundant, to extend the woodland habitat generally found only on steep slopes and in river bottoms.

Songbirds

The great number of songbirds that occupy hedgerows have two recognized values, the esthetic and the economic. The esthetic value received by people from hearing and seeing them is noncontroversial and real. While we might be able to get along without the song and appearance of songbirds, it is doubtful that Americans would concede this. Generally the songbirds that occupy hedgerows are not destructive.

The economic vaue of many songbirds is a controversial subject. They are recognized as great insect-eaters. The question is, if sufficient habitat were available, to what extent could songbirds control harmful insects compared to pesticide applications? Dambach (1948) found an average density of 29.0 pairs of breeding birds per acre of shrub field borders or 45.4 pairs per 100-acre farm in Ohio. He further calculated that the breeding songbirds and their progeny on this area could theoretically consume about 8,700,000 insects, which exceed the number of insects that over-winter in crop fields and borders. However, no study has been conducted during summer on the actual consumption of insects by songbirds and quail together. Other workers have reported a few instances where insects were controlled sufficiently by songbirds to permit crops to be grown economically without resorting to an intensive insecticide program (Cottam and Uhler, 1950 and Kalmbach, 1952).

The real economic value of songbirds in controlling insects remains to be determined. Few Wisconsin farms have fencerows totaling an acre even when scattered shrubs in the vicinity of dwellings are included in the total. If we consider the esthetic value together with whatever insect-control benefits accrue, songbirds have to be considered an important contribution of hedgerows. Without hedgerows, it would appear that songbirds on farms would be greatly reduced.

Small Mammals

Generally the species that occupy hedgerows such as the white-footed mouse and short-tailed shrew are beneficial. In contrast, grassy field borders provide habitat for the destructive field mice. The damage caused to all agricultural crops by field mice (*Microtus* spp.) is well known (Hamilton, 1940 and others). Dambach (1948) in Ohio reported that 88 per cent of the mammals found in bluegrass sod are known to be injurious to crops whereas these species compose only 25 per cent of the mammals present in shrub borders. Petrides (1942) in a New York study found no field mice in his studies of 15,900 feet of hedges, while Linduska (1950) reported that grassland field borders support more injurious small mammals than hedgerows.

Insects

In recent years great concern has been expressed by some conservationists and health authorities over the increasing use of pesticides to control insects. At the same time the production of agricultural crops requires efficient control of insects, and this at least for the time being necessitates chemical treatments. While many studies have been conducted to show that with proper use insecticides are generally not harmful to wildlife, the long-term and particularly indirect effects of chemical treatments of crops may be highly destructive to wildlife (Rudd and Genelly, 1956). Ideally, biological control of insects would avoid such problems as these. Thus, while in the past only limited consideration has been given to this method of controlling insects, significant efforts are being turned in this direction now (Poznanin, 1954; Briggs, 1960 and Fleschner, 1960).

Generally, hedgerows adjacent to grain and forage crops contain more beneficial insects than do field borders composed of grassy and broad-leaved species, but the opposite may be true for truck crops and orchards (Dambach, 1948). Crop damage by destructive insects found in hedgerows is sporadic depending on the occurrence of various conditions. For example, in 1959 migrating aphids which carried the virus that damaged Wisconsin oat crops settled in hedgerows. However, this sporadic condition alone does not justify the destruction of hedgerows (R. J. Dicke, pers. communication).

Hedgerows composed of a variety of shrubs present an almost constant source of flowering plants required by the all-important pollinating insects. However ,the importance of the flowers of shrubs to bees has not been quantitatively measured in Wisconsin. Pollinating bees use those shrub species with pithy stems such as sumac (*Rhus* sp.) for cell nests where the plant materials they gather are stored (J. R. Medler, pers. communication and Bohart, 1952).

While sufficient information on the precise relationship of brushy hedgerows to insects is lacking, the important point is that the available knowledge as indicated above shows that the relationship can be at times very beneficial to agricultural and horticultural crops.

Rights-of-way

Brushy hedgerows along rights-of-way can provide wildlife cover, esthetic value and also reduced roadside maintenance if located sufficiently far from roads to reduce or eliminate problems resulting from vision obstruction and drifting snow. Naturally such hedgerows would have to consist of species that develop a dense low growth of good ground cover in order to provide reasonable protection against erosion and at the same time decrease tree encroachment. Such sites can generally be found along sloping road banks, roadsides with wide shoulders and under communication and power lines. On the latter sites, shrubs can effectively prevent tree encroachment. An effective right-of-way maintenance program based on this principle was developed by Egler (1949). The treatments involved a combination of selective chemical application to kill trees and to permit the growth of desirable shrubs. This program also has application along roadside rights-of-way, and is generally very beneficial to wildlife.

The Wisconsin Highway Commission has informed the Interagency Working Group of the Wisconsin Natural Resources Committee of State Agencies that low-growing, self-maintaining brushy growth could be an important substitute for grassy rights-of-way along roadsides if the proper shrub species were available. Grassy roadsides require expensive mowing operations, hence the interest in low-growing, self-maintaining shrubs (Aten, 1960). Hedgerows along roadsides, if composed of the right shrub species and properly located can have windbreak values and also serve as living snow fences (Edmin-

This roadside hedge, left for wildlife under a selective brush control project, will benefit upland game birds and mammals, songbirds, and pollinating insects, as well as provide esthetic and soil and water conservation values.

ster, 1938 and 1939). Such a program would have to be carefully planned, but the effort required to fully exploit this possibility in view of the potential benefits is highly justifiable.

Soil and Water Conservation and Farm Operation

Hedgerows when located along field borders can serve as windbreaks for reducing soil erosion and for water conservation by trapping wind-driven snow which would otherwise end up in drifts along roadsides, farmyards and in other unwanted sites, and holding it to melt in the fields (Harper, 1937). In some cases the right kind of "living fence" can be used as a livestock barrier.

Some of the objections to hedgerows are that they appear to take up considerable space, require maintenance and handicap equipment operation. Hedgerows vary greatly in width. In the early 1930's, when quail reached their highest density level in the history of the Prairie du Sac study area, hedgerows averaging 12 feet in width occupied 1.4 acres out of each 150 acres of land with approximately half of this shrubby cover being located along roadsides. Since the field borders between fenced fields which contain only vegetative cover occupy 2–4 feet of space anyway, hedgerows can hardly be considered as wasting too much cropland, particularly if some form of incentive reimbursement is provided to the landowner for the nominal loss of tillable acres.

There isn't any question that hedgerows inside the boundaries of a farm at times have serious nuisance value. They frequently must be removed to allow the establishment of strip crop and contour-strip layouts. However, for the most part, the "nuisance" hedgerows have already been removed. Further, brushy cover need not be confined to hedgerows. It can be allowed to remain or be established on woodland edges, streambanks, gullies and in any other place where it does not interfere with normal farm operation. Line fences are other places where hedgerows will provide valuable wildlife cover and simultaneously create only a minimum of interference to farm equipment operation.

In addition, the shading effect of hedgerows has to be recognized. To reduce shading effects, tall-growing shrubs and trees would have to be controlled in hedgerows.

Conclusions

In view of the many possible benefits derived from the presence of hedgerow cover, it seems clear that the advancement of a program for preserving and restoring hedgerows is highly warranted.

In agricultural areas, for the most part, hedgerows have already been removed. If the remaining hedgerows were adequate to support populations of wildlife comparable to those of the mid 1950's, a program aimed at preserving these hedgerows could reasonably be undertaken. Unfortunately, this is not the case. The number of hedgerows currently in existence in many areas is so low that the loss of only a small additional percentage could result in the extirpation of quail.

What can be expected in the state-wide quail population is indicated in the history of cover loss at Prairie du Sac. During a period of only 8 years, from 1951 to 1959, the Prairie du Sac population collapsed. The cover loss required to bring about the collapse amounted to only an additional 15 per cent over that which occurred from 1936 to 1951. This indicates that wherever the extent of cover loss is comparable to that at Prairie du Sac, and other factors being equal, quail will disappear. Along with the quail will go other species of wildlife, songbirds, and beneficial insects that are dependent on hedgerows.

When we consider what has happened to the quail in Wisconsin where we have a record of the cause and effect relationship of hedgerow cover, we can understand why a winter such as that of 1958–59 could take the disastrous toll that it did. Periodically many wildlife species are drastically reduced by the occurrence of very unfavorable weather. But, as long as favorable habitat exists they rebound to their previous levels within a few years. However, we cannot expect that the next upswing of wildlife populations from the present low will bring about a recovery that will even begin to approach the peak reached in the period of 1951–59. Thus there is no alternative to launching an all-out campaign to preserve existing hedgerow cover and to restore at least some of that previously lost if we are to regain any semblance of former quail populations.

There is even more at stake than saving and increasing wildlife on farmlands for esthetic benefits and other values described in the previous section. Sport hunting alone is recognized as an economically important source of income to the state.

In the past, several wildlife species were greatly favored by land-use practices. At the present time, however, there are few areas of the state where the recent population levels of wildlife species are not threatened by current land-use practices. The exception includes only the southwestern part of the state and even here woodland grazing by cattle should be greatly curtailed. Waterfowl habitat is diminishing at an alarming rate, particularly in the breeding areas of the United States. The growth stage of vegetation in the forested area of the state is generally unfavorable to the forest game species. Fortunately deer and ruffed grouse populations, still relatively abundant in Wisconsin compared to many other states, can be stabilized at present levels, but this will require a coordinated wildlife and forest management program (Wisconsin Conservation Department, 1962).

It is still possible to stop the downward trend in wildlife populations and even bring about increases. But, this can be done only through the activation of a total land-use program designed to mutually benefit forest, agricultural, and wildlife production.

Some of the key factors concerning quail population management, specific habitat requirements, and methods of habitat restoration for quail will be presented in the next sections.

Population Management

In Wisconsin as in many north central states, thorough consideration has been given to the questions of whether quail could stand a hunting season, stocking would increase the population, refuges had any value, and restocking with wild birds was beneficial. Only a brief discussion will be presented here on the pros and cons of these questions.

Closed Seasons

The reasons for closing hunting seasons on any wildlife species vary, but generally they center on an observed drastic decline. The decline may be the result of unfavorable weather conditions, over-shooting and habitat deterioration. The reason for the 1896 closing of the Wisconsin quail hunting season probably involved a combination of drastic winter losses and habitat change although the importance of the latter was probably not recognized as to its full role in the decline of this species at that time. Similar reasons were involved in the closing of the quail hunting season by 1917 in four out of the eight north central states listed by Leopold (1931). Of these four states, only one that had a reasonable quail population remained closed in later years. This was Ohio where a considerable effort was initiated in the mid-1950's to open the season (Allton, Stickel and Dustman, 1957).

At one time (1860–70's) prior to Wisconsin's closing, commercial hunting was a factor in the decrease of quail, but hunting was not closed until many years later.

Up to the 1930's when many states began to conduct surveys and studies on quail and other game species, the closing of hunting seasons seemed like the ideal method for solving the problem of low populations. Up to a point this belief was valid. Good citizens, who realized that game populations were declining, felt that something had to be done and decided that closing the hunting season was the simplest action that could be taken. The pitfall of this kind of action was that it salved the public into thinking that all they needed to do now was sit and wait until the affected species made its recovery.

The many observations and studies that have been made in the last three decades have shown the danger of this approach in contrast to accepting the complete responsibility of managing a given species. While short-term declines can be related directly to adverse weather, the long-term decline is caused by habitat deterioration. Once a hunting season is closed, the real reason why the species declined and what needs to be done about this frequently receive little attention, particularly when there are other species which are more popular to hunt. Thus habitat continues to deteriorate until the point is reached when nothing within practical limits can be done to perpetuate it. As long as the affected species has hunter interest, at least some efforts are made to improve its welfare.

The closing of quail hunting seasons involved another factor which is unique for this species. Landowners and ornithologists put a high premium on the esthetic value of quail. Since the bird is primarily produced on private land, it was natural that a landowner would not want to see "his birds" hunted. Unfortunately the habitat requirements of quail are such that the modern practices of good farming are not sufficient to restore cover. Deliberate practices have to be carried out to provide habitat for quail. These techniques which require the participation of all people will be described in the following sections.

It is now well known that the annual mortality (70–90 per cent) on both hunted and protected areas in the north central states is so much greater than that caused by hunting alone that the latter factor generally is insignificant (Errington and Hamerstrom, 1935 and 1936; Errington, 1945; Marsden and Baskett, 1958; this study, and many others). Further, our Wisconsin studies from 1929 to 1959 show that as long as the habitat requirement is satisfactory quail will recover from drastic winter declines in a two- to four-year period regardless of whether or not hunting is involved.

Quail as well as other wildlife species can't be stockpiled. Once they reach a certain level, the phenomenon of inversity operates to decrease breeding efficiency. While they do not eat themselves out of "house and home" as do deer (Dahlberg and Guettinger, 1956) and muskrats (Mathiak and Linde, 1954), they quickly show intolerance which operates to reduce the breeding potential.

Refuges

The concept of closing hunting on selected areas where a species could increase and spread to surrounding lands, which has been advanced over the years from James I, 1509–26 (Leopold, 1933), hardly applies to Wisconsin quail. As pointed out above, quail declines occur on hunted and unhunted areas in almost equal proportions. The Prairie du Sac population decreased from a level exceeding 400 in 1929 to zero in 1959, although hunting is so insignificant in this area that in some years there were no records of any kill whatsoever. Simultaneously the quail population increased on some of the heavily hunted areas in the rest of the occupied range.

The annual average movement of approximately 1 mile, most of which occurs between April and July, is another factor that complicates refuge establishment. The smallest area on which a quail population might be relatively self-contained, and this would be only for the inside 5,000 acre portion, appears to be at least 15,000 acres. The possibility of establishing and maintaining many such units is not practical. Albeit units of this size could be set aside as refuge units, the surrounding land area would also have to contain good quail habitat or the egressing birds would have a low survival in this area. Small refuges, 2 to 10 acres in size, established to benefit several species, were developed in Indiana (Bushong, 1961) at a cost of $311 each. The cost for each unit of game produced on these areas was estimated at $20.

Open Seasons

The theory of setting hunting seasons for all game species has been thoroughly presented by many authors such as Leopold (1933), Grange (1949), and Errington and Hamerstrom (1936). Therefore in this section we will present only those factors concerned with quail.

The principle on which hunting regulations are based is that once a population reaches a certain level, it becomes self-sustaining and a harvestable surplus is produced. In quail, if the fall population exceeds the amount of good habitat, some coveys will have to settle in poor range where their winter mortality will be very high. Also while the cover in a selected covey range may be ample, winter food supplies frequently will be in short supply as the result of normal agricultural practices. All of the birds that occupy poor coverts are surplus birds. Also quail on unshot areas were found to have a higher winter mortality than on shot areas (Errington and Hamerstrom, 1933).

If hunting pressure on quail was as great as it is on waterfowl, considerable caution would have to be taken to protect this species by limiting hunting to a level considerably below the past 10 years. Actually quail hunting pressure is relatively light as indicated below.

Occasionally a few hunters may fail to use discretion and reduce a covey to a level where its opportunity to survive in winter is threatened. Under experimental conditions, Gerstell (1939) found that larger coveys (12 birds) survived well at low temperatures while small coveys (4 birds) succumbed. However, even this type of overshooting is not serious because small November coveys often join other birds to form larger coveys before the middle of winter. Therefore, in setting hunting seasons to properly harvest quail, consideration should be given to the effect of hunting on the total population rather than on individual coveys.

Errington and Hamerstrom (1935) concluded that 30 to 40 per cent of the quail can be shot, based on losses sustained in winter on unshot areas. A harvest of 20 to 55 per cent of the quail on areas studied in Oklahoma by Baumgartner (1945) during a five-year period did not prevent a high population from maintaining itself. Probably the simplest evaluation for determining the allowable harvest of quail is to contrast the kill under varying lengths and opening dates of hunting seasons with the impact on the population level over a period of years. In Wisconsin, hunting seasons varied in length from 21 to 44 days from 1951 to 1957, and the estimated kill increased from 14,000 to 52,000. During this period, the state-wide quail population also increased to reach its highest level in

1958, indicating no adverse impact of hunting on the population level.

Another factor that operates to naturally guard against overshooting is hunter interest. This decreases when wildlife populations become relatively scarce, especially when they remain widely scattered as are quail and ruffed grouse in Wisconsin (Dorney and Kabat, 1960).

Dates

Several factors are involved in setting opening dates. The first of these is the date when most young reach the stage of growth when they provide good sport hunting. In Wisconsin by October 15, 85 per cent of the young quail in the fall population are 8 weeks or older in age and 50 per cent exceed 14 weeks (Table 16). At 16½ weeks of age, young quail are considered as being full size. Eight-week-old quail are about half grown. If size alone were considered in setting the opening date for hunting, a mid-November date would be ideal.

A second factor concerns mortality rates. Our data show that there is some loss of quail throughout the fall (Fig. 9). Thus if the hunting season opened in mid-November there would be fewer birds to hunt than if the opening was in mid-October.

Other factors, although of only minor importance, which concern the setting of opening dates, are the weather conditions which would provide optimum hunting conditions. Experience has shown that any time in October dewy mornings may be expected, a condition that facilitates "dog-work" and hunter comfort. All through the month of October leaves fall, and the autumn weather elements knock down rank growths of vegetation producing better chances for flushing and retrieving birds.

Generally the season is set to run long enough to provide ample opportunity to hunt the birds, yet is closed in time to avoid expected snow falls which make the birds extremely conspicuous, especially when roosting in the covey circle. This could lead to occasional overshooting as some hunters would be tempted to make a "pot shot". At earlier dates, quail hunting is a sport-hunting proposition since the value of the meat, even as a delicacy, is hardly commensurate with the cost of obtaining it. Only the most interested hunters continue their sport after the first weekend or two. Hence if snow is avoided, the late season harvest is a small part of the total under Wisconsin conditions.

Quail hunting seasons in Wisconsin usually begin about October 15 or later. This date results in some sacrifice of size in quail but reduces the number of birds that would be lost through natural mortality occurring between October 15 and November 15. The presence of many small quail in the population on October 15 is not a problem. Hunters readily pass up the squealers. Also the very immature birds that are shot do not materially reduce the population since these are late-hatched birds which have a very high winter mortality anyway.

A last factor that is recognized in setting seasons is having concurrent opening dates on several species. Thus any damage that might come from overshooting, which could occur when a single species receives all the hunting pressure, is reduced by simultaneous openings. Several species occupying the same range as quail which are ready to hunt in Wisconsin at about the same time include pheasants, ruffed grouse, cottontail rabbits and squirrels.

Quail add variety and sport to any hunter's bag!

Zones

There is no sound biological reason why every county that has occupied quail range extending throughout most of its area should not have a hunting season on this species. Overharvest in border counties is not a problem because of low hunter interest. Those counties that are located on the boundary line of the better range and which have some scattered coveys can be either included with or excluded from those which have a season. The decision here might be entirely administrative based on the need to "block in" a group of bordering counties which have comparable populations of other species or to take advantage of natural borders such as highways, rivers, etc.

Bag limits

The basic purpose of a bag limit is to prevent overshooting and to equitably distribute hunting opportunities of the available surplus among the largest number of hunters. Wisconsin's bag limit has varied from 3 to 5 birds. A secondary consideration here involves setting a bag limit that will be reasonably attractive to interest hunters. However, even though the quail is a relatively small bird (most of those shot range from 4.5 to 7 ounces), it is still a trophy bird in our state. Thus the consideration to make the bag limit large enough to provide a little meat is not a factor of significance. Again the best test of whether the size of the bag limit is serving its purpose is to determine the effect on the fall population. We have seen no detrimental effect from either the 4- or the 5-bag limit. The lower limit prevailed from 1942 to 1949 and the larger from

1950 to 1958. In 1959 the bag limit was lowered to 3 because of a drastic winter population reduction. A further reduction in the winter of 1961–62 resulted in the decision to close the 1962 hunting season. This was entirely a precautionary measure based more on public attitude than on biological factors.

Stocking

Pen-reared Birds

Quail used in stocking programs are either obtained from game farms (artificially propagated) or by trapping wild birds. The former have been used primarily for "stock-shoot" purposes and secondarily to replenish areas where wild birds disappeared because of adverse weather and temporary habitat losses.

With the exception of a few efforts made by clubs for field trial purposes, Wisconsin has not had a stock-shoot program. Based on the vast experience of other states, and the availability of and interest in other game species, it is apparent that Wisconsin should not have any part in this type of effort.

The use of pen-reared quail for restocking depleted areas appears to be even more futile than their use for stock-shoot purposes. The results of a survey by Buechner (1950) on stocking pen-reared quail in 17 states showed that the method is costly and does not materially increase the shootable population of bobwhites. The cost of putting a pen-reared quail into the hunter's bag ran from $2.80 to $55.56. Stanford (1952) tried a unique approach of releasing wild-trapped adults with game-farm-reared young. The wild adults readily adopted the young birds in the following percentages: Cocks—46.7, hens—23.1 and pairs—15.3. However, the cost of putting such young and adult birds in the hunter's bag was $50.26 and $37.63 each, respectively. Latham and Studholme (1952) selected breeders to be used in an artificial propagation program that survived on a vitamin-deficient diet. The returns on the progeny reared by these adults was 5 per cent in comparison to 22 per cent for native birds.

Even the native-hatched bird with "experienced" adults to guide them have a difficult time surviving. The intricate pattern associated with covey organization and breeding behavior, the capacity to find food and to use available cover, the high annual mortality and dispersal habits allow only the most superior birds to survive in Wisconsin. For example, coveys are formed by the combining of two or more broods, together with the surviving adults who reared them. It is highly improbable that incubator-raised birds form coveys as readily as do wild birds. However, it is known that some pen-reared young will join wild broods to form coveys (Pierce, 1951b and Reeves, 1954).

Compared to the stocking programs of southern states, only small-scale releases of pen-reared quail have been made in Wisconsin (Appendix D), with the exception of some made by Gustav Pabst early in the 1900's, which were reported to be large and widespread. No follow-up studies were made to precisely measure the results of these releases, but at the same time there was no conspicuous evidence that any of these efforts were successful in establishing self-sustaining populations of quail. Some of the larger Wisconsin releases consisted of quail from several other states. In at least a few cases these southern birds survived the first winter after their release. The contribution of these stocking efforts seemed negligible (Schorger, 1944). All of the releases made before 1900 appeared to be made for restoration purposes.

The only way in which pen-reared birds could make a significant contribution to the establishment or increase of a local population of birds would be to have a high survival, to pair and to produce broods. This leaves the problem of when to stock. Fall stocking, even assuming that the gamefarm birds had the same capacity to form coveys and survive as well as wild birds, would still be followed by the usual heavy winter mortality (50 per cent under average conditions) and further mortality in spring and summer.

Thus, it is apparent why fall-stocked birds have little chance to make a contribution toward establishing a local population. Actually, the size of the contribution would probably be even lower than that indicated above because it is very likely that game-farm-reared young would show a lower survival rate than native-hatched birds upon which the above computations were based. An estimate of the survival of pen-reared fall-stocked birds was reported by Reeves (1954) in one of his intensive studies which showed that the harvest for 14-week-old birds was computed to be 38 per cent as effective as for wild birds. Of those surviving to the hunting season, 81 per cent were bagged and a maximum of 3.6 per cent of those stocked were left as breeders.

To escape the winter and spring losses, full-grown, pen-reared quail have been stocked in late winter or early spring. Since only 31 per cent of the native quail survive from spring to fall, the fate of pen-reared birds is apparent. This low survival of wild birds occurs even though these birds are adjusted to environmental conditions. The wild quail have the unique social organization of covey formation from which spring dispersal begins. Pen-reared birds are at a complete disadvantage when released. They are usually very tame (Reeves, 1954); this is a characteristic that makes them vulnerable to wild and domestic predators. From this brief discussion, then, it seems apparent why full-grown, pen-reared quail when released in late winter or spring have had a poor record of survival. Therefore, stocking mature pen-reared birds in spring to establish quail populations, using past techniques, is just as inferior a game management practice as is the fall or summer release of young birds.

Wild Transplants

It is obvious that the number needed and cost of procuring wild quail required for general stock-shoot purposes make this type of project completely impractical in Wisconsin. Therefore, we will concern ourselves only with the use of wild transplants for restoration purposes.

The studies reported in previous sections and those presented in the Appendix D on quail transplantations have shown that restoration with wild birds is possible and may be practical under some conditions but only when releases are made within the occupied range (Fig. 4).

Since 1929, when intensive studies were begun in Wisconsin, there were only about seven years (1936–38, 1943, 1948, 1951 and 1959) when restoration efforts with wild transplants should have received some consideration. These years were characterized by heavy winter losses. Even in those years, with the possible exception of 1958–59, the quail populations recovered generally from their lowest points within a three-year period to their levels existent in the years preceding the heavy losses, showing that transplantation efforts were not needed. We found no year when losses were abnormally high other than in the winter season.

The extreme losses which occurred in the winter of 1958–59 appeared to justify transplantation efforts. Before further consideration could be given to this possibility a careful spring survey was required to determine whether there were relatively large areas of 10,000 or more acres in size with good cover, lacking birds now but previously occupied by quail. The 1960 whistling survey showed that, while quail populations were very low, birds were still present throughout their range and that there was no need for restocking.

If transplantings are attempted, the following guidelines are proposed. Releases should consist of whole or nearly whole coveys containing at least 10 birds in good condition. The release point should be within a half-mile of residual coveys, and the best success would be expected to result from late winter efforts. In no cases should transplantations be made at points where the closest surviving covey is located as far as a mile or more away. Also the release point should be in an area where there are not less than approximately 100 quail per 4,500 acres (the size of the Prairie du Sac area) in the fall population with not less than 1 mile of hedgerow per 550 acres of area. While these figures may not be precise, experience has shown they are good base figures, the best now available.

Fortunately Wisconsin winters rarely invoke severe conditions on the entire occupied quail range of the state. Even in the extreme winter of 1958–59, while most of the quail range was experiencing very adverse weather, the northwest counties largely escaped the killing blast. These areas had relatively high quail populations in the fall of 1959 providing a focal point from which quail could spread. This condition should be recognized in making transplantations. Thus to expedite the rate of spread of quail from occupied range into empty coverts, transplants should be released on the periphery of such areas providing that there is public interest and that transplant stock is available.

There are several good arguments against transplantation projects. The first is that in those years when such a practice might be beneficial, the areas where wild birds are still present also need them. The second concerns the possibility of reducing losses in adverse winters through feeding programs to be described in the next section. Finally, habitat preservation and restoration can ameliorate losses to forestall transplantation needs.

Habitat Management

Background

The studies at Prairie du Sac have shown not only how much cover is required to sustain given densities but also the level at which quail disappeared entirely from areas within their Wisconsin range. When the intensive studies began (1929–36) there were 18.45 miles of hedgerow cover along fences and roads. This amount of cover allowed quail populations to reach a level slightly above 400 birds. When the hedgerow cover declined to 7.12 miles by 1959, a change of 62 per cent, the quail population declined to "0" even though weather conditions in winter were very favorable for survival, particularly from 1951 to 1958 (Tables 6, 7 and 11).

Other changes took place in land use at the same time that were unfavorable, such as the change in corn harvesting methods. Prior to the development of the corn picker, corn was hand or machine cut and then shocked before it was removed from the field. In many fields these shocks were left through the winter, providing an excellent source of both cover and food. As the mechanization of corn harvesting developed, the corn shock began to disappear. Even with this detrimental change, however, studies of covey survival showed that only in the severe winters was food shortage a serious problem, and while this condition is becoming more critical, large quail losses have always occurred when prolonged periods of deep snow occurred. This does not mean that winter food sources can be neglected as will be pointed out later in this section.

Annual spring censuses and hunting success have shown that between 1951 and 1958 when the Prairie du Sac quail population was shrinking drastically, the species was holding its own level or increasing in many other areas where cover losses were light in the state. Conversely, in other areas such as eastern Green Lake County where cover was constantly being lost from 1955 to 1958, the quail population decreased proportionately (Table 6). These observations sustained the findings of the Prairie du Sac studies.

Based on the studies of the correlation between quail populations and cover conditions, we can conclude that a deliberate program is needed to preserve existing hedgerows and to restore a sufficient amount to bring up the total on any area to a level of about 1 mile per 450 acres of rural land. Otherwise quail will permanently disappear in many parts of Wisconsin in the near future. The loss of paramount habitat features has an insidious effect. Favorable weather conditions can offset the habitat loss and thus temporarily allay the actual impact of such an environmental change on a wildlife species. Then when unfavorable periods of weather prevail, catastrophic losses occur which provoke wild guessing on "what happened". Predators, poisonous effects of pesticides, overharvesting during hunting season, etc., are blamed. The part played by habitat loss often goes undetected. It is only when continual studies are carried on to follow the trends in wildlife populations and habitat that it is possible to pinpoint the real cause of the catastrophic declines.

While the specific purpose of this subsection is to present concepts and means of preserving and increasing the basic quail habitat, general objectives first need to be clarified. Some of the pertinent findings on habitat status and requirements will be summarized to establish the point that we have sufficient knowledge and facilities to manage quail in Wisconsin. Fortunately, hedgerows, the main cover requirement of quail habitat, have many other values which are compatible with a sound total land-use program.

First we will discuss what appears to be the necessary cooperation, understanding and the acceptance of certain practices by all people involved in pertinent land-use programs, and then a proposed program for achieving the objectives of quail management.

Requirements and Fundamental Habitat Concepts

It is well known that quail are currently a species of those agricultural lands in which the climate is mild enough to readily permit the growing of crops such as corn every year. Generally woodlands are present on almost every farm where quail are found. Since to date the type of farming carried out in this state in the area occupied by quail has produced enough food for them in the form of weed and domestic crop seeds, it has not been necessary to resort to special practices to sustain this species in most years. The exceptions are those years in which severe winters occur, about once every five years.

Within this type of agricultural land it is necessary to have a good distribution of shrubby hedgerows. Based on the Prairie du Sac studies, approximately 1 mile of hedgerow per 550 acres of land area is required to support the lowest level at which a fall quail population (about 1 bird per 42 acres) can be sustained without danger of extirpation (Table 43.) In addition, numerous scattered thickets of shrub growth apparently are required to supplement the hedgerows. These thickets vary greatly in size, from as small as 10 square feet to one-fourth of an acre. At Prairie du Sac these thickets were found on the river bank, on hillsides, in ravines and gullies and on the edges of three abandoned gravel pits. The amount of such supplemental cover required by a covey of quail is impossible to measure precisely, but several such spots existed per mile of hedgerow in the Prairie du Sac area and were periodically used as roosting sites. In the absence of supplemental cover the minimum amount of hedgerow cover would have to be increased. Shrubby edges of woodlands and swamps bordering crop fields also have cover value comparable to that of hedgerows on roadsides and between fields.

The hedgerow cover cannot be restricted to islands of land units. It must be contiguous with similar cover types in the surrounding areas. The distance that separates areas having hedgerows and quail from other similar areas has not been accurately measured. But general observations on covey locations and the average annual movement of these birds indicate that one or more miles of coverless land would be sufficient to interrupt the continuity required to sustain populations of these species. This does not mean that quail completely occupy their general range. On the areas which have a sufficient amount of hedgerows to sustain them, quail usually have an irregular distribution. They occupy the sites containing the hedgerows but not the coverless areas.

Thus far we have not emphasized the value of farm woodlands as components of quail habitat. Their main contribution appears to be in supplying scattered thickets and occasional shrubby borders which provide supplementary roosting cover. Quail are frequently found in farm woodlands but only when the woodlands are dispersed in areas where hedgerows are present in field borders and along roadsides.

Pine plantations in the early years of development, up to 10 years of age, also provide excellent roosting cover. Their outer edges have the same value as hedgerows consisting of deciduous shrubs. Once the coniferous trees reach the height where their lower branches begin to die, the cover value decreases proportionately.

Nesting cover is apparently not a conspicuously limiting factor in the distribution and abundance of quail in Wisconsin. The direct correlation between the location of quail coveys and areas with hedgerows indicates that this species will find enough nesting sites if shrubby cover is present. While we did not conduct any nesting studies, virtually all of the broods and the coveys we did find in late summer and early fall were located in or near hedgerows.

The cover provided by shrubby hedgerows composed of woody plants is frequently supplemented by herbaceous growths of species such as cattails, *Phragmites,* giant ragweed and standing corn. However, the value of these plant species as roosting cover is limited to utilization during certain periods of the year.

Finally, there is strong evidence that hedgerows are as valuable for brood habitat as they are for winter cover. This conviction is based on the many observations we have made on the location of coveys utilizing hedgerow cover in late summer and early fall. While herbaceous cover is adequate at this time of the year to conceal quail broods and coveys, they are usually found in or near hedgerows and thickets composed of woody species.

The value of hedgerows as required for quail brood habitat may be comparable to the value of moderately pastured woodlands and tag alder swamps to ruffed grouse in northern Wisconsin (Dorney, 1959). These components of quail habitat may facilitate brood movement, provide access to feeding sites and possess the general value of "edge".

It is the total value of hedgerows—to other wildlife species, songbirds and beneficial insects and mammals, for water storage (drifting and melting snow), and as windbreaks and living fences—that provides the justification for advancing a state hedgerow preservation and restoration program. The important point is that this program must be accepted first by all of those agencies which are involved in developing and advancing practices that either favorably or unfavorably change the landscape for wildlife and other conservation interests, and then by the landowners and the general public. Along with the benefits, the liabilities of having hedgerows on farms must be recognized and balanced by special programs to offset any disadvantages arising for landowners.

Nesting Cover

According to Klimstra (1950a) in an Iowa study, quail select grassy nest sites in close association with breaks in the cover pattern such as field edges, clearing, roadsides and gullies. He found 36 out of 46 nests (78%) in nonproductive lands. These studies are sustained by our observations on the location of broods in late summer and early fall in hedgerows or brushy thickets. The strong preference for this type of habitat for cover is demonstrated by the fact that although adult quail move about a mile in spring from their own winter cover, they select comparable habitat for nesting at their new locations.

In recognition of the nest site preference of quail, it is necessary to deliberately maintain some grassy cover in the vicinity of the brushy growths that are distributed within cultivated crop land occupied by these birds. Fortunately this requirement generally is a natural feature of practical land-use programs. Grassy vegetation is more prevalent than shrubby growths along roadsides, and other rights-of-way and field borders. It will encroach in some openings in woodlands and occurs naturally on edges of swamps and throughout marshes. The practices of establishing sod for erosion control in gullies, along streambanks and on slopes and the improvement of permanent pastures are all beneficial to quail. Generally while relatively undisturbed nesting cover is far from being overabundant, the amount available is adequate as compared to brushy cover.

Hayfields and roadsides and other rights-of-way such as under communication lines also provide nesting cover, though hayfields do not afford an opportunity for management. Some mortality occurs during mowing operations, but, it is only the early nesting quail that are affected by first hay cuttings. Fortunately most quail hatch well after the peak of the first hay-cutting period in the middle of June, and the period between the first and second mowing is long enough to permit most of the Wisconsin quail to complete laying and incubating their clutches.

In contrast to hayfields, roadsides and other rights-of-way can be more easily managed to benefit quail without detrimentally affecting the purpose for which they were constructed. For example, where mowing can be either eliminated, delayed or the number of cuttings reduced on highway rights-of-way, quail will benefit since nesting in these sites is common—highest on an acreage basis compared to other lands even though lowest in hatching success (Klimstra, 1950a). Specific game habitat management on rights-of-way will be described in the section on hedgerows.

Generally there will be few places where shrubby vegetation will need to be sacrificed for development of grassy nesting cover. However, in certain parts of some counties such as western Green Lake and Marquette, a considerable amount of land previously under cultivation is being allowed to revert to wild lands. Here, some deliberate effort to control shrub growth by mowing or herbicide treatment to prevent the plant succession from reaching the woody stage is desirable. Such efforts, however, are warranted only if food sources are available.

Late Summer, Fall and Winter Cover

Fortunately the same basic type of shrubby roosting cover is required at all three of these seasons. This is significant for through a program for the preservation and restoration of this cover type alone, it is possible to maintain the main component of quail habitat for most of the year. While the value of winter cover has long been known, the importance of hedgerows in late summer and fall either has not been recognized in the past or for one reason or another has failed to receive much emphasis from other workers.

In the past, quail cover management was handicapped by the lack of knowledge, not on what was required but on how much. Our Prairie du Sac studies provide the source of the best quantitative information applicable to Wisconsin conditions. We now have quantitative data on how many quail a given amount of hedgerow cover, at least in one area, can maintain. Also the reliability of the Prairie du Sac *quail: hedgerow-mile index* in quail management programs in other areas is sustained by our general observations on quail populations, on the utilization of this type of cover and on the amount available in other areas of the state.

Before determining how much and where hedgerow cover should be preserved or developed in any given area, two conditions must be met. First, the area under consideration must be located within the occupied range where some part of most of the farms are devoted to cultivated crop production. Secondly, in the selected area landowners must accept and carry out or have carried out on their land the practices required to maintain or establish hedgerows or supplementary cover.

If these two conditions are fulfilled, then the first step in a hedgerow management program is to conduct a survey of the actual and the potential amount of hedgerows and supplementary brushy cover. The status of the latter cover type must be known to determine either that the required hedgerow amount needs to be increased to compensate for the lack of scattered brushy thickets or that it does not need adjustment.

The second step is to determine how much hedgerow cover is necessary and desirable. Since some goals must be set to have an objective program, we recommend the following basic considerations.

While the minimum amount of hedgerows required to sustain quail is 1 mile per 550 acres, we recommend 1 mile of hedgerow approximately 12 feet wide per 450 acres of land in all areas. This amount of cover is expected to sustain a quail population of about 1 bird per 20 acres. This will vary somewhat between individual areas depending on differences in land use and topography. High priority should be given to the maintenance or restoration of hedgerows and shrubby cover on sites where little conflict exists with agricultural land management (for example, woodland borders, streambanks, roadsides and line fences). Further increases in permanent cover beyond the minimum requirement, however, depend on the ease of creating more and the interest of local landowners and others.

The initial action required at Prairie du Sac is to save the existing hedgerows and then to determine the number of miles of low-conflict sites and their location on which cover can be restored or created. The sites where shrubby cover would be in least conflict with agricultural practices in this area are along woodland borders. A survey of the woodland borders as determined from an aerial photo shows there are 18 miles of sites for this cover type. This is equal to the total miles of hedgerows that were existent on the Prairie du Sac area in the early 1930's (Table 43). While the distribution of shrub borders along existing woodlands would not be an exact substitute for hedgerows which could be established in ideally selected locations, 21 out of 24 covey ranges would benefit (Fig. 17). About 5 miles of the woodland borders are remote from covey ranges and would not benefit quail. However, several other covey ranges which were low in total hedge cover in the 1930's would be considerably improved. Thus, through the establishment of shrub borders, the equivalent of hedgerows in this case, in only low-conflict sites, it is possible to restore the amount existent in the early 1930's.

Ideally some additional hedgerow cover should be restored along field borders and roadsides to provide better distribution and thus improve the over-all quality of the quail habitat. For this the restoration of only a small amount of hedgerows, about 1 mile out of the 4 miles bordering fields or, in the case of roadsides, 2 out of the 7 miles lost since 1935 would suffice. This would also be beneficial to all other animals occupying this cover type, and would simultaneously attain other goals of total land management by providing some soil and water conservation advantages through windbreaks.

The immediate question facing representatives of natural resource agencies, landowners and other interested people in the Prairie du Sac area is how much effort can be reasonably expended to maintain and develop cover in all of the potential sites. Since so many low-conflict sites are available in this area, the ultimate goal should be toward the 100 per cent mark. Naturally such an attempt should be made in steps. Two methods are available for establishing cover. The first merely is to protect areas to permit natural plant succession to take place. Based on our experience at Prairie du Sac, this would result in cover establishment in from 5 to 10 years in some sites. Not all sites would respond in this length of time. The second is to plant sites which with proper care might provide some relatively good cover in 5 years.

Food Patches and Feeding Program

Spring to Fall

At the present time in areas where parts of all farms are in cultivation, no extra effort is required to manage land to produce food for quail and other wildlife. In areas where the cover requirements are generally ample but where whole farms have been retired from cultivated crop production, some food management measures may be desirable (Errington and Hamerstrom, 1936). Where only a few scattered farms have been retired, the decision to cultivate some part of any one farm for a food patch would depend on whether a specific landowner were interested in having some quail or other wildlife species with similar habitat requirements on his own land at all seasons of the year.

Where there are several places within an area in which two or more adjacent farms have been retired from cultivated crop production, some food patches are required for quail maintenance. The least costly food patch, but one which provides sufficient food only in very mild winters, involves merely plowing strips of land of about 1 to 2 acres in size and allowing the natural growth of annual plants that bear seed eaten by quail (Jackson, 1951). For the number of quail found on any one farm in Wisconsin this should be enough food to carry these birds from spring to fall. The planting of cultivated crops, and the only one we know that will provide year-round food is corn, is more costly but naturally yields more feed.

The cost of planting food patches on a farm varies from about \$15 to \$50 per acre, depending on how much of the work and equipment required has to be hired. Since not more than about two patches 1/8 to 1/4 acre in size are needed, the cost of a food patch that will provide food year-round should not be more than \$20 per farm. It is also possible that if corn is used and left standing, it can provide enough food for a second year of feeding (in areas where few deer are present), thus reducing the cost of establishment to \$10. This is a relatively low cost, particularly if we add the value of the edge effect that is created and needed in wild land to produce optimum levels of farm game and other wildlife species. When cultivated crops are planted for the food patch on wholly retired farms, an area of 1/4 to 1/2 acre of additional land should be plowed adjacent to these sites and left fallow to fully create the necessary edge effect. Of course, noxious weeds would have to be controlled.

Food patches can also be developed by using a combination of herbicides that will control both grasses and broad-leaved plants (Hamilton and Buchholtz, 1953). Such treatment will suffice for seed-bed preparation and weed control. Or, if desirable, the seed bed can be prepared by plowing and then after the food patch is planted, weed control can be obtained with pre-emergent herbicide treatments.

There are many other details to consider in establishing food patches, but only the more basic aspects could be profitably discussed here. The detailed problems are well known to game managers and other personnel such as Soil Conservation Service farm planners who can give guidance on this subject.

At present, food sources for quail are still adequate wherever cultivated crops are grown from spring to fall (Korschgen, 1958). But, it is probable that in the future with continued improvement in weed control and crop harvesting methods food patches will have to be deliberately created on many farms. This is now true in areas where truck crops are grown exclusively; however, these places are very limited in number and quantity. Some studies are needed to evaluate these conditions constantly.

Winter

The value of feeding programs in severe winters for increasing the survival of quail has long been recognized (Leopold, 1931 and Errington and Hamerstrom, 1936). Although on a state-wide basis in Wisconsin the need for winter feeding occurs about 1 year in every 4, it is this periodic critical year which controls the quail population. It takes about 3 favorable years for a quail population to recover from a severe winter. The average percentage of quail lost in mild winters is 37, in moderate winters it is 58 and in severe winters, 77.

Although some benefits would accrue from conducting an intensive feeding program every winter, we do not consider such an effort as being practical. Fortunately, some landowners enjoy feeding wildlife, particularly quail, and thus, with a minimum of effort involving putting out grain up to ten times a year, they have increased survival by 20 to 60 per cent in severe winters. However, unless this effort is planned and persistently followed up, it may at times be more damaging than beneficial. This can happen because birds may become attracted to sites by a few feedings and become reliant on them for winter feed. Then if feeding is suddenly stopped when the need for food is urgent the birds will continue to range around such places instead of foraging farther and eventually will starve.

Since there is no way of determining whether a winter will be severe or mild, how can one plan and be ready to conduct a practical feeding program when it is needed? There is only one answer to this. Precise arrangements have to be made in advance to have facilities ready whenever they are needed. There is no one approach to accomplishing this; at the same time there are many possibilities for planning and conducting an effective feeding program.

A feeding program can be divided into three steps: (1) convincing the landowners and the public of its importance, (2) determining the effort that responsible and obligated governmental agencies and public cooperators can undertake, and (3) working out the mechanics of providing and getting feed to the birds by interested people.

The first step requires reliable information on what needs to be done and what can be accomplished. Fortunately we have more such information on quail than on any other game bird. By feeding approximately 1 out of 4 coveys in an adverse winter on an area the size of Prairie du Sac, 4,500 acres, the percentage of birds surviving in the fed covey could be increased enough to place the winter loss for all four coveys in the moderate category (Table 11). Projecting this effort to a township basis where the average population consists of 1 bird per 20 acres (state average in better range), approximately 15 to 20 coveys would have to be fed. The operation of 15 to 20 stations would involve the feeding of about 200 to 260 birds, most of which would survive. The over-all result of the feeding effort in good range would be that quail populations could recover from severe winters to previous high levels in from one to two years rather than from two to five; and in marginal range quail populations could at least be kept from disappearing.

Cornshocks, now rare, were once invaluable winter feeding and cover sites for most wildlife. These will have to be replaced by special practices if wildlife is ever to return to previous levels.

In many instances pheasants and other wildlife species would benefit from the quail feeding operations or vice versa. In years when mast crops are in short supply, squirrels would be fed, and at all times feeding stations would serve wintering songbirds and mourning doves.

The role of conservation departments in such efforts would vary, but at all times they should provide the direction required to organize and guide the basic effort. In Wisconsin the Conservation Department does annually conduct a winter-feeding program. However, it is apparent that no agency of this type has enough facilities, funds and manpower to take on the entire effort alone. The bulk of the effort must come from cooperators.

The number of potential cooperators that could carry out an emergency winter-feeding program is great. Landowners, 4–H clubs, Future Farmers, Boy Scouts, sportsmen, ornithologists, civic groups and others all have participated in past efforts to varying degrees. Leaders of these groups together with teachers, county agents, highway supervisors and patrolmen and personnel from the Soil Conservation Service are some of the possible persons who could help and guide an emergency crash winter-feeding program.

While everyone is "busy" with their own jobs, it may be possible in some areas to solicit help from people who routinely pass through areas where feeders could be located. These include truckers, mailmen, school bus drivers, highway patrolmen, etc. While these people could not be expected to carry out the whole program, they should be able to supplement the efforts of others.

A crash feeding program would involve the acceptance of commitments to supply feed to coveys in designated areas. Efforts would have to be made to locate 15 to 20 coveys per township and place or at least have feeders ready for each of these coveys. Many kinds of feeders can be used. A simple type is one constructed from a milk can filled and placed to operate as a self-feeder and used in conjunction with brush shelters. The use of small grains and cracked corn will prevent animals such as deer, mice, rabbits, and squirrels from eating or carrying away large amounts of the feed. This operation will involve filling the feeders from 3 to 10 times per winter and clearing away snow. Placement of the feeders is important to avoid drifting snow which necessitates frequent cleaning efforts.

The locating of coveys requiring winter feed is basic to a successful program. Again there are many ways in which this can be accomplished. Most farmers know whether they have coveys on their lands by late fall. Mail questionnaires could be sent to them soliciting such information. Hunters are also an important source of information. Local newspapers could aid by publicizing the required information and effort. The solicitations and commitments to feed would have to be made each year. Feeding would not have to start until a day or two after the first heavy snowfall of 4 or more inches. If the first snow melts readily or is light and in many places is readily blown exposing bare ground, feeding need not be started until the next snowfall. However, once feeding is started, it must be continued. Feed must be made constantly available when ground snow depths exceed an average of 4 inches for two or more days.

Coveys should be selected which are located where natural feed is scare and access is good. There is no point in trying to feed quail in remote places, long distances from roads.

At times disinterest might be a problem, especially when a long period of mild weather prevails, as from 1951 to 1958. However, even in this period there were local areas where birds were hard put for 1 or 2 months. While having a standby program ready at all times seems complicated and burdensome, this same problem prevails in snow removal programs on streets and highways and is effectively handled. The fact that little or no special equipment is needed for this effort is a special advantage. A source of feed is also required but usually it would be possible to obtain enough voluntary contributions to supplement stocks from conservation departments.

When we consider the cost of land acquisition and cover maintenance, and the many hours spent hunting or viewing wildlife, the expenditure for a feeding program is low particularly since the benefits include other wildlife species. While such an effort in the past seemed to attract only a moderate interest, we must recognize that in modern land-use programs wildlife can no longer be taken for granted. They must be included in basic land-use plans. Even with dwindling habitat, there will be many years when excellent coverts will lack food. One of the paramount reasons now for conducting an emergency winter-feeding program is that the bulk of our present quail habitat comes close to being marginal, but as long as we can carry 30 per cent or more birds through the winter and maintain the existing cover, we can sustain the species in any area. However, if we allow an adverse winter to "knock out" a quail population, it may never come back in many areas.

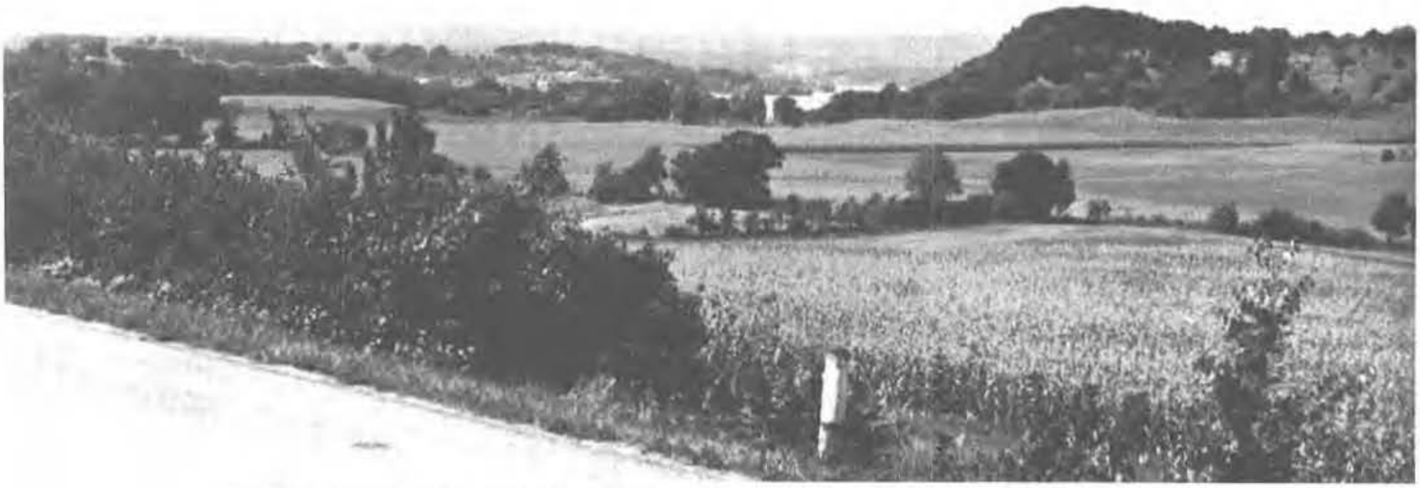
Food patches should be used to supplement the emergency feeding program. There is no way of guaranteeing that a food patch will be used; however, when the quail population is relatively high, most good coverts will have birds and this will not be much of a problem. Unfortunately, there are very few crops that will remain erect to expose seed during periods of heavy snow. Corn is the main crop that will do this. Corn shocks are excellent but costly to erect and maintain. Some varieties of soybeans are fairly good, particularly if planted where snow drifting is at a minimum.

Programs for Hedgerow Maintenance and Establishment

Agency Responsibilities

The success of getting the representatives of appropriate land-use agencies to evaluate, coordinate, and advance natural resource programs depends on having an officially sanctioned organization through which all can cooperate. In Wisconsin there are three major state organizations which have been established by legislation to serve this purpose. They are the State Soil and Water Conservation Committee, the Natural Resources Committee of State Agencies and the Department of Resource Development. The latter was created by the Legislature in 1959.

Six of the major land-use or implementing agencies have voluntarily signed a Six-Agency Agreement to advance land-use programs cooperatively: the University of Wisconsin College of Agriculture and Extension Service, State Soil and Water Conservation Committee, Agricultural Stabilization Conservation Committee, Farmers Home Administration, Conservation Commission and Soil Conservation Service. On a more local level there are Soil and Water Conservation Districts which are concerned with the conservation of soil and soil-related resources; they are aided in their work by the State Soil and Water Conservation Committee. This committee also has the



This landscape is scenic, represents good conservation, and contains fine wildlife habitat. The minimum goal of 1 mile of hedgerow per 450 acres of land in an area such as this will occupy only ½ acre of land out of a 150-acre farm.

supervisory responsibility over programs provided by P.L. 566, which established the small-watershed program.

There are a large number of other organizations and programs established formally and informally to cooperate with and assist landowners in carrying out specific and integrated conservation practices on their lands. These are far too numerous and ramified to describe here in detail. Some of the basic programs are described later in this section.

The all-important point here that must be emphasized again and again is that the management of hedgerows as well as the management of any other natural resource is an *interagency responsibility*. This includes acceptance, advancement or rejection of the whole or any part of a program for managing natural resources. Naturally basic responsibilities must be assumed by agencies, groups or individuals in proportion to their equity in the programs under consideration. While quail are the responsibility of the Conservation Commission, hedgerow maintenance and establishment must be formally recognized and accepted by all rural land-use agencies, since this habitat type exists in all areas. To date this has not been done on a total basis. Some progress has been made through voluntary cooperation and in some cases specific phases of hedgerow management have been formally endorsed under the Agricultural Conservation Program and the Soil Bank.

Official sanction of state agencies must go further than merely endorsing the preservation of hedgerows and the practices necessary to establish them. It must also endorse the actual placing of the recommended minimum of 1 or more miles of hedgerow per 450 acres on the land. In some cases this will mean advocating hedgerows for field borders depending on the location of desirable sites required to attain optimum distribution. It will also mean providing assistance and support for developing incentives for landowners to accept recommended plans.

On the other hand, if the recommended plan or certain aspects of it are deemed impractical, this decision must be made on the interagency level and be clearly spelled out even if it means signing the death knell for quail in our state. It is more gainful to determine what can and what cannot be done and operate accordingly than to be deluded into expending funds and energy on a hopeless program. Such efforts could be best diverted into more fruitful activities. This is a most important point because even the landowners' acceptance of such practices as those affecting basic soil conservation is relatively slow. Their acceptance of some basic soil conservation and hedgerow management practices is described below.

The Soil Conservation Service recently reported that 40,817 out of approximately 177,000 farms in the state (Ebling *et al.*, 1948) were cooperators in their program. This means that approximately 23 per cent of the state farm owners took advantage of the opportunity to get assistance for improving their farms during a period of about 25 years of operation by the Soil Conservation Service. Included in this record were reports of planting 540 miles of hedgerows. Most, if not all, of the planting stock was obtained from the Conservation Department. While this materially is not an impressive record when one recalls that on the 4,500-acre Prairie du Sac area 11.3 miles of hedgerows were lost during the same period, the 1959 record does show that a significant number of landowners are still willing to at least plant this type of wildlife habitat.

Some question can be raised on the actual contribution made by these plantings. If all these shrubs and trees planted in hedgerows survived and resulted in the production of 23 quail per mile of hedgerow, the 540 miles planted has a potential productivity of 12,420 birds. Obviously not all of these plantings survived or were maintained. A Conservation Department study for the period 1931–53 (Woehler and DeByle, 1954) showed that only about 20 per cent of the wildlife tree and shrub stock obtained from this agency by landowners and cooperators remained alive 5 or more years after planting. And, of these 20 per cent, only 10 per cent showed good survival. Furthermore, many of these wildlife shrubs and trees reported by the Soil Conservation Service were not planted within the occupied quail range.

In 1959 the Conservation Department distributed 2,045,000 shrubs for game food and cover plantings. Of this total 776,525 were planted in counties located within the occupied quail range. Based on a 1-foot spacing this would be approximately 36 miles of hedgerows. The hedgerows planted through the Soil Conservation Service are generally included in this total.

The possibility that it will be mandatory in the future to carry out basic conservation practices that affect the welfare of the state, or nation for that matter, is indicated in the following regulations. For almost a century, rural landowners have been legally obligated to control noxious weeds on their property. Recently state legislation was passed requiring landowners to control forest insects on noncrop lands. Permits to burn vegetation on private lands are required in forest protection districts. In 1923 legislation was enacted allowing counties to adopt ordinances to zone certain lands. One of the major consequences of the zoning legislation that affected natural resources in large areas was the program aimed at eliminating agriculture in areas more suitable to forestry. In the last decade some counties have adopted zoning ordinances that restrict the use of flood plain lands for residential development. One county, Waukesha, has set up conservancy districts that include the designation of wetland use for wildlife purposes (Rowlands, 1957 and Kabat, 1957).

Probably the most forceful measure used to achieve a designated land-use practice, though on a more restricted area basis than the others previously described, is the employment of the authority to condemn lands. Highway and military agencies, for example, probably have used this authority more often than other organizations.

The above regulations were designed to help people in the long run to achieve the best use of their lands for themselves and simultaneously for the welfare of the nation. It is doubtful that education and extension alone will convince the majority of rural landowners of the importance of accepting and carrying out soil and water and related resource-conservation practices. For example, we all know how important it is to educate our children, yet this and other nations have felt it was necessary to make this a compulsory activity. Further, many landowners are not in a position to carry out programs for natural resource management under existing conditions.

However, even if soil-conserving and possibly some basic cultural practices for producing agricultural crops were eventually accepted as mandatory practices by landowners, we must still assume that for some time to come the best support that could be expected for hedgerow management would be greater financial and other incentives together with stronger moral encouragement. Even without official endorsement on specific goals by representatives of major state agencies concerned with the use of natural resources, some significant progress has been made. There is much to be gained, therefore, in requesting formal support for hedgerow management from these groups.

At the present time no specific protocol has been established as to which agency or agencies the Conservation Department should first appeal to get a specific endorsement for a state-wide hedgerow management program. Since it is urgent that a start in this direction be made now and since the Natural Resources Committee of State Agencies has been considering many related problems concerning natural resources, hedgerow management in its entirety or at least in part could be presented first to this unit for appraisal and endorsement. While it is imperative that this request be made soon, it should be recognized that this effort should be a part of an integrated, rural land-use program. The proponents of any one land-use program aimed at advancing a single-purpose objective have to accept the responsibility of the impact of these efforts on the pursuits of other people. This is particularly true where agriculture and wildlife crops are concerned.

Let's assume now that it would be possible to obtain a complete inter-agency and landowner endorsement for the production of enough new hedgerows to achieve the goal of 1 mile per 450 acres of rural land. Before this could become a reality a considerable period of time, from 3 to 10 years, would be required to establish new hedgerows. The actual length of time required would depend on the condition of selected sites. Therefore, the first goal should be the preservation of the hedgerows now in existence. Second, the sites having the highest potential for rapid hedgerow growth, such as areas where debrushing practices have recently been applied and live root stocks still remain, should be protected from further mowing. Third, highly desirable sites where no hedgerows now exist should be protected from mowing and grazing to allow shrub growth to develop through natural plant succession. Shrub plantings should be made simultaneously to speed development of hedgerows.

Key agencies in the program described above are the Conservation Department and Soil Conservation Service. The

The value of the brushy cover for wildlife on both sides of this field depends on the connecting "in-field" hedgerow. This type of hedgerow cover must be preserved by special programs such as easements, private game farms, or cost sharing in the ACP program.

former produces wildlife shrubs that can be procured at minimum costs by landowners and also provides planting instructions or direct help in some cases for hedgerow development. The Soil Conservation Service provides planning assistance. Cost-sharing in some cases is available through the Agricultural Conservation Program for planting stock, preparing seedbeds, mulching and for fencing planted areas in woodland borders and along streambanks where protection against grazing is required. The results of this program were previously reported.

The Wildlife Management and Botany Departments of the University of Wisconsin, the Soil Conservation Service and the Conservation Department directly and through various cooperative projects conduct research and test trials of various shrub and tree species to be used in hedgerow management programs. The Agricultural Research Service also conducts related research projects requested by the Soil Conservation Service. For example, in its 1960 report to the Agricultural Research Service, the Soil Conservation Service recommended research projects on shrub cover development and an evaluation of the effect of hedgerows and border developments on insect, rodent and weed pests.

Several other agencies which are concerned with shrub management, particularly those involved in the maintenance of rights-of-way, will be discussed in a following section.

While the Wisconsin Conservation Department and the Soil Conservation Service are concerned with all lands where hedgerows exist or could be established, some agencies are concerned only with specific sites. Thus a discussion on specific hedgerow management programs will be presented later in this section on the basis of site location and will include the problems, possibilities and progress.

Citizen Responsibilities

Before a realistic program can be adopted for helping landowners manage hedgerows, the contribution made in support of wildlife by all people and the responsibility of each person benefiting from wildlife on farms must be assessed.

While Wisconsin rates relatively high in the United States for its agricultural assets, recreational values also run very high. Fine and Werner (1961) estimated an expenditure of \$581,296,311 which includes \$74,183,809 for hunting by people taking vacation-recreation trips in a 12-month period in 1959 and 1960 in Wisconsin. Their figures may be high because they did not make adjustments for nonrespondents in their study. All people make a direct or indirect contribution to the wildlife resources of the state. For example, during an 8-year period from 1948–49 to 1956–57 the governmental costs for farm price and income support programs alone in the United States were \$8,711,000,000 (MacFarlane, 1960). This included \$1,758,000 for Agricultural Conservation Program payments and the Soil Bank. All people contributed directly to this program through tax dollars. However, the magnitude of the total contribution made by rural landowners, urban hunters and all other people varies.

Agricultural programs are supported by all people, not only by providing markets for farm produce but also through taxes which are channeled into agricultural cost-sharing and support of research and extension programs. These latter contributions, to date, have only indirectly been available for producing wildlife habitat on farm lands. If the land-use practices developed to enhance agricultural production were favorable or even compatible with those for wildlife crops, there would be no problem. This is not the case, and in many instances they are strictly detrimental.

The portion of the revenue derived from the sale of hunting licenses that is devoted primarily to habitat management is expended on state-owned or controlled lands. Other facets of game management for which license money is used include law enforcement, land acquisition, propagation, education and information. Generally there are no public funds directly available for wildlife management other than those from license money, the sale of duck stamps and the excise tax on sporting arms and ammunition. Private contributions, while substantial from the standpoint of individual donors, are meager considering the total needs.

Farmers provide the bulk of the habitat and the space for seeing and hunting wildlife. They also buy hunting licenses and pay taxes. Hunters buy hunting licenses and equipment and also pay taxes. Nonhunters who make a special effort to enjoy nature pay taxes but do not buy hunting licenses or incur expenditures specifically for hunting. There are many people who do not have either the opportunity or interest to hunt or to enjoy the outdoors and thus seemingly do not benefit from wildlife but who still pay taxes. Actually this latter group of people also benefit considerably from the impact of recreational spending to the state economy and from the contributions that the upland game, songbirds, beneficial insects, small mammals and plant species inhabiting hedgerows make to the balance of nature and over-all educational values.

Without a quantitative evaluation, it is impossible to determine accurately whether any of the above groups fail to carry their fair share of the management of the wildlife resource. However, the responsibility that people have to posterity is a factor that should be recognized by all. We inherited a relatively rich legacy of wildlife and, if we wish to sustain this natural resource, we are obligated to do all we can to preserve and increase this value now and for the future.

The foregoing considerations suggest that the nonhunters are getting more for their investment than rural landowners and hunters. If a careful study of this condition proves that this is the case, then what can be done to eliminate this inequity? Ideally there would appear to be no alternative but to tax the favored group in proportion to their benefits. In practice this assessment would be a complicated, if not an impossible task.

The simpler approach would be to determine the contribution of wildlife to the state's recreational and conservation values. Theoretically this contribution should be financed out of an apportionment of the general tax source and should be used as a fund for conducting a basic wildlife management program since all people benefit from wildlife generally. The revenue accrued from hunting licenses then could be additive rather than the source of the basic fund. This approach is used by the federal government which supports the work of the U. S. Fish and Wildlife Service with funds appropriated by the Congress and supplemented by revenue obtained from the sale of waterfowl stamps. If this cannot be done by states, then it is questionable that there is any way to achieve an equitable distribution of the costs of managing our wildlife resources.

One approach to obtaining additional funds for conservation purposes was the placement of a 1-cent tax on cigarettes in 1961. This tax is expected to accrue approximately $50,000,000 in the next 10 years. It is being used primarily for the acquisition of land having scientific and recreational values (scenic, fishing and hunting) and the development of plans for utilizing natural resources before they are converted to other uses. Actually this bill was not designed to obtain revenue from any specific group of people but is a general form of revenue.

As laudable and apparently desirable as are these objectives, sufficient knowledge and the physical facilities required to satisfactorily preserve and enhance the natural values of lands being acquired are still necessary. In fact, land acquired now for public use, if not paralleled with a considerably expanded program of resource conservation, may become a fiscal burden for a single agency to manage and maintain.

The question of whether the rural landowner should have a moral or legal obligation or no obligation at all to manage some part of his land for wildlife is complex. Support programs for producers of agricultural crops generally exclude any reference to wildlife management, but in 1961 the ACP program was amended to provide cost sharing directly for wildlife practices. Prior to this time the agencies which administer these programs nevertheless encouraged practices that were beneficial to wildlife. This was especially true in the Soil Bank Program.

There are many taxpayers who feel that the dollars they contribute to support agricultural programs morally impose an obligation on landowners receiving these benefits to practice some wildlife management. Rural landowners at present do not feel that they have such responsibilities particularly if their own investments in land development are relatively great. This attitude in many cases results in areas formerly having a high wildlife production value being turned into wildlife deserts. If wildlife habitat were abundant, these situations would have only a negligible effect on this resource, but the reverse is true. As an economist said at a meeting of the Soil Conservation Society several years ago, "You cannot wish away this problem; it will have to be worked out by representatives of both interests."

Finally, the recent redirection set forth in the U.S. Food and Agricultural Act of 1962 toward converting some agricultural land to other uses rather than merely paying for "idling them" is a major step toward formulating a clearer perspective on wildlife and agricultural land-use relationships. This action and machinery in turn will aid our citizenry to evaluate and accept their inevitable responsibility in those land-use problems. This program and its ramifications were excellently summarized by Timmons (1962) at the National Conference on Land and People.

Even if rural landowners recognized a moral responsibility to carry out wildlife-management practices, would they be compelled to do something about this? Does society have any right to even contemplate the use of coercive means to force landowners to maintain and create wildlife habitat? Further, even if rural landowners are willing to manage parts of their land for wildlife, do they have any moral or economic obligation to provide hunting space for others on their property? We feel that nobody would argue that the rural land-owner has this responsibility. This would be as illogical as insisting that the man who owns urban property is obligated to provide free playground space on his lawn. Because of the importance of wildlife to our way of living, however, we believe that if the rural landowner receives more public funds to support his farm operation than he contributes to other programs benefitting the public, he is obligated to provide a reasonable amount of hunting opportunity on his lands. He can easily accomplish this by allowing his acquaintances and a few other well-behaving hunters who obtain his permission to trespass on his lands. On the other hand, the rural landowner needs protection from the rowdy hunter who disrespects property values. This attitude has been cited by farmers as the main reason for posting their lands against treaspassing and why they do not establish and maintain wildlife food and cover.

We have included the above discussion here because this problem has been a major obstacle to wildlife management in the past on private lands. We believe that rural landowners meeting with representatives of the hunting public could solve this problem. If it cannot be solved, our system may evolve into that of some European countries where the landowner is the proprietor of all the wildlife on his land. Such an action, however, would further estrange the farmer and the urban public leaving a totally undesirable situation. To date we have considered that wildlife is public property and every effort should be made to keep it this way. However, it is apparent that the philosophies and programs adhered to in the past in our nation have not been successful in maintaining and increasing our wildlife heritage.

Shrub Species for Hedgerow Plantings and Management

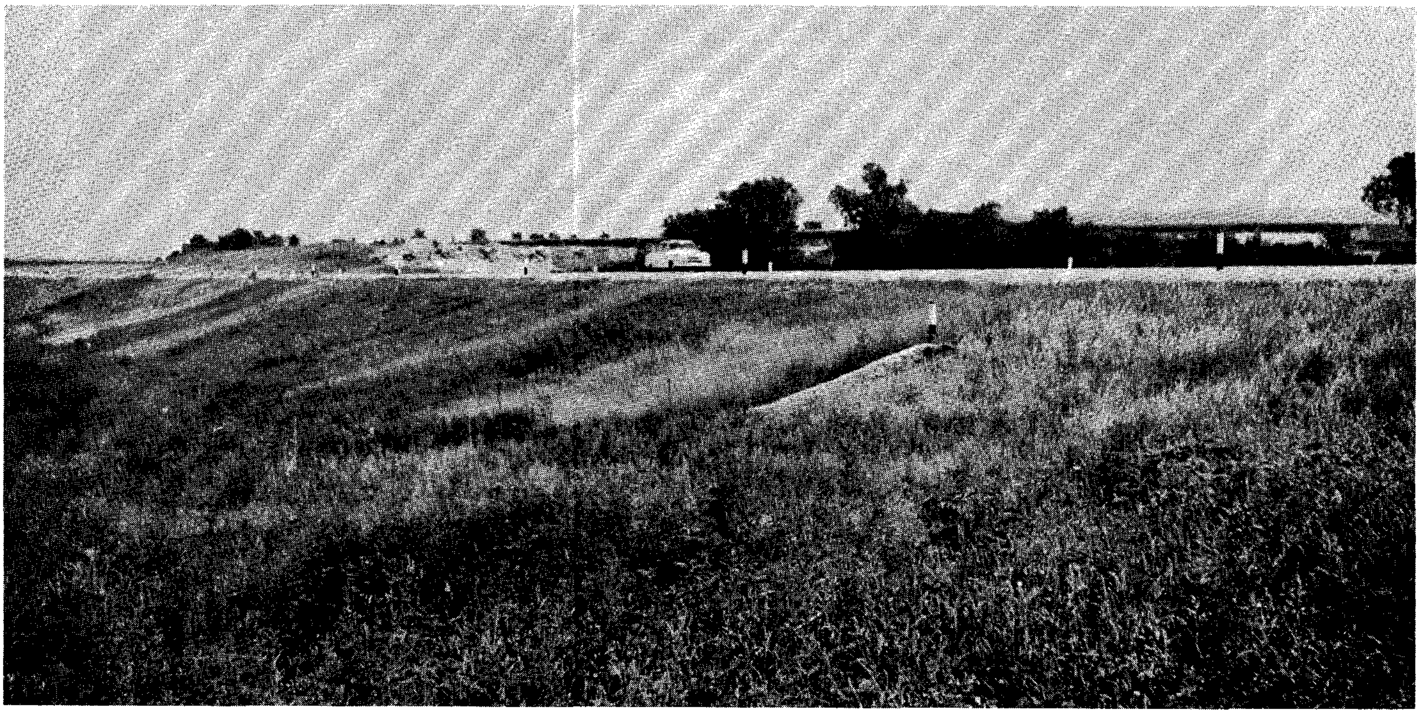
Since quail appear to be nonselective in the shrubs they use for cover, the best species to use will depend on the requirements of the various sites in which they are planted or allowed to grow. At present there are a relatively large number of shrub species that would make good hedgerows (Edminster, 1950 and Appendix E). None of these are completely satisfactory, but several will serve the present purposes. The late Prof. John T. Curtis, Botany Department of the University of Wisconsin, proposed (pers. communication) that game technicians start locating naturally growing shrubs that have the characteristics of good wildlife cover and food value. These could then be transplanted to a nursery where they could be further evaluated, and those that maintain the originally observed desirable characteristics could then be produced on a large scale.

The above proposal was based on the recognition that some species have a variety of growth characteristics which are maintained in their progeny. For example, certain members of a species of wild plum may be found growing tall in some places, low in others and may or may not spread by vegetative growth. Other species may have clones that either grow densely or remain sparse. An experimental shrub nursery for testing and producing native species with desirable wildlife values is needed because much of the stock now grown for habitat improvement purposes in Wisconsin may not be native and may lack the desirable characteristics.

Native shrubs also have the advantage of being adapted to Wisconsin environments. Some of the native plum and rose species, for example, might serve the purpose of a living fence better than the stock of multiflora now grown commonly, which is limited to the southern part of the state and is handicapped by "die-back" in winter. Until such time as native stock with a known history can be produced, that which is now available should be used. However, emphasis should be made on establishing plantings not in widely scattered places, but where they can contribute significantly to the improvement of wildlife habitat.

The width of hedgerow plantings can vary considerably depending on the site. Under the Soil Bank program it was necessary to place shrubs for hedgerows in 4 rows with a 4-foot spacing between rows. This amounts to a basal width of a minimum of 12 feet. Naturally the wider the hedgerow the better, but this type of cover has made valuable contributions at times when the width was as narrow as 4 feet. However, narrow hedgerows must be densely planted if they are to provide good quail cover. A 12-foot-wide hedgerow would occupy about ½ acre of land per average 150-acre farm at our recommended goal of 1 mile to 450 acres of land. When we consider that only a fraction of this would occupy field borders on tillable land, the loss to farmers under a hedgerow-management plan is not great, particularly if some form of compensation can be provided to them for this contribution to wildlife habitat improvement.

The establishment of hedgerows on new sites or their restoration on old "cleaned-out" sites requires the same cultural practices as for any cultivated crop. Where available, planting machines should be used. Weed control can be secured through mulching, cultivating or by properly applying herbicides, making doubly certain that valuable shrubs and wildlife are not damaged. Maintenance will require a selective woody species' control program (USDA, 1959). This involves destroying undesirable species, particularly trees, which will cause shading handicaps. The right combination of dense shrub growth will reduce tree encroachment to a minimum. Conifer-



Roadside fill section in the interagency roadside development project in Dane County. The bands on the bank are plots of grasses, legumes and shrubs.

ous trees make the most rapid usable cover but will be a management problem later.

In sites along rights-of-way bordering new or improved roads a practice proposed by the late Prof. John T. Curtis may be feasible. This involves taking the top soil from areas previously occupied by shrub species, which is normally removed in constructing new or improving old roads and which contains roots of woody species, and spreading this on new rights-of-way. This practice has not been tested but could possibly develop into a rapid method for getting woody species established on rights-of-way.

Within the occupied quail range, sites selected for establishing new hedgerows shouldn't be isolated from others already present. The location should be based on a unit-area management plan. This does not mean that landowners who are interested in having hedgerows for wildlife species other than quail or for basic soil and water conservation benefits should be discouraged from maintaining or establishing them. However, only those hedgerows that form a continuous network will, within the occupied quail range, produce and maintain this species. Short interruptions of a few rods in an otherwise continuous hedgerow are not particularly objectionable since quail will readily cross such openings.

Rights-of-way

Rights-of-way along roadsides are an important source of habitat for quail and other wildlife. It was the roadside hedge that was involved in the Prairie du Sac area having considerable numbers of quail prior to 1935 and also in their disappearance between 1935 and 1959 when this cover type was destroyed (Table 42). Of the 11.3 miles of the hedgerow cover destroyed between 1935 and 1959 in this area, 65 per cent consisted of roadside hedges. The hedgerows in these sites were removed because it was believed by many prior to 1950 that they were obstructions to roadside maintenance and handicapped travel on the roads. In many cases hedgerows were destroyed incidentally during the process of noxious weed control, but often the destruction was aimed directly at the hedgerow.

In 1953 a Working Group on Noxious Weed Control and Brush Management of the Natural Resources Committee of State Agencies, consisting of representatives of all agencies responsible for rights-of-way, was assigned the task of evaluating the problems and potential of these sites for multiple use. This group agreed formally on the importance of and methods for noxious weed control in right-of-way areas and also agreed that brush should be left for wildlife wherever it was not an obstacle to other land uses (Natural Resources Committee of State Agencies, 1958). It was recognized that there were many sites in rights-of-way where the existence of shrubs (brush) did not interfere with maintenance programs.

It has been proven that selective brush control (Egler, 1949 and USDA, 1959) in right-of-way areas has been more economical and effective in noxious weed elimination and woody vegetation management than have the usual mowing and blanket spraying programs. Selective brush control involves cutting out and chemically treating undesirable shrubs and trees and permitting low-growing woody species to become predominant in rights-of-way. The Wisconsin Power and Light Company has employed this practice on all of their lines and is very effectively controlling undesirable woody species while simultaneously creating good wildlife habitat.

The Working Group has launched a two-fold noxious weed control and brush management program. The first effort is state-wide and concerns all rights-of-way, and at this time consists primarily of an extension and education program. The second concerns a specific effort in a study area in three southwest townships in Columbia County and in one area in Dane County. Weed control demonstrations, cooperation and assistance with county and town weed control officials, designation of areas along roadsides where shrubs can be left to grow and their growth selectively controlled are parts of this unique program. The principles of the program have been presented to town and county officials, and the specifics are now receiving attention. The whole program will be presented to the landowners for review and consideration. The Prairie du Sac study area is located in one of the three townships, making possible the measurement of whatever success is achieved in hedgerow restoration and establishment in terms of quail production.

Unfortunately in this area most road rights-of-way are narrow. It will probably be necessary to secure additional strips along the narrow roadsides to provide a space for hedgerows to be established that will not interfere with other land uses. The mechanics of procuring the extra width of land on the right-of-way have not been worked out. Additional land to widen road rights-of-way may be procured by purchase, acquiring easements or leases. Some brush cover may be maintained along the railroad rights-of-way in this area but this possibility remains to be fully explored. The Wisconsin Power and Light Company has already created some good wildlife cover on their rights-of-way in this area. Other rights-of-way such as those under telephone and other electrical lines are in the same status of evaluation as the railroad sites.

Emphasis on brush management in rights-of-way is along the town and county roads where traffic is less than on state and federal highways. However, even on the latter rights-of-way, there are places where brushy growth can be tolerated. Generally the high-speed roads are sites where significant numbers of wildlife species are killed by vehicles. While this is a factor to be recognized in resource management, it is secondary in importance to producing and maintaining wildlife cover wherever possible. By careful site selection such as along fills and cuts, shrubs can be allowed to grow along even the main highway rights-of-way without significantly endangering wildlife or handicapping maintenance operations.

A cooperative study has been set up in Dane County just north of Sun Prairie on Highway 151. At this site, combinations of grasses, legumes and shrubs have been established in a series of demonstration experimental plots, on both sides of cut and fill sections. The purpose of these plots is to get more information on desirable vegetative and woody plant species that will provide roadside bank protection, attractiveness, cover for wildlife and beneficial insects and low maintenance cost. Ideally a low-growing, erosion-controlling and self-maintaining shrub could replace grass cover, which requires frequent mowing in most sites.

The amount of right-of-way hedgerows needed for effectively managing quail in any one area will depend on the available potential sites. In some areas right-of-way sites will hardly exist, in others they will be so abundant that establishment of hedgerows along a fraction of them will be adequate.

Field Borders

Of all the sites where hedgerow management requires interagency support, the field borders rate among the foremost. This applies to all the phases of managing these sites: maintaining those still existing, restoring those previously destroyed and creating new hedgerows. In the past the attitude of agricultural agencies was based on getting rid of the hedgerows to facilitate field work and to destroy the habitat of crop-damaging insects and diseases. This view was natural and sound as long as hedgerows were abundant and their value to wildlife and other beneficial animals and plant life was relatively unknown. That day is past.

A moratorium of some sort is needed on hedgerow destruction until such time as a mutual agreement can be reached that their existence is profitable or irrefutably intolerable. In the interim every effort should be made to maintain the remaining hedgerows and encourage development of others in new sites. At the same time every effort has to be made to take advantage of the possibilities for using hedgerows in biological insect and noxious weed control and for soil and water conservation. If subsequent studies clearly show that hedgerows in field borders are generally impractical, an interagency agreement is needed on this aspect so that conservation departments can concentrate on other game management practices; or, if they are acceptable, an all-out program can be launched to preserve and increase them.

While the above pragmatic problem is being attacked, landowners must be queried to learn how many are planning to leave or destroy remaining hedgerows and how many would allow improvement of poorly stocked sites and restoration or establishment in new sites. There are several methods for doing this; these include mail questionnaires, personal contact and distribution of questionnaires at meetings. Simultaneously, information should be obtained on the incentives landowners feel are necessary in order to accept hedgerow management for wildlife. This doesn't mean that landowners would necessarily demand or get financial remuneration. Incentives could include added hunting opportunities, remuneration for hunter damage to property, and assistance in how to perform cultural practices. Above all, landowners must be informed of the total benefits of having hedgerows on their farms over and above hunting values, and the availability of planting stock. Recognition of the contribution that landowners make by managing hedgerows is necessary since the accruing benefits are in part public.

The results of the above surveys will provide guidelines for determining the management efforts and the type of incentives required by landowners for maintaining old and producing new hedgerows on their properties.

Woodland Borders

Practically all of the philosophical and technical material covered under the section on "field borders" applies to woodlands, although some difference in selection of species and site and site preparation will have to be considered. For example, in poorly stocked woodlands that had been previously pastured, the planting of aggressively spreading species such as multiflora rose in bordering hedgerows would be objectionable. Conversely, this would not be as serious if the bordering woodlands contained enough large trees to form a canopy that would tend to shade the rose and prevent it from successfully spreading.

Logically the planning requirements for establishing hedgerow borders along woodlands should be a cooperative function of foresters, game managers, and soil conservationists. This cooperation now exists but will have to be intensified if this practice is to be adequately accomplished. Since woodland borders on many farms offer the greatest number of sites for shrub borders that do not conflict with other land uses, a greatly expanded program is warranted. Such problems as whether to plant shrubs adjacent to the woodland or as part of the understory just inside of the peripheral edge of the forest trees will require a forester's and an ecologist's guidance and approval.

Ungrazed woodlands with shrub borders, along with their timber and watershed values, would provide additional cover, feed, and nesting sites for some wildlife species and thereby approach the maximum of multiple use.

Stream and Other Waterway Banks, Gullies and Other Odd Areas

Since cover is required along stream and other waterways for erosion control, these sites offer special advantages for wildlife. The banks of streams and other waterways, where possible, should be used as the foci for establishing a permanent network of hedgerows. Other sites such as field borders are much more vulnerable to land-use changes that could sooner or later result in their removal. The value of these sites for multipurpose interests has been recognized in the provision of cost-sharing for establishing streambank cover under the Agricultural Conservation Program. While the considerable number of miles of cover established on these sites show the interest in this practice to date, the potential hasn't even been scratched.

Many streambanks are located in permanent bluegrass pastures which frequently are barren of vegetation and are virtually biological deserts. These pastures produce neither a significant amount of forage for cattle nor cover for wildlife. This situation thus offers an ideal site for vastly improving the wildlife habitat and for soil erosion control.

Streambanks also offer an ideal opportunity for advancing multiuse recreational programs since these sites provide habitat for both fish and wildlife. They could be used as the basic land type around which to establish a system of fish and game management units.

The banks of drainage ditches are comparable in many respects to natural streambanks as ideal sites for wildlife habitat improvement. In planting stream cover, shrub species should be selected that will not encroach into the ditch channels. Through a combination of species selection, herbicide treatment, and improved mechanical devices, it should be possible to develop the necessary means for establishing and controlling ditchbank vegetation so that it will serve multipurpose interests.

Other waterways along which hedgerows can be manually established or allowed to develop naturally are ponds, rivers and lakes.

In gullies and odd corners, shrub cover is being planted or allowed to develop naturally at a higher rate than in probably any other location. A great many such sites still exist, however, where this habitat improvement practice can still be advanced.

Special Problem Areas

The cover requirement of quail and other wildlife species for an extensive distribution of hedgerows poses a special problem in the management of habitat on selected areas. This applies especially to state-owned lands but also to some private areas. There are many relatively small scattered areas which lend themselves to management because of natural features, public ownership and landowner interest. Unfortunately such areas regardless of the excellence of their habitat are not large enough to contain most species of wildlife, particularly upland game birds, because of the dispersal behavior of the birds. This problem is so important that every effort should be made to determine whether movement could be controlled even though the opportunities to develop the necessary techniques seem remote in the light of our present knowledge.

A research project for this purpose is proposed later.

Summary

Quail have been gradually declining in Wisconsin for about 100 years. The primary factor affecting this loss has been the destruction of the main component of quail habitat: hedgerow cover. If the rate of hedgerow loss observed on the study area at Prairie du Sac continues in other places, quail will disappear from many parts of Wisconsin in about 10 years, particularly on the borders of the occupied range. Winter weather will be a conditioning factor on the length of this period.

The success of preserving and restoring hedgerow cover in the future depends on the total value of this cover type to game birds and mammals, songbirds, other mammals, beneficial insects, and soil and water conservation. An evaluation of the pros and cons of hedgerow values indicates that an all-out effort for a preservation and restoration program is warranted.

The success of a hedgerow management program, which

includes shrub borders adjacent to woodlands, depends upon both an interagency and a landowner acceptance of the philosophy and goals of maintaining and increasing this cover type: the presence of hedgerows approximately 12 feet in width in a ratio of 1 mile to 450 acres of rural land in the presently occupied quail range of the state. An approach is proposed to obtaining an interagency evaluation of the program required to attain these goals. Generally we know what is needed to manage quail on extensive areas; still required is information on how to control the movement of quail and related species to manage them on small areas.

The present Wisconsin quail population can still sustain hunting seasons. Closing the hunting season, except for extreme emergencies as was the case in 1962, can be expected to result in public disinterest in the need for managing quail and to hasten their extirpation in the state. Length of seasons, refuge and stocking values and specific habitat needs are discussed.

Emphasis in this section is placed on hedgerow preservation and restoration, including a philosophical appraisal of the program and methods for obtaining support to conduct an all-out management program for this cover type.

FUTURE RESEARCH

As with all studies, this one ends with recommendations for further research concerning Wisconsin quail, related species and land use. Emphasis in the future, however, should be primarily on methods of preserving and establishing habitat.

1. Surveys of the population and habitat status, basic components of any wildlife study, must be continued. Time-taking studies on for example movement and mechanics of population changes are not needed, at least not in the near future. However, surveys to determine population status and trends are always needed to set hunting seasons and constantly measure the impact of habitat changes. Intensive winter surveys can be omitted since year-round population trends can be calculated from whistling counts and winter weather records.

2. Precise information on the current plans of landowners for their remaining hedgerows and factors affecting the acceptance of management practices is an immediate need. Of equal or greater importance is an interagency research project on the liabilities and advantages of having hedgerows along roadsides and woodland and field borders. This information is specifically available for wildlife interests, but not for other animals or recreational, biological and conservation values. Included in this study should be an economic appraisal of advantages and disadvantages to landowners.

3. Research should be expanded to get more information on the best shrub species for hedgerows and cultural methods of establishing them. For this purpose a collection of native species with desirable characteristics is required. Such collections should then be transplanted to an experimental nursery where they can be observed to determine whether these characteristics would persist and to develop methods for propagating them in nurseries. The best species should then be made available to other nurseries with instructions on how to propagate and maintain them for mass production. Considerable information is also required on how to successfully and economically establish shrubs in hedgerows.

4. One of the major difficulties in habitat development lies in the dispersal behavior of many species, particularly quail. The spring movement averaging about 1 mile by Wisconsin quail necessitates the maintenance and establishment of cover over a wide area, a minimum of 15,000 acres. At the same time the amount of cover development required on areas where hedgerows have been drastically reduced is relatively great. Despite the great loss of cover since the mid-1800's when habitat was optimum, scattered remnants exist on many farms. A small addition of hedgerow cover on a series of adjacent farms could be sufficient to satisfy the requirements of several coveys of quail if these birds did not disperse the distances they do in spring.

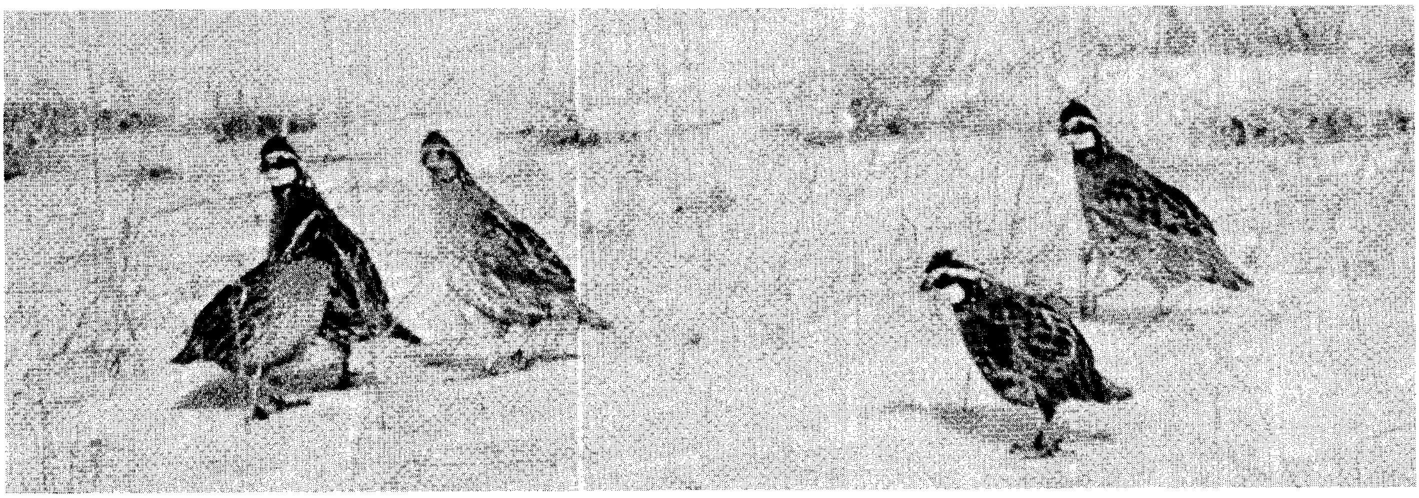
This problem applies to all wildlife species, but particularly to upland game birds. Therefore, if a method could be developed that would control the movements of upland game bird species such as quail, intensive habitat development practices could be successfully performed on isolated units of land, providing the owners were interested and natural niches for maintaining and establishing cover existed. Obviously this would also apply to state-owned and controlled lands.

Research on the problem described above would probably require considerable effort and time before any usable results accrued. However, the potential application warrants the effort. The research required in such a project would include detailed examination of habitat features and quail behavior to determine what motivates movement. It is possible that movement could be controlled through artificial means such as planting caged females, trapping and holding wild birds in captivity through the dispersal period, manipulating food and cover, operating calling devices or treating vegetation with chemicals that would attract or repel either sex, or even employing such elaborate techniques as beaming various light rays and sound waves of varying intensity and length. Such approaches may seem remote and complicated, but if wildlife is to be perpetuated in this highly developed world, techniques of this type may be the solution.

If such a research project were to be undertaken it should be a cooperative venture with either several states participating through coordinating groups such as the U.S. Fish and Wildlife Service and the U.S. Department of Agriculture or any one of the fish, game and conservation commissioners associations. It should include related species, since the findings could apply to most upland game birds. This effort could be combined with current studies on developing methods for controlling the crop depredations of waterfowl, blackbirds, etc.

5. A study is also needed of agricultural support programs to determine how much of a contribution is made by the general public to farmers in relationship to the question of how much responsibility farmers have in managing their lands for wildlife. Likewise, information is needed on how much of a contribution hunters and the nonhunting public benefitting from wildlife directly or indirectly make to rural landowners and to the management of the wildlife resource.

6. Finally, two basic interagency studies are needed concerning rural land-use: (1) the impact of present agricultural and wildlife land use practices on each other; and (2) a listing of all agencies concerned with natural resources, the authority which established them, their functions and responsibilities.



APPENDIX A

Whistling Counts as a Survey Technique

While fall and winter censuses provide invaluable statistics for population trends on study areas, more extensive methods were desirable for state-wide surveys and additional area data. A review of whistling counts by Hawkins (1936) at Faville Grove near Madison, a report by Bennitt (1943) and personal discussion with him on whistling and hunting success relationships suggested a technique for obtaining state-wide quail population statistics. Hawkins' counts are shown in Table 55.

The relatively large number of males heard whistling appeared to offer promise of a quantitative method which could be used to census quail in early summer. In the past some doubt existed that counts of whistling males would represent spring and summer quail numbers, as Stoddard (1931) had deduced that generally only unmated males whistled the familiar "bobwhite". In a later report, Bennitt (1951) summarized ten years (1938–48) of studies on bobwhite whistling and agreed with Stoddard that it was probably the surplus (unmated) males that called. His deduction was based on a comparison of summer whistling cocks and fall quail densities on study areas. His studies also showed a significant correlation between whistling count indices and hunting success.

During the spring and summer of 1943–45, we made many incidental observations on whistling males on the 4,500-acre Prairie du Sac quail study area. Though our preliminary counts were made on only parts of the study area in any one day's census, it appeared that the area as a whole had almost as many males whistling as were present in our spring populations on April 1. The seasonal distribution of whistling in these preliminary studies was comparable to that recorded by Hawkins (1936).

In 1946 and 1947, we intensified our efforts to get total counts on all of the birds whistling in the area. Our counts were made by cruising in an autmobile and stopping often and long enough to listen for males whistling in all parts of the area. Fortunately, there were access roads throughout the Prairie du Sac study area that were within audibility range of most of the whistling males. We listened 3–5 minutes at each stop to assure ourselves that all birds that were whistling at each point would be heard and counted. The results of these counts are shown in Tables 55 and 56. The 1946 and 1947 counts sustained our earlier deduction on the relationship of the number of whistling quail and the spring surviving males. Actually the count of 42 males whistling on June 8 in 1946 exceeded the April 1 population of 33 males. On June 24, 1947, a total of 52 whistling "bobs" was recorded in comparison to the 56 males composing the April 1 population, and on July 6, 1948, 20 whistling males were counted and the April 1 population contained 31 males.

The increase in bobwhite males from April to June in 1946 was undoubtedly the result of an ingress of males which at least temporarily exceeded the egress. As was reported earlier, quail movement is relatively great and seemingly unoriented during this period. A whistling count on a surrounding 8,000-acre area revealed 64 birds. This density was approximately one and three-fourths times greater than on the primary study area.

The difference between the behavior of Wisconsin quail, where evidently most or all of the males whistle at the peak period of this activity, and the behavior reported in the Missouri studies where only the unmated males are alleged to whistle may involve both a phenological and a density relationship. The Missouri counts are made in mid-July and by this date the intensity of whistling has declined (Tables 55, 56 and 57). However, this would not appear to account for the total difference, for even though Wisconsin quail densities are considerably below those for Missouri the counts obtained on our transects are equal to or higher than whistling counts made in Missouri. Stoddard's observations (1931) on whistling by unmated males were also derived from experience with much higher populations than are found in Wisconsin.

Additional information on quail whistling behavior in Wisconsin was also obtained by direct observation of males during

TABLE 55

Quail Whistling Counts

Faville Grove* 1936		Prairie du Sac 1946	
Date	No. Males Whistling	Date	No. Males Whistling
April 1	1		
April 15	5		
April 25	3		
April 26	1		
May 5	6		
May 10	1		
May 15	4		
May 20	9		
May 25	7		
June 1	2	June 6	19
June 5	6	June 8	42
June 10	12	June 20	23‡
June 15	7	June 22	36‡
June 25	3	July 25	10
July 1	23	July 26	8
July 4	6†	July 27	8
July 11	19	July 31	6
July 12	15	Aug. 1	0
July 13	2	Aug. 2	4
Aug. 14	5	Aug. 4	6
Aug. 15	2		
Aug. 16	4		
Aug. 23	3		

*The Faville Grove counts are taken from Hawkins (1936). All counts were made between 4:30 a.m. and 8:00 a.m.
†Drouth effect implied.
‡Two-thirds of area checked.

TABLE 56

Spring Quail Observations and Whistling Census, Prairie du Sac, 1947
(½ hour before sunrise to 8 a.m.)

Date	Total No. Males Whistling	Single Males Observed		Paired Males Observed	
		Whistling	Silent	Whistling	Silent
4- 1	0				
4- 8	0				
4-12	0				
4-15	0				
4-19	1				
4-22	2	1			
4-26	4	0	0	0	3
4-29	3	0	1	0	6
5- 1	0	0	6	0	2
5- 3	25	0	1	0	1
5- 6	6	0	3	0	3
5- 9	6	0	3	0	5
5-11	3	2	0	0	3
5-14	8	1	2	1	3
5-16	6	3	0	2	3
5-21	5	1	0	0	2
5-31	10	1	0	0	0
6- 3	29	3	0	0	0
6- 6	32	0	0	0	1
6-10	21	2	1	0	0
6-14	19*	3	1	0	1
6-17	30	3	0	0	0
6-20	30	2	0	0	2
6-24	52	6	0	1	0
6-28	50	4	0	0	0
7- 2	48	0	0	0	0
7-12	18*	0	0	0	1
7-13	5*	0	0	1	0
7-26	0	0	0	0	0
8- 9	1	0	0	0	0

*Partial counts.

the 1947 counts (Table 56). The location of all the whistles heard and birds observed was recorded. These observations show that as whistling intensity increased, practically all unaccompanied males were whistling. More paired birds were seen early in the breeding season than later. Generally males accompanied by hens did not whistle, but there were some exceptions. While it was difficult to determine whether or not most of the single males seen in June and July were mated, it appeared that during this period mated males also whistled, but only when they were not accompanied by their hens.

These observations were the basis for establishing a statewide system of transects in 1948 to inventory quail in many of the counties within the quail range. To determine whether the county transect technique required refinement, two approaches were used. First, more detailed studies of quail whistling behavior were set up at Prairie du Sac and then these results were compared with the data from the county transects.

At Prairie du Sac we first followed the daily pattern of whistling during late June and July in groups of birds within hearing distance of selected locations. An understanding of the daily pattern of whistling activity would point out the most effective time of day for making whistling counts and indicate the magnitude of deviation which might be expected at other times. Two 8-hour morning periods of observation and three afternoon periods were used for this, and the total number of bobwhite calls was recorded for each listening station by half-hour intervals. The number of individuals calling was also noted when possible. Richard Pillmore, a University of Wisconsin research assistant at that time, was largely responsible for gathering information on this study.

Next, a transect route was run 15 times on the Prairie du Sac study area between June 2 and August 11. Stops were made at 42 pre-selected points with a 3-minute listening period at each. The results obtained are plotted in Figures 27 and 28 for the morning and evening hours, respectively. The intensity of whistling was greatest from 4:30 to 5:30 a.m. It tapered off between 5:30 and 6:00 a.m. when there were lulls in activity. After 6:30 activity was sporadic, giving rise to a sawtooth pattern. There were even some half-hour periods later in the morning when no calls were heard. The pattern in the afternoon period continued to be sporadic in nature, but at times was quite intense. There was a late afternoon lull and a slight pick-up as evening set in. These two figures also reflect a seasonal pattern in intensity, June and early July showing more intensity than late July. The seasonal picture will be presented in later paragraphs.

Finally to obtain further data on daily pattern, the county transects were examined by 15-minute intervals post-sunrise, averaging the total individual birds heard. Total calls were not recorded. Also, the results obtained from the 15 transects run on the Prairie du Sac area were separately analyzed by 15-minute intervals. Both the results from the county transects and the Prairie du Sac transects are shown in Figure 29 as 3-point moving averages. The data were not combined into one curve, for the Prairie du Sac transects run over the same route might affect the result due to an area pattern of quail distribution. To partially allay this effect, we regularly alternated the direction in which the Prairie du Sac transect was run. In the county data this area effect could not be present, because each transect was over a different territory and all are averaged together. Actually the results obtained are not dissimilar. The lag in the early part of the Prairie du Sac curve is due in part to a lack of birds at both ends of the territory covered by the transects, and alternating direction of the transect could not eliminate this effect.

A comparison of this pattern of morning whistling activity with that shown in Figure 27 displays good agreement. Both are at a peak soon after sunrise and are at a high level of intensity for an hour to an hour and a half after sunrise. Figure 29 does not show the sporadic peaks displayed later in the morning as in Figure 27 of course, because the former is averaged from a number of counts.

From these data it is evident that for maximum counts, transects should run no longer than about 1 hour and 15 minutes after sunrise. This procedure is not adhered to in running the county transects, because it was desired to cover a more extensive area than this permitted, though in 1957 a change to 20-stop transects was adopted. Since the results were regarded

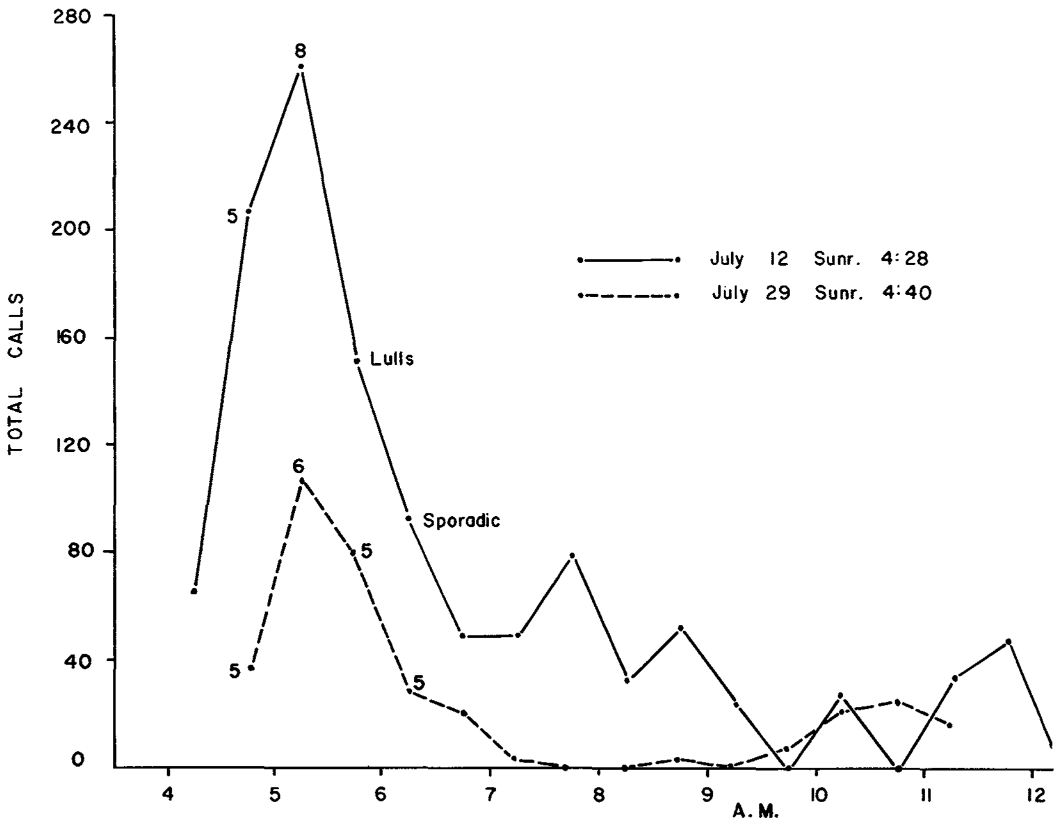


Figure 27. Daily pattern of whistling activity, morning hours, C.S.T., (1948). (5, 8, etc. are number of individual birds calling where known. Total calls per half-hour interval).

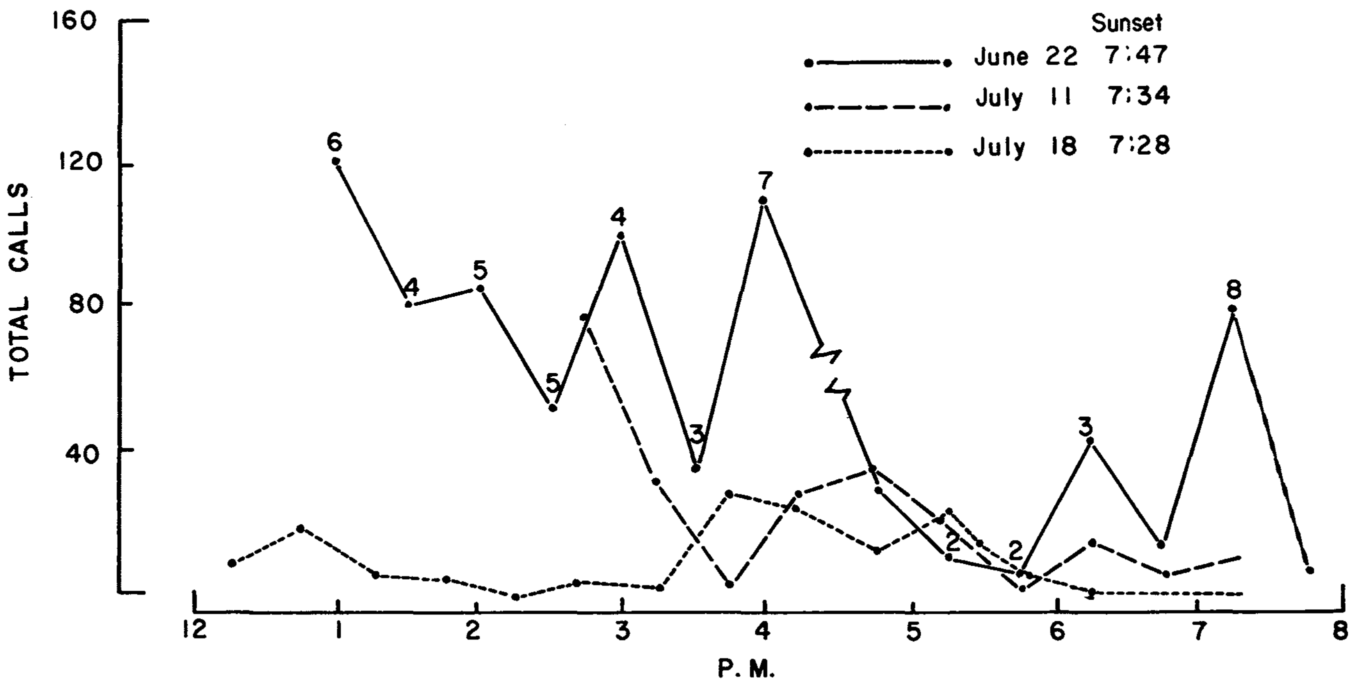


Figure 28. Daily pattern of whistling activity, afternoon hours, C.S.T., (1948) (6, 4, etc. are number of individual birds calling where known. Total calls are per half-hour interval).

TABLE 57

Results of Transects on a Standard Route on the Prairie du Sac Area, 1949*

	No. Bobwhites Whistling at Each Stop															
	June							July						Aug.		
Stop No.	2	4	10	13	17	20	30	5	10	18	20	25	30	3	11	Avg.
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
2	0	0	0	3	0	0	2	0	2	0	0	0	0	0	0	0.5
3	1	1	0	1	2	0	2	1	1	0	0	0	0	0	0	0.6
4	2	3	3	4	1	0	3	2	1	0	0	3	0	0	0	1.5
5	3	2	3	2	2	0	2	1	3	0	3	1	0	0	0	1.5
6	0	0	4	3	2	0	2	1	2	0	1	0	0	1	0	1.1
7	2	1	0	3	1	0	3	0	4	0	1	0	0	1	0	1.1
8	4	5	1	2	4	0	2	4	3	0	0	2	0	0	1	1.9
9	5	4	1	4	4	3	3	5	3	0	4	2	0	0	5	2.9
10	1	4	1	4	4	2	1	0	1	0	3	1	0	1	0	1.5
11	1	0	2	6	1	1	2	0	3	1	1	3	0	2	0	1.5
12	2	4	0	4	3	2	5	3	5	0	2	1	3	1	2	2.5
13	1	2	2	3	1	3	5	0	2	0	3	3	2	2	1	2.0
14	4	3	3	6	3	1	6	5	7	0	1	4	2	2	1	3.2
15	3	4	8	4	3	2	5	1	5	1	1	0	3	2	0	2.8
16	1	4	2	4	3	2	2	0	0	0	1	0	0	0	0	1.3
17	3	3	5	2	5	3	1	0	2	0	1	0	0	0	0	1.7
18	3	0	0	0	2	1	0	0	1	0	0	3	0	0	0	0.7
19	2	1	2	3	0	5	2	0	2	3	2	2	5	0	1	2.0
20	3	3	4	3	1	3	2	1	2	3	3	1	3	2	0	2.3
21	2	3	0	1	3	8	3	2	5	1	0	1	2	0	0	2.1
22	4	1	1	3	3	2	4	2	3	0	0	0	2	0	0	1.7
23	1	0	5	3	3	4	2	3	0	0	0	1	1	0	1	1.6
24	0	3	6	1	3	5	2	3	3	0	0	0	2	0	1	1.9
25	0	1	9	2	4	6	3	3	5	2	2	0	3	2	1	2.9
26	3	1	5	4	0	4	5	6	4	0	2	1	3	4	1	2.9
27	2	0	7	4	1	3	8	7	2	2	7	1	3	3	3	3.5
28	0	0	2	0	2	2	2	2	2	0	0	0	0	1	1	.9
29	0	0	2	0	2	2	1	3	2	0	1	0	0	1	0	.9
30	3	2	7	6	6	5	6	5	2	5	3	0	0	1	5	3.7
31	5	6	6	4	5	4	2	0	3	4	2	0	0	0	2	2.9
32	0	0	6	5	0	2	1	1	0	0	0	0	0	0	0	1.0
33	0	1	2	2	3	2	0	2	0	1	1	0	1	0	0	1.0
34	1	3	4	5	2	6	0	2	0	1	0	0	0	1	4	1.9
35	0	2	4	4	2	3	3	2	2	2	3	0	0	1	2	2.0
36	2	1	7	3	1	9	0	1	0	7	2	0	0	0	5	2.5
37	0	0	5	4	3	8	6	4	0	5	3	2	0	0	1	2.7
38	0	1	4	1	1	4	0	5	0	0	2	0	0	0	0	1.2
39	0	0	3	0	0	1	0	0	1	0	0	1	0	0	0	0.4
40	3	3	3	1	1	6	0	0	2	0	1	2	0	0	1	1.5
41	1	0	3	2	2	5	0	0	3	0	0	0	0	0	0	1.1
42	0	0	4	0	1	5	0	2	2	0	0	0	0	0	0	0.9
Total	68	72	136	116	90	124	98	79	90	38	56	35	35	28	39	1.8

*The direction of the route was reversed each time it was run.

only as an index, it was not necessary that full activity prevail during the entire run.

The "bobwhiting" of male birds has a phenological basis, and hence there is a strongly developed seasonal pattern of whistling activity. It is necessary to determine this pattern and the factors that affect it, as well as the daily pattern, to compare and evaluate the results obtained on whistling count transects.

The 15 transects run over the same route on the Prairie du Sac area were conducted primarily for the purpose of documenting the phenological pattern. The route with 42 standard listening points was laid out, and this was run at intervals during June, July and early August. The route was 24 miles in length. Each run of the transect was commenced at sunrise, with the direction of the transect alternated regularly. Three-minute stops were made at each of the 42 points, and the total number of individual birds whistling at each point was recorded. The transects were completed in 3 hours. Temperature was recorded at start and finish, and only calm mornings (wind velocity under 6–8 mph) were selected for making the runs.

The results of these transects show that a definite position or area effect is present, the average number of birds heard at each point through the series varying from no birds at Stop 1 to 3.7 birds for the average at Stop 30 (Table 57). There is also a wide variation present at the same stops on different runs, other than that related to the seasonal factor. At Stop 25, for example, 9 birds were heard on June 10, whereas only 1 and 2 were heard on June 4 and 13, respectively. This is partially the result of movement of birds and partially due to lulls in whistling. In other cases, stops showed very great consistency as, for example, Stop 31 over the first six runs. The variations noted are greater at their extremes than can be accounted for by chance alone (Table 58).

The seasonal trend in whistling activity as based on total individual birds heard whistling is shown in Figure 30 (based on data from Table 57). Reference may again be made to Figures 27 and 28 where the curves for the different dates reveal the seasonal intensity of whistling as based on total calls heard, rather than individual birds calling.

Also in Figure 30 the maximum and minimum daily temperatures and the daily rainfall for the season, as recorded at the dam at Prairie du Sac, are presented.

Only one point on this seasonal curve is badly out of line with the general trend. This is for June 17. There is no apparent explanation for this low count other than to note that it took place on a day having a "low overcast" sky. Also it followed a cool spell. The low count on July 18 was possibly induced by the "light drizzle" depressing the "enthusiasm" of the birds.

Three transects over the same route were also run on the Dunn County study area. The results were:

June 7—29 individuals whistling
June 15—38 individuals whistling
June 22—42 individuals whistling

Comparison of these seasonal counts with Table 58 suggests that the peak season of whistling activity occurred between mid-June and early July in 1949; the county transects, therefore, were scheduled to be run when it became apparent that the peak had been reached. In 1947 and 1948 less specific studies indicated that the peak was reached in late June and early July and was perhaps sharper.

A number of studies have been conducted in other states to evaluate the effect of various factors relating to whistling counts such as length of time spent listening at each stop, wind velocity, temperature, dew, and cloud condition. Elder (1956), for example, reported that only 20 per cent of the daily variation in whistling was due to weather. However, his study was based on comparing whistling counts at only two stations.

The variation in whistling counts (calls) obtained on different dates but on the same area superficially indicated that censuses of bobwhite quail using this technique are subject to excessive error. However, these were made under a wide range of conditions. An experienced census-taker would avoid days when conditions were not right and, by recognizing the difference between sporadic and active whistling, would obtain counts with much lower variation. Ideally the range of dates within which the call-survey is made should be determined each year from the trend of whistling activity in a test area. It is necessary for this purpose to sample an area large enough to eliminate the daily variation resulting from movement. Currently our general recommendation for Wisconsin is that the transects be run between June 15 and July 4.

TABLE 58

Minimum Differences in Transect Totals Required for Significance of Difference at the 5 Per Cent Level

Mean of the Two Transect Totals Being Compared	Minimum Difference in Totals Required	Mean of the Two Transect Totals Being Compared	Minimum Difference in Totals Required
200	41	50	21
180	39	45	20
160	37	40	19
140	34	35	18
120	32	30	17
100	29	25	15
90	28	20	14
80	26	15	12
70	25	10	10
60	23	5	8

The census-taker may over a period of years acquire an experience with plant phenological items that he can tie in with whistling activity. A number of such relationships were observed in this study, but none appeared to be simple enough to serve as an indicator of when to begin making whistling counts.

Three general statistical methods may be used to compare differences in transect results (total birds heard), within a year or between years. All require the assumption that the population is the only variable and that all other factors are constant. Since this is patently untrue, an attempt must be made to select standard conditions for conduct of the transects. The analyses can be used only as guides since it is not possible to duplicate the conditions exactly between transects.

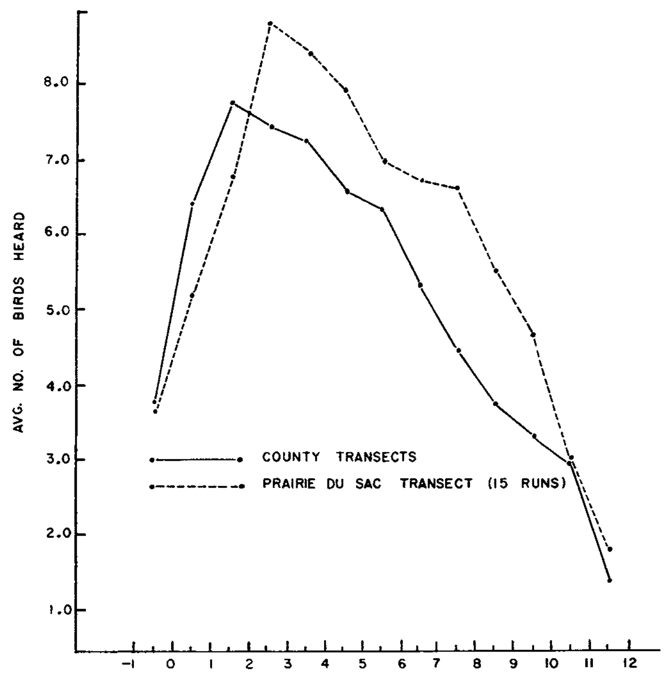


Figure 29. A comparison of the average number of bobwhites whistling at Prairie du Sac and on various county transects throughout the state.

One method involves a computation of the mean number of birds heard per stop and its standard error for each transect. Comparisons of transects would then be made through t values computed from mean differences and the standard error of the differences. This method suffers from the great variability introduced by nonrandom variation within the transect; i.e., the various stops do not sample a homogeneous population due to local differences in range quality. A second method, involving extra effort, would be to make 3 or more runs of each transect and compute the mean of the transect totals and its standard error. Again comparison of means could be made through the t test as above. A third method, perhaps the most direct, is a Chi-square test under the hypothesis that the two transect totals being compared do not differ from their mean. Deviations from their mean greater than expected by chance alone lead to the conclusion that a real difference exists.

For comparison of a number of such results it is convenient to use a table (Table 58). It is derived from Chi-square computations. It lists minimum differences in totals needed to give a probablity of drawing so large a difference at the 5 per cent level of expectation ($p < .05$) for various mean values of transect totals under comparison. For example, if A yielded 58 and B totalled 84, the mean is 71. The difference is 26. Entering the table at 70, we see that this difference just exceeds the requirement for a probability beyond the 5 per cent level. Again, the statistical test is applicable only if factors other than population did not affect the results. The application of this significance test is the responsibility of the technician who must appraise the degree to which other factors may have contributed to the difference.

In Table 6 transect comparisons are made between years by this procedure. If the minimum difference specified above is not achieved, the runs are judged as "same". This only means that we are unable to claim a difference (we accept the "null hypothesis"), though it must be clearly understood that we do not imply that there may not be a difference.

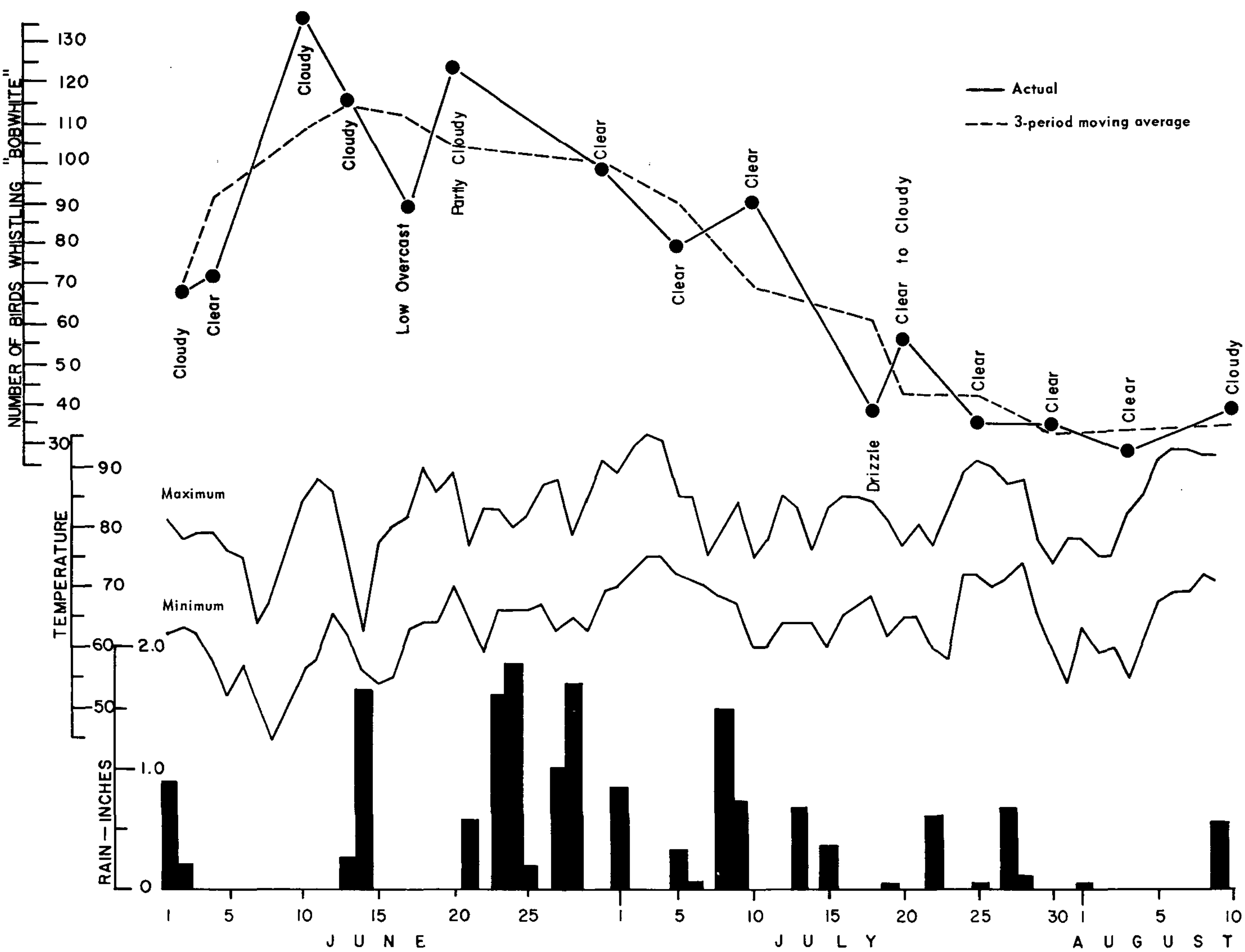


Figure 30. Seasonal pattern of whistling in bobwhite quail at Prairie du Sac, 1949, occurring under different weather conditions. (Weather data gathered at Prairie du Sac.)

APPENDIX B

Reproductive Behavior of Pheasants in Pens

Introduction

When a population of animals is reduced by some short-term factor or combination of factors, recovery is often quite rapid. But once the population reaches a certain level, it tends to become static, or it may decline. This was first illustrated by Errington (1945) in the bobwhite quail under the "inversity" concept. What factors operate to limit the size of the population of a species once it reaches saturation levels in its own habitat has long been the object of speculation.

Einarsen (1942) observed a spectacular increase of pheasants from an original stocking of 2 cocks and 6 hens in 1937 to 1,540 in the fall of 1941 for an average, annual gain of 277 per cent per year on Protection Island, Washington. The percentage increase declined from about 400 for the first three years to 100 in the fifth year. There was no hunting on this area.

On Pelee Island, In Lake Erie in Ontario, a pheasant population grew from an estimated 36 stocked birds in 1927 to a fantastic high by the mid-1930's, estimated to be between 50,000 and 100,000 (Clarke, 1947). Stokes (1954) believed this estimate was too high and that 50,000 was the peak level reached. Explanation of population behavior that is seemingly density-dependent continues to be one of the main objectives of current game research.

Our studies reported here were conducted primarily to get some additional leads on the specific effects of density on the reproduction phase of wild quail populations. Because facilities, equipment, and experimental birds were available, the pheasant was used in these pen studies on reproductive behavior. This species also reproduces readily in captivity. It was expected that the results of these studies would also help to interpret the population behavior of other gallinaceous species. Since the relationships of these studies were covered in previous sections of this report, discussion here is limited to the basic findings and only a few generalizations on population dynamics.

The effect of density on reproduction was investigated in a series of four studies. The first (I) and second (II) were conducted as the result of fortuitous conditions. Pheasants used in other studies provided the opportunity to learn whether density affected mating behavior and whether extremely high density affected egg laying and nesting. A third (III) study was then designed to determine whether high density, controlled at two levels, resulted in a measurable effect on reproductive success and, if so, the possible mechanics operating in the occurrence of such a condition. Finally the reproductive performance of 1- and 2-year old or older birds was compared (IV).

Density Effects on Mating Behavior (Study I)

On May 18, 1948, the study to determine the effect of extreme crowding on mating behavior and the implications of this on reproduction was initiated. Twenty hens and 4 cocks (all 1 year old) were transferred from 12′ x 12′ breeding pens, to 75′ x 25′ enclosures. While still in the 12′ x 12′ pens, these birds were confined at the rate of 5 hens to 1 cock. These hens had previously laid an average of 25 eggs each.

First, 10 hens and 2 cocks were placed in the large pen. The cocks immediately engaged in violent fighting and pursuit of the hens. Then 5 more hens and 1 more cock were placed in the pen, and the strife decreased greatly. The moment the remaining 5 hens and single cock were transferred to the large pen all strife ceased, although the cocks continued to pursue the hens. The experiment was completed in less than 1 hour.

While this experiment was conducted under artificial conditions, it demonstrated the sensitivity of birds to density and its effect on mating behavior. The cocks reacted immediately to the presence of the hens by exhibiting sexual drive and intolerance of each other. Then as the density of birds was increased, the cocks ceased fighting but maintained interest in the hens. Apparently the increase in hens suppressed the competition among the cocks, because the ratio of hens to cocks remained the same and the only change in pen conditions was the increase in the number of birds.

Possibly the procedure used in this experiment was responsible for a part of this behavioral reaction; we did not test this possibility. Density changes would not appear to affect egg fertility since the cocks mated with the hens under all densities.

Effects of Extreme Density on Egg Laying and Nesting Behavior (Study II)

The purpose of this study was to make some observations on the egg laying and nesting of artificially propagated pheasants penned in small enclosures at high densities. Adult pheasants were penned on June 11 at the rate of 18 cocks to 18 hens in six large wire enclosures which were approximately 100′ x 30′ x 7′. This is a density of about 500 birds per acre. This density is far higher than in any natural population, but it was thought that under this extreme condition, density effects would be sharply brought out. These adult pheasants had been used for egg production earlier in the year in breeding pens (12′ x 12′ enclosures, 1 cock to 5–6 hens). Most if not all of these hens had been laying eggs steadily from mid-April up to the time they were transferred on June 11. While the hens were in the breeding pens, the eggs they laid were removed daily. The large pens, after the hens were transferred into them, were not examined again until July 17.

On July 17, most of the hens were still laying or were incubating nests. An average of 6–7 nests was found in each of the pens. The total number of eggs laid in nests by the 108 hens was 435, and there were also many scattered eggs which had not been laid in nests. The frequency distribution for the number of nests and the number of eggs in each is as follows:

Number of eggs	1–5	6–10	11–15	16–20	Total Nests
Number of nests	4	16	8	10	38

Gross examination of the eggs in nests showed that many of the nests contained eggs laid by two or more hens. The frequency distribution for nests containing eggs laid by a minimum of from 1 to 3 hens was as follows:

Minimum number of hens laying	1	2	3
Number of nests	13	18	3

A later study planned for these pheasants required that the eggs in the nests be removed, permitting all of the eggs to be broken and their contents examined. As many as four different stages of embryo development were found in the eggs in some nests. Lack of development was regarded as a stage, also. The frequency distribution of nests having multiple stages of embryo development was as follows:

Number of stages of embryo development found	1	2	3	4
Number of nests	11	12	8	7

Eggs found in the nests were also classified for presence or absence of an embryo, whether it was fresh or decayed, and the age of the embryo. The results are shown in the following table:

	Eggs Showing No Development		Eggs Containing a Developing Embryo			
			Age of Embryo in Days			
	Decayed	Fresh*	1–6	7–12	13–18	19–24
Number of eggs	79	127	23	62	83	61

*No evidence of deterioration.

It was impossible to determine how many hens incubated a given nest. Hens were found sitting on almost every nest we examined. In many cases the hens permitted the observer to stand directly over them without flushing. In other cases the hens fled from the nest upon our approach. In one instance two nests were found which were located less than 6 inches apart. Each one of these nests contained eggs with 10- and 22-day-old embryos. From the external characteristics of the eggs, we were able to deduce that the 10-day-old embryos in each of the nests had been laid by the same hen and the 22-day by another. The reason for these two hens laying in each other's nests may be that their proximity resulted in the failure of the hens to recognize their own nests. Although most of the other nests in the pens contained eggs which were laid by more than one hen, these nests were at least 5 feet apart, and it would be expected that nest recognition by the hens would be easier.

The consequence of hens laying in nests in close proximity is indicated in the following conjecture:

Hen pheasants in dense populations lay eggs in each other's nests. If only one hen incubated each nest, would she hatch the oldest embryos and then take her chicks and abandon the rest of the developing embryos? Such nest abandonment would result in the hatching of only a few of the total eggs laid, and the waste of the rest. It is only remotely possible that another hen might be physiologically and psychologically ready to adopt the nest and continue to incubate the remainder of the eggs.

In another experiment in 1948, incidental to this study, 10 hens and 1 cock were penned in a 25x75′ enclosure devoid of cover in early April. All of the hens laid eggs at the usual rate, 1 egg per 1.3 days (Buss, Meyer and Kabat, 1951). The hens laid in each other's nests but only one hen attempted to incubate the eggs in one of the nests, a dump nest containing 58 eggs, located in a corner next to the gate where we entered the pen almost daily. The hen covered about half of the eggs in the nest. After 23 days of incubation the hen left the nest with one chick, the only one that hatched. We broke the remaining eggs and found four different-aged living embryos.

This experiment showed that while one of the hens possessed the necessary drive to incubate an abnormally large clutch, more important, she ceased incubating as soon as the first egg hatched. Six of the eggs contained embryos about 21 days of age. Although the pen condition, density and lack of incubation by all but one hen comprised an abnormal situation, it indicates that under very high density and inadequate cover conditions low production results.

Similar desertion behavior was observed in wild quail by Klimstra (1950b). Stanford (1953) observed quail hens deserting nests after some chicks were hatched but deduced that the early-hatched eggs had been laid on hot ground which initiated incubation before the clutch was finished. Linder and Agee (1963) found that a high proportion of wild hen pheasants abandoned the clutches they were incubating when captive chicks were placed where they could be seen and contacted. However, these hens did not react to captive chicks that were penned where they could be heard but not seen. Nest desertion of partially hatched clutches was also observed in three species of the Rallidae family, including the takahe, *Notornis manteli* (Williams, 1957), the American coot (Gullion, 1954) and the European coot (Alley and Boyd, 1947).

The degree to which varying levels of density causes reduced reproductive rates in wild populations will be discussed in greater detail in Study III. However, we do know that wild pheasants in natural habitat lay eggs at random, in each others' nests and leave unhatched eggs in nests (Buss *et al.*, 1951; Stokes, 1954; and Trautman *et al.*, 1959). In addition to the desertion of partially hatched clutches, wild bobwhite quail also displayed some of the same breeding characteristics (egg dropping and laying in dump nests) as did the pheasants described above (Stoddard, 1931). The latter also reported that when quail are abundant and cover is scarce, 2 or 3 quail commonly lay in the same nest.

In summary, hen pheasants penned under a very high density level dropped many eggs at random, laid in each others' nests and incubated nests in which 2 or more hens had laid eggs. At least one hen had the drive to incubate a clutch under very adverse habitat conditions, but left the nest with the first chick that hatched and abandoned the remaining living embryos. This type of behavior results in a greatly reduced productivity and a prolongation of the reproductive stresses.

Effect of Controlled Density Levels on Pheasant Reproduction (Study III)

This study was conducted in 1948 and repeated in 1949 to compare the effect of two density levels of pheasants on their reproductive performance under pen conditions. Two pens of equal size, 75′ x 100′, were used. Five hen pheasants and 1 cock were placed in the first pen for a density of 30 hens per acre. In the second pen, 15 hen pheasants and 3 cocks were used (90 hens per acre), which was a density threefold greater than that in the first pen. For identification purposes, the pen with the lower density was named "Density I" and the other "Density II." The type, quality, and density of the ground cover in both pens, consisting of annual and biennial weeds, grasses, domestic hay, and grain species, were very similar and offered adequate nesting cover.

In both years, the birds were placed in the pens during the last week in March, and left to lay eggs in nests and hatch young. The pens were checked weekly for: the number of eggs laid, nest location and phenology, and the number of young hatched. The only difference between the 1948 and 1949 experiment was in the number of cocks living in each of the pens.

In 1948, within a few days after the birds were placed in the Density II pen, one cock became dominant and killed the other two. In 1949, as soon as a cock became dominant in the Density II pen, he was replaced by a subdominant cock from another pen. After this process had been repeated a few times, three cocks were found that would cohabit the same pen more or less amicably. Some fighting occurred sporadically but it was not so severe that the birds killed each other. Probably the dominant cock in the 1948 study would have left his pen mates alone if they had avoided his territory. However, they persisted in entering it to pursue the hens which stayed with the dominant cock. On such occasions they were attacked and badly beaten.

Generally in both years the hens first dropped some eggs at random before beginning to lay in nests. Next, the hens laid some eggs in nests and incubated them for a few days but then abandoned these, and finally, they settled down to steady incubation and hatching their clutches.

The reproductive phenology for the two groups of 1948 birds was as follows:*

Group*	Date of First Nests	Date of First Incubation	Date First Clutch Hatched	Hatching Date of Last Clutch Incubated
Density I (5 hens, 1 cock)	April 27	May 12	June 22	July 7
Density II (15 hens, 1 cock)	April 27	May 25	June 30	July 29

*All of the dates given are averages for the groups.

The reproductive phenology and the reproductive performance presented above and in Table 59 show that in the Density II pen the hens started laying on the same date but dropped a greater proportion of eggs and took a longer period of time to settle down to nesting than the hens in the Density I pen. However, the reproductive success per bird for both pens was very similar. All hens, except one in Density II pen, brought off broods of young. When consideration is given to total eggs laid, eggs laid in nests, and hatching dates, it is apparent that the breeding success of the Density I pheasants would be more conducive to population increases. This is because the extra effort of laying and incubating more eggs constitutes a stress that would weaken the higher density birds more than those in the Density I pens (Kabat *et al.*, 1956).

In 1949, these experiments were repeated, but as previously described the number of cocks in the Density II pen was maintained at three. Generally the reproductive phenology for 1949 differed from 1948 in that the Density I hens were earlier and the Density II hens later.

Group*	Date of First Nests	Date of First Incubation	Date First Nest Hatched	Hatching Date of Last Clutch Incubated
Density I	April 28	May 5	May 27	June 24
Density II	April 28	May 27	July 3	Aug. 12

*All of the dates given are average figures.

However, the results in Table 60 showed that a great difference occurred in reproductive success between the pheasants in the two density pens. In 1949 the hens in the Density I pen again laid a greater proportion (58 per cent) of their eggs in nests, and again each hen was successful in bringing off a brood. In contrast, the hens in the Density II pen laid only 18 per cent of their eggs in nests and only about one-third of the hens nested successfully.

A comparison between the over-all results of the 1948 and 1949 study showed that most of the phases of reproduction considered here were similar for the Density I trial. However,

* At the time the material for Study III was prepared for publication, the original data were not available for statistical analysis. However, very little overlap occurred in the ranges for each of the different phases of reproduction compared.

TABLE 59

Breeding Behavior of Pheasants in Density Experiment Pen I and II, 1948

Group	No. Eggs Dropped at Random	No. Eggs Laid in Nests	No. Eggs Hatched	Total Eggs Produced	No. of Clutches Laid*	No. of Clutches Hatched
Density I (5 hens and 1 cock)						
Avg. per hen	12.0	25.4	5.6	37.4	2.4	1
Per cent of total eggs (187) produced	32	68	15			
Density II (15 hens and 1 cock)						
Avg. per hen	25.3	17.9	6.6	43.1	1.3	.9
Per cent of total eggs (647) produced	59	41	15			
Density I x 100 / Density II	47	142	85	86	185	111

*Number of nests containing eggs produced by each hen.

in 1949 the hens had an earlier reproductive phenology, laid fewer eggs and built fewer nests, which indicates a differential response to the seasons in the two years involved.

From these studies, we concluded that density had a measurable effect on the different phases of reproduction. When the number of cocks was increased, the reproductive success was proportionately lower. Observations made at the pen sites indicated the type of density reaction that was responsible for the low reproduction. In 1949, the cocks in Density II pen, in competition with each other, continually chased the hens and attempted copulation. It appeared that under this perpetual harassment the hens were never able to carry on normal nesting activities so that the final production was inversely proportional to the cock density. In Pelee Island pheasants, Stokes (1954) reported a breeding behavior of wild birds that was qualitatively similar to that of the penned birds in these studies.

Reproduction of Young and Old Pheasants (Study IV)

A few observations by various authors on wild bobwhite quail and a few other species indicated that birds 2 or more years old may lay eggs earlier than 1-year-olds. In our study we sought to determine if there was any actual difference in the breeding behavior of young and old hens, and if it occurred, if there was any impact on reproductive success. The term "young hen" refers to a hen in her first breeding season, while an "old hen" is one in the second or later breeding season.

The experiment was started on March 25, 1949, by dividing 25 young and 25 old hens into 10 groups of 5 each and placing them in 12′ x 12′ breeding pens. One cock pheasant was also placed in each pen. At this time the birds were debeaked to prevent egg eating. The debeaking was repeated on April 8.

Egg-laying records were kept for these hens until they reached maximum production on May 5. At this time, 2 groups of 20 hens, each consisting of equal numbers of young and old, were transferred to 25′ x 100′ holding pens. Two cocks were placed in each of the two pens. The pens were checked weekly, and the number of eggs laid was tallied. The birds were allowed to nest and bring off young. Nests were located, their phenology recorded, and a count was made of the number of young produced.

TABLE 60

Breeding Behavior of Pheasants in Density Experiment Pen I and II, 1949

Group	No. Eggs Dropped at Random	No. Eggs Laid in Nests	No. Eggs Hatched	Total Eggs Produced	No. of Clutches Laid*	No. of Clutches Hatched
Density I (5 hens and 1 cock)						
Avg. per hen	10.8	12.0	5.8	22.8	1.2	1.0
Per cent of total eggs (115) produced	48	52	26			
Density II (15 hens and 3 cocks)						
Avg. per hen	27.9	5.6	2.3	33.5	0.5	0.3
Per cent of total eggs (510) produced	82	18	6			
Density I x 100 / Density II	39	200	300	68	240	333

*Number of nests containing eggs produced by each hen.

Date of First Egg. The old hens started to lay on April 8, when two hens came into production (Table 61). It was not until 5 days later, April 13, that the first egg was produced by young hens. As more hens in both groups came into production, the young hens continued to show this 5-day lag in first-egg production. However a chi-square test of the mean difference was not significant ($X^2 = 4.10$, 26 d.f.)

Egg Production. The mean difference between the egg-laying rates for young birds and the old hens for the dates shown was highly significant ($X^2 = 19.83$, 6 d.f.) (Table 62). This lag in egg production continued until peak production was reached the first week in May, at which time all hens were laying as many as 3 eggs during each of the 4-day intervals.

Nesting, Broodiness and Hatching. After the hens were transferred to the holding pens, some hens began to lay eggs in nests almost immediately. However, the majority dropped eggs indiscriminately about the pens for some time before laying in nests. Then too, once nesting was started, it was not uncommon to find three or four hens depositing their eggs in the same nest. Similarly, incubation began in a haphazard manner. Hens incubated a clutch for a few days and then abandoned it. Finally, incubation began in earnest and continued until hatching. The breeding behavior described here is similar to that in Studies I-III.

The reproductive phenology which was generally similar for these two groups of birds is shown below:

Group	Date of First Nests	Date of First Incubation	Date First Clutch Hatched	Date of Hatching for Last Clutch Incubated
Young	May 13	May 20	June 20	Aug. 3
Old	May 13	May 13	June 10	Aug. 3

However, the more detailed material presented in Table 63 shows a difference in reproductive capacity for the two groups. While the old pheasants built more nests, laid a larger number of eggs in nests and had a greater number of successful clutches, these differences were not significant at the 5 per cent level. The difference between the number of eggs hatched per old hen was significantly greater.

In this study, the old hens showed an advantage in all phases of breeding behavior. This superiority in reproductive success was climaxed by 40 per cent more successful clutches being produced by old hens, and the fact that the over-all effort required per egg hatched was less.

TABLE 61

Periods When Young and Old Hen Pheasants Produced First Eggs

Group (25 Hens in Each)	Hens Producing First Eggs: 4-Day Periods						
	April 8–11	April 12–15	April 16–19	April 20–23	April 24–27	April 28–May 1	May 2–5
Young							
New Hens Laying	0	1	4	5	5	6	4
Total Hens Laying	0	1	5	10	15	21	25
Old							
New Hens Laying	3	3	6	5	4	2	2
Total Hens Laying	3	6	12	17	21	23	25

TABLE 62

Egg Production Record of Young and Old Hen Pheasants

Group (25 Hens in Each)	Egg Production: 4-Day Periods							Total Produced
	April 8–11	April 12–15	April 16–19	April 20–23	April 24–27	April 28–May 1	May 2–5	
Young	0	1	12	36	55	67	73	244
Old	5	5	37	49	63	72	76	307

TABLE 63

Breeding Behavior of Young and Old Hens Under Pen Conditions*

Group	No. Eggs Dropped at Random	No. Eggs Laid in Nests	No. Eggs Hatched	Total Eggs Produced	No. of Clutches Laid	No. of Successful Clutches
Young						
(20 hens)	270	157	59	427	15	10
Avg. per hen	14	8	3.0	21	0.7	0.5
Old						
(20 hens)	229	183	88	412	18	14
Avg. per hen	11	9	4.4	21	0.9	0.7

*The figures used in this table are only for the holding pens (25′ x 100′) and do not include the eggs laid in the breeding pens.

APPENDIX C

Hunting Season and Harvest Records

Quail Hunting Seasons, 1851–1960

1851*	Protected February 1 to August 1 (6 months)
1858	Open October 1 to February 1
1860	Open September to December 1
1867	Open August 20 to December 15; game bird nests protected
1870	Open August 20 to November 15 (applies to 10 counties; others apparently open all year)
1871	Open August 20 to November 15
1878	Open August 25 to January 1
1880	Open August 15 to January 1
1881	Open August 15 to January 1
1887	Open September 1 to December 1
1893	California quail protected
1895	Open August 20 to December 1
1897 & 1901	Protected until September 1, 1901
1895–1931	Closed season throughout the state
1932	October 1, at noon, to October 3, 5 p.m. In Crawford and Richland counties only. Daily 4, possession 8
1933	September 30, noon, to October 4, 5 p.m. In Crawford, Jackson, Juneau, LaCrosse, Monroe, Richland, Sauk, Trempealeau, and Vernon Counties only. Daily 4, possession 8
1934	September 29, noon, to October 2, 5 p.m. In Clark, Columbia, Crawford, Dane, Grant, Iowa, Juneau, LaCrosse, Marathon, Marquette, Pepin, Richland, Sauk, Vernon, Waukesha, Waushara, and Wood Counties only. Daily 4, possession 8
1935	October 19 to October 24 In Columbia, Crawford, Dane, Green Lake, Juneau, LaCrosse, Marathon, Marquette, Monroe, Richland, Sauk, Vernon, and Waushara Counties only. Daily 4, possession 8
1936–1940	Closed
1941	November 3 to November 7 In Adams, Crawford, Dane, Iowa, Juneau, LaCrosse, Monroe, Richland, Vernon and Wood Counties only. Daily 4, possession 8
1942	November 11 to November 15 In Adams, Buffalo, Crawford, Dane, Iowa, Juneau, LaCrosse, Monroe, Pepin, Richland, Sauk, Trempealeau, and Vernon Counties only. Daily 4, possession 8
1943	November 8 to November 12 In Crawford, Dane, Iowa, Richland and Vernon Counties only. Daily 4, possession 8
1944	November 1 to November 5 In Dane, Iowa, LaCrosse, Richland and Vernon Counties only. Daily 4, possession 8
1945	October 31 to November 4 In Buffalo, Crawford, LaCrosse, Richland, Trempealeau, and Vernon Counties only. Daily 4, possession 8
1946	October 24 to October 28 In LaCrosse, Richland, Trempealeau, and Vernon Counties only. Daily 4, possession 8
1947	October 23 to October 27 In LaCrosse, Pepin, Richland, Sauk, Trempealeau, and Vernon Counties only. Daily 4, possession 8
1948	November 2 to November 5 In Crawford, LaCrosse, Richland, Sauk, and Vernon Counties only. Daily 4, possession 8
1949	October 31 to November 4 In Buffalo, Crawford, Jackson, Juneau, LaCrosse, Monroe, Pepin, Pierce, Richland, Sauk, Trempealeau, and Vernon Counties only. Daily 4, possession 8
1950	October 14 to October 29 In Buffalo, Crawford, Dane, Grant, Green, Iowa, Jackson, Juneau, LaCrosse, Lafayette, Monroe, Pepin, Pierce, Richland, Sauk, Trempealeau, Vernon and Wood Counties only. Daily 5, possession 10
1951	October 13 to November 11 In Adams, Buffalo, Clark, Columbia, Crawford, Dane, that part of Eau Claire County lying south of U.S. Highway 12, Grant, Green, Iowa, Jackson, Juneau, LaCrosse, Lafayette, Monroe, Pepin, Pierce, Richland, Sauk, Trempealeau, Vernon, and Wood Counties only. Daily 5, possession 10
1952 (a)	October 18 (1:00 p.m.) to November 11 In Adams, Buffalo, Columbia, Crawford, Dane, that part of Eau Claire County lying south and west of U.S. Highway 12, Grant, Green, Green Lake, Iowa, Jackson, Juneau, LaCrosse, Lafayette, Marquette, Monroe, Pepin, Pierce, Richland, Sauk, Trempealeau, Vernon, and Wood Counties. Daily 5, possession 10

* Quail seasons from 1851 to 1932 are taken from *Laws of Wisconsin.* They do not show shooting hours or bag limit. Some annual laws show nothing relating to seasons; the assumption is that laws of the previous year or years are continuous.

TABLE 64

Rank of Counties in Quail Harvest, 1932–57

Rank	County	Years Open	Kill 1932–57	Rank	County	Years Open	Kill 1932–57
1	Richland	16	36,000	18	Buffalo	11	6,100
2	Sauk	14	28,400	19	Dunn	3	5,400
3	Dane	14	20,900	20	Wood	10	4,500
4	Trempealeau	14	20,700	21	Green Lake	5	3,900
5	Vernon	19	17,300	22	Eau Claire	5	3,700
6	La Crosse	14	16,700	23	Waushara	4	3,100
7	Crawford	18	14,600	24	Pepin	11	2,500
8	Marquette	6	13,600	25	Pierce	8	2,300
9	Iowa	13	13,000	26	Rock	2	1,800
10	Columbia	8	12,300	27	Portage	2	1,100
11	Adams	9	10,600	28	Taylor	1	900
12	Monroe	13	10,000	29	Chippewa	3	800
13	Grant	9	9,100	30	St. Croix	3	500
14	Juneau	13	8,800	31	Waukesha	1	400
15	Green	8	7,600	32	Clark	3	300
16	Jackson	10	6,900	33	Marathon	2	200
17	Lafayette	8	6,400	34	Waupaca	2	100
					Miscellaneous		38,400
					Total		328,900

TABLE 65

Annual Quail Harvest, 1932–60*

County	1932	1933	1934	1935	1936–1940	1941	1942	1943	1944	1945	1946	1947	1948	1949
Adams	—	—	—	—		250	326	—	—	—	—	—	—	—
Buffalo	—	—	—	—	C	—	239	—	—	23	—	—	—	315
Chippewa	—	—	—	—		—	—	—	—	—	—	—	—	—
Clark	—	—	49	—	L	—	—	—	—	—	—	—	—	—
Columbia	—	—	1,809	1,560		—	—	—	—	—	—	—	—	—
Crawford	207	549	212	193	O	419	634	212	—	143	—	—	292	418
Dane	—	—	2,608	2,846		769	821	503	467	—	—	—	—	—
Dunn	—	—	—	—	S	—	—	—	—	—	—	—	—	—
Eau Claire	—	—	—	—		—	—	—	—	—	—	—	—	—
Grant	—	—	409	—	E	—	—	—	—	—	—	—	—	—
Green	—	—	—	—		—	—	—	—	—	—	—	—	—
Green Lake	—	—	—	981	D	—	—	—	—	—	—	—	—	—
Iowa	—	—	316	—		408	339	367	272	—	—	—	—	—
Jackson	—	368	—	—		—	—	—	—	—	—	—	—	801
Juneau	—	1,030	418	—		210	236	—	—	—	—	—	—	378
La Crosse	—	1,242	884	559	S	161	381	—	282	252	619	841	1,474	662
Lafayette	—	—	—	—		—	—	—	—	—	—	—	—	—
Marathon	—	—	79	153	E	—	—	—	—	—	—	—	—	—
Marquette	—	—	1,324	1,165		—	—	—	—	—	—	—	—	—
Monroe	—	324	—	166	A	212	339	—	—	—	—	—	—	446
Pepin	—	—	345	—		—	111	—	—	—	—	207	—	207
Pierce	—	—	—	—	S	—	—	—	—	—	—	—	—	279
Portage	—	—	—	—		—	—	—	—	—	—	—	—	—
Richland	344	755	515	1,018	O	938	908	480	698	120	841	771	356	954
Rock	—	—	—	—		—	—	—	—	—	—	—	—	—
St. Croix	—	—	—	—	N	—	—	—	—	—	—	—	—	—
Sauk	—	2,028	1,464	1,822		—	970	—	—	—	—	808	815	1,508
Taylor	—	—	—	—		—	—	—	—	—	—	—	—	—
Trempealeau	—	1,491	—	—		—	544	—	—	103	1,127	841	—	711
Vernon	—	256	185	155		359	339	287	461	229	397	437	1,355	554
Waukesha	—	—	361	—		—	—	—	—	—	—	—	—	—
Waupaca	—	—	—	—		—	—	—	—	—	—	—	—	—
Waushara	—	—	821	26		—	—	—	—	—	—	—	—	—
Wood	—	—	364	—		195	—	—	—	—	—	—	—	—
Miscellaneous	—	2,128	333	204		1,137	1,749	1,595	1,561	1,467	3,786	1,081	857	1,359
TOTALS	551	10,171	12,496	10,848		5,058	7,936	3,444	3,741	2,337	6,770	4,986	5,149	8,592

*Estimated or reported.

(b) No open season
In all other counties

1953 (a) October 17 at 1:00 p.m. to November 11
In Adams, Buffalo, Crawford, Dane, Grant, Green, Iowa, Jackson, Juneau, LaCrosse, Lafayette, Monroe, Pepin, Pierce, Richland, Sauk, Trempealeau, Vernon and Wood Counties. Daily 5, possession 10

(b) No open season
In all other counties

1954 (a) October 16 (1:00 p.m.) to November 14
In Adams, Buffalo, Columbia, Crawford, Dane, Grant, Green, Iowa, Jackson, Juneau, LaCrosse, Lafayette, Monroe, Richland, Trempealeau, Vernon and Wood Counties. Daily 5, possession 10

(b) No open season
In all other counties

1955 (a) October 1 (12 noon) to November 13
In all that part of Chippewa, Dunn, and St. Croix Counties lying north of State Highway 64. Daily 5, possession 10

(b) October 15 (12 noon) to November 13
In Adams, Buffalo, that part of Chippewa County lying south of State Highway 64; Columbia, Crawford, Dane, that part of Dunn County lying south of State Highway 64; Eau Claire, Grant, Green, Green Lake, Iowa, Jackson, Juneau, LaCrosse, Lafayette, Marquette, Monroe, Pepin, Pierce, Richland, that part of St. Croix County lying south of State Highway 64; Sauk, Trempealeau, Vernon, and Wood Counties. Daily 5, possession 10

(c) No open season
In all other counties

1956 (a) October 20 (12 noon) through November 11
In all that part of the state of Wisconsin lying westerly of a line beginning at the junction of State Highway 64 extended westerly to the west boundary of the state, thence easterly along said Highway 64 to its junction with State Highway 27, thence southerly along said Highway 27 to its junction with U.S. Highway 12, thence southerly along said Highway 12 to

(TABLE 65 Cont.)

County	1950	1951	1952	1953	1954	1955	1956	1957	Rank 1958*	1959*	1960*
Adams	—	907	978	903	1,425	1,604	1,782	2,464			
Buffalo	437	323	489	570	538	828	1,072	1,256			
Chippewa	—	—	—	C	C	203	338	281			
Clark	—	176	—	C	C	C	16	73			
Columbia	—	942	1,054	C	1,660	1,875	1,279	2,086			
Crawford	746	791	1,035	1,021	1,539	1,679	1,666	2,830			
Dane	1,481	716	857	1,561	1,592	2,809	1,832	2,037			
Dunn	—	—	—	C	C	3,042	1,097	1,220		1	1
Eau Claire	—	534	692	C	C	753	1,064	659		2	
Grant	368	151	330	481	985	1,702	2,516	2,123			
Green	547	277	419	881	1,228	1,416	1,345	1,476			
Green Lake	—	—	514	C	C	1,386	578	488			
Iowa	676	423	476	1,591	1,395	1,958	2,574	2,184			
Jackson	810	343	394	784	637	1,130	710	963			
Juneau	790	277	445	740	682	1,431	940	1,159		5	
La Crosse	934	408	660	2,035	1,167	1,039	990	2,111	2	3	
Lafayette	288	262	267	525	963	986	1,634	1,464			
Marathon	—	—	—	—	—	—	—	—			
Marquette	—	—	1,010	C	C	4,111	2,731	3,245	3	4	
Monroe	860	549	1,130	577	705	1,318	1,535	1,867			
Pepin	119	262	203	207	C	339	190	354			
Pierce	283	302	229	289	C	211	99	622			
Portage	—	—	—	C	C	C	792	354			
Richland	1,889	1,033	1,238	4,366	3,441	5,971	4,818	4,538	1		
Rock	—	—	—	C	C	C	1,006	805			
St. Croix	—	—	—	C	C	346	91	110			
Sauk	2,962	2,263	1,467	2,531	C	3,321	2,962	3,477			
Taylor	—	907	—	—	—	—	—	—			
Trempealeau	1,332	721	1,619	2,753	2,448	2,026	1,980	2,989	4		
Vernon	765	—	1,257	1,739	1,925	2,086	2,211	2,342	5		
Waukesha	—	—	—	—	—	—	—	—			
Waupaca	—	—	—	C	C	C	41	12			
Waushara	—	—	—	C	C	C	858	1,415			
Wood	462	287	222	163	508	1,175	346	793			
Miscellaneous	2,738	1,225	2,197	2,398	2,471	3,200	2,599	4,257			
TOTALS	18,487	14,079	19,182	26,115	25,309	47,945	43,692	52,054	47,400	15,100	8,500

*In 1958 a highway boundary system of zones was established so that only parts of some counties were opened. In addition the Department ceased listing hunting kill by counties. Hence for these years only the rank of the first five counties is listed. For 1960 the harvest was so small only the chief county is indicated.

its junction with U.S. Highway 10, thence easterly along said Highway 10 to its junction with State Highway 49, thence southerly along said Highway 49 to its junction with State Highway 23, thence westerly along said Highway 23 to its junction with State Highway 73, thence southerly along said Highway 73 to its junction with U.S. Highway 51, thence southerly along said Highway 51 to its junction with the south boundary of the state. Daily 5, possession 10

(b) No open season
In all other parts of the state

1957 (a) October 19 (12 noon) through November 12
In all that part of the state of Wisconsin lying westerly of a line beginning at the junction of State Highway 64 extended westerly to the west boundary of the state, thence easterly along said Highway 64 to its junction with State Highway 27, thence southerly along said Highway 27 to its junction with U.S. Highway 12, thence southerly along said Highway 12 to its junction with U.S. Highway 10, thence easterly along said Highway 10 to its junction with State Highway 49, thence southerly along said Highway 49 to its junction with State Highway 23, thence westerly along said Highway 23 to its junction with State Highway 73, thence southerly along said Highway 73 to its junction with U.S. Highway 51, thence southerly along said Highway 51 to its junction with the south boundary of the state. Daily 5, possession 10

(b) No open season
In all other parts of the state

1958 (a) October 18 (12 noon) through November 30
All that part of the state lying westerly of a line beginning at the junction of U.S. Highway 51 with the south boundary of the state, thence northerly along said Highway 51 to its junction with State Highway 73 thence northerly along said Highway 73 to its junction with State Highway 23 thence northerly along said Highway 23 to its junction with State Highway 49, thence northerly along said Highway 49 to its junction with U.S. Highway 10, thence westerly along said Highway 10 to its junction with U.S. Highway 12, thence westerly along said Highway 12 to its junction with State Highway 27, thence northerly along said Highway 27 to its junction with State Highway 64, thence westerly along said Highway 64 and a westerly extension of said Highway 64 to the west boundary of said state. Daily 5, possession 10

(b) No open season
In all other parts of the state

1959 (a) Same as 1958–59; Daily 3, possession 6

(b) Same as 1958–59

1960 (a) October 22 (12 noon) through November 6
All that part of Wisconsin lying westerly of a line beginning at the junction of State Highway 78 with the south boundary of the state, thence northerly along said Highway 78 to its junction with State Highway 22, thence northerly along said Highway 22 to its junction with State Highway 23, thence easterly along said Highway 23 to its junction with State Highway 73, thence northerly along said Highway 73 to its junction with State Highway 22, thence northerly along said Highway 22 to its junction with State Highway 10, thence westerly along said Highway 10 to its junction with U.S. Highway 12, thence westerly along said Highway 12 to its junction with State Highway 27, thence northerly along said Highway 27 to its junction with State Highway 64, thence westerly along said Highway 64 and a westerly extension of said Highway 64 to the west boundary of said state. Daily 3, possession 6

(b) No open season
In all other parts of the state

APPENDIX D

Quail Restoration with Wild Transplants

Efforts made in Wisconsin to stock quail are shown in Table 66. With the exception of a series of releases at Two Rivers which definitely were pen-reared birds, it is not known whether the imports comprising the releases of quail in Wisconsin obtained from southern states were wild or pen-reared birds. From 1950 to 1955 several attempts were made to transplant birds into four different areas described below. These consisted of wild birds except for one release.

The University of Wisconsin Arboretum, a 1,000-acre area, had a relatively good quail population with an estimated peak of 171 birds in the winter of 1938–39. By the early 1950's there were no more wintering quail on this area, but there were some coveys located within a few miles. These were gone by the 1960's. Horicon Marsh, a 30,000-acre area consisting mostly of marsh and some upland had not been occupied by quail for many years. River Hills, an area of about 2,000 acres had not had a quail population since about 1900. The Southern Unit of the Kettle Moraine State Forest, about 20 miles long and 3 miles wide, had a few scattered coveys in the southern end at the time of the releases.

All transplants were held in gentle-release pens for 2 days before liberation. At least 15 birds were released at a time. The releases generally held together as coveys for the remainder of the winter and into early spring. The transplanted quail with a few exceptions consisted of almost whole coveys which were trapped in their native habitat. One exception to this was the Kettle Moraine release of September 1953 which consisted of game-farm-reared birds. We were unable to determine whether these birds formed coveys or joined wild coveys. Reeves (1954) found that fall releases of pen-reared quail frequently joined wild coveys.

The releases in the Arboretum and at Horicon disappeared within one year. The breeding success of the transplanted quail at Horicon was at least fair with 3 broods reported produced in the first summer after release. However, there were no birds found at Horicon in the following spring of 1951.

The River Hills birds showed very good survival the first year after release. Eight different males were heard whistling in June of 1950; only 9 had been released. Two or three coveys of about 15 birds were seen in the winter of 1950–51, and only 2 to 4 birds were heard in the spring of 1951.

A maximum of 17 males was heard whistling in the River Hills area in June and July of 1952. These consisted primarily of survivors of the 1952 late winter release. Only a few casual observations were made in 1953 but no birds were seen or heard. In 1954 a whistling survey was made which indicated that there were no survivors left. Residents of the area cooperated in reporting both winter and spring observations. The 1952 releases apparently disappeared in less than 2 years.

The area in which the Kettle Moraine birds were released was more difficult to census than the Milwaukee area because there were some native birds a few miles south of the release

TABLE 66
Quail Introductions in Wisconsin

Year	No.	Per Cent Males	Source	Release Area
1884–85	?		Tennessee	Ripon, Fond du Lac Co.
1886	?		Texas	Oshkosh, Winnebago Co.
1887	?		Louisiana	Racine, Racine Co.
1890	About 20 pairs	50	?	Whitewater, Walworth Co.
1892	84	?	Kansas	Sheboygan, Sheboygan Co.
1892	"a few"	?	Plymouth	Sheboygan Co.
1894	?	?	Texas	Two Rivers, Manitowoc Co.
1895	120	?	Kansas	Two Rivers, Manitowoc Co.
1897	Several hundred	?	Kansas	Two Rivers, Manitowoc Co.
1897	?		?	Palmyra, Jefferson Co.
1898	?		?	Prairie du Chien, Crawford Co.
1899	140	?	Kansas	Sturgeon Bay, Door Co.
1902	?		?	Washington Island, Door Co.
1903	?		?	Outagamie Co.
1932–33	?		?	Poynette, Columbia Co.
Jan. 1950	42	50	Dunn Co.	Univ. of Wis. Arboretum, Dane Co.
Jan. 1950	26	58	Dunn Co.	Horicon Marsh, Dodge Co.
Jan. 1950	24	40	Dunn Co.	River Hills, Milwaukee Co.
Mar. 1952	17	70	Dane and Columbia Cos.	River Hills, Milwaukee Co.
Mar. 1953	25	⊤	Dunn Co.	So. Unit Kettle Moraine State Forest, Eagle, Waukesha Co.
Sept. 1953	43	56	Eastern U.S. (pen-reared)	So. Unit Kettle Moraine State Forest, Eagle, Waukesha Co.
Mar. 1955	18	⊥	Dunn and Columbia Cos.	So. Unit Kettle Moraine State Forest, Eagle, Waukesha Co.

Note: 1884–1933 releases were probably pen-reared birds in most cases; the 1950–55 releases, except 1953, were wild transplants. The records from 1884–1900 are from Schorger (1944).

A large number of quail were released in various parts of the state by Gustav Pabst around 1900.

area and dispersion of the birds after the release was greater. Two coveys of birds containing young produced by these releases were found from 2–3 years after each release. While the available coverts were ample, they occurred only in a north-south pattern. Birds that dispersed either in a westerly or easterly direction found themselves in poor range.

The failure of the birds in all the areas to establish sustaining populations was attributed to the lack of quail in the surrounding areas. The dispersing birds simply failed to find mates with which to pair.

These studies showed that wild transplants of the size we liberated located winter coverts after release, produced broods the first summer and appeared to thrive as well as did wild birds in their native habitat. Apparently releases of the size of our test groups are adequate to insure good survival the first year of release.

These studies suggest why quail disappeared from the southeastern part of Wisconsin. As shrubby cover was destroyed during agricultural expansion, only islands of good habitat remained. These were the last sites occupied by quail. Because of the movement behavior and high turnover of quail, they gradually disappeared first from the most disturbed areas, and then from the islands of remaining good habitat.

APPENDIX E

Wisconsin Shrubs of Value for Roadside and Wildlife Use

Compiled by

J. T. Curtis, U. W. Plant Ecology Laboratory

Species*	Special Habitat	Food Value	Fence Value	Cover Value
Alnus crispa	Acid, cool	———	Fair	Good
Alnus rugosa	Wet, cool	———	———	Fair
Amelanchier sp†	Acid, cool	Berries	Fair	Fair
Amorpha fruticosa	Wet, warm	?	———	Fair
Aronia melanocarpa†	Acid sands	Berries	———	Good L
Betula glandulosa†	Wet, alkaline or acid	Rabbit browse	———	Good L
Betula sandbergii	Wet, alkaline	Rabbit browse	———	Good L
Ceanothus americanus	Dry, alkaline	?	———	Good L
Ceanothus ovatus	Dry, acid, cool	?	———	Good L
Cephalanthus occidentalis	Wet, warm	?	Fair	Good
Cornus alternifolia†	Mesic, rich	Berries	———	Good
Cornus purpusi	Wet, alkaline	Berries	———	Good
Cornus racemosa†	Upland, warm	Berries, rabbit	Fair	Good
Cornus rugosa	Upland, cool	Berries	———	Fair
Cornus stolonifera†	Wet	Berries, rabbit	———	Good
Corylus americana†	Upland	Nuts	Fair	Good
Corylus cornuta	Upland, acid	Nuts	Fair	Good
Crataegus sp†	Alkaline	Berries	———	Good
Diervilla lonicera	Upland	Deer?	———	Fair L
Euonymus atropurpureus	Upland	———	Fair	Good
Hamamelis virginiana	Upland	?	———	Good
Hudsonia tomentosa	Sterile sand	———	———	Good L
Hypericum kalmianum	Wet sand	———	———	Fair L
Ilex verticillata†	Wet to mesic	Berries	Fair	Good
Juniperus horizontalis†	Dry sands	———	Good	Good L
Juniperus virginiana†				
Lonicera canadensis	Acid, cool	Berries	———	Fair
Lonicera villosa	Acid, wet	Berries	———	Good
Myrica asplenifolia	Acid sands	———	———	Good L
Nemopanthus mucronata	Wet to mesic	Berries	Fair	Good
Physocarpus opulifolius	Anywhere	———	Good	Good
Potentilla fruticosa†	Wet, alkaline	———	———	Good L

Species*	Special Habitat	Food Value	Fence Value	Cover Value
Prunus americana†	Mesic	Berries	Excel.	Good
Prunus nigra	Wet, acid	Berries	Fair	Good
Prunus pumila†	Acid sand	Berries	———	Good L
Prunus virginiana†	Anywhere	Berries	Fair	Good
Pyrus iowensis†	Dry	Berries	Excel.	Good
Rhus aromatica	Dry sites	Berries	———	Good L
Rhus copallina	Mesic	Berries	———	Good L
Rhus glabra†	Dry	Berries, rabbit	———	Fair L
Rhus typhina†	Mesic	Berries, rabbit	Good	Fair
Rosa arkansana†	Dry, alkaline	Berries	———	Fair L
Rubus parviflorus	Mesic, cool	Berries	Good	Good
Rubus pubescens†	Anywhere	Berries	———	Good L
Salix bebbiana	Wet, alkaline	———	———	Good
Salix adenophylla	Mesic	———	Fair	Good
Salix discolor†	Wet	———	———	Good L
Salix humilis†	Dry	———	———	Good L
Salix interior	Wet	———	Fair	Good
Salix lucida†	Mesic	———	Fair	Good
Salix sericea	Wet, alkaline	———	———	Good
Sambucus canadensis	Anywhere	Berries	Fair	Fair
Sambucus pubens†	Cool	Berries	———	Fair
Shepherdia canadensis	Acid, cool	———	———	Fair L
Spiraea alba	Wet, alkaline	———	———	Good L
Spiraea tomentosa	Wet, acid	———	———	Good L
Staphylea trifolia	Mesic, rich	———	———	Fair
Symphoricarpos albus	Dry	Berries	———	Fair L
Symphoricarpos occidentalis	Dry	Berries	———	Fair L
Viburnum acerifolium	Acid, cool	Berries	———	Fair
Viburnum lentago†	Mesic	Berries	Fair	Good
Viburnum opulus	Wet to mesic	Berries	Fair	Fair
Viburnum rafinesquianum	Mesic	Berries	Fair	Good
Zanthoxylum americanum	Mesic	Berries	Good	Good

*Nomenclature after Gleason.
†Known or suspected to possess desirable ecotypes.
L = Low shrub.
Recommended lists for rich upland soils of southern Wisconsin:

A. Tall, hedge-row type, for fence lines and as automobile crash-barriers: *Cornus racemosa, Corylus americana, Physocarpus opulifolius, Rhus typhina, Salix adenophylla, Sambucus canadensis, Viburnum lentago, Zanthoxylum americanum, Prunus americana, Crataegus* sp., *Pyrus iowensis.*

B. Low, ground cover-type, for self-maintaining roadsides and rest cover: *Ceanothus americanus, Diervilla lonicera, Rhus aromatica, Rhus copallina, Rosa arkansana, Salix humilis.*

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