Relation of weather, parasitic disease and hunting to Wisconsin ruffed grouse populations. Number 20 1960

Dorney, Robert S.; Kabat, Cyril
Madison, Wisconsin: Wisconsin Conservation Department, 1960

https://digital.library.wisc.edu/1711.dl/XH7TSSBK2SF4O9D

RELATION OF WEATHER, PARASITIC DISEASE AND HUNTING TO WISCONSIN RUFFED GROUSE POPULATIONS

STATE CONSERVATION COMMISSION OF WISCONSIN

TECHNICAL BULLETIN NUMBER 20

Wisconsin Conservation Department
Madison 1, Wisconsin

1960

CONSERVATION COMMISSION

ARTHUR R. MacARTHUR, Janesville
Chairman

RUSSELL D. STOUFFER, Shell Lake
Secretary

JOHN R. LYNCH, Gordon

PAUL J. OLSON, Madison

GUIDO RAHR, Manitowoc

CHARLES F. SMITH, Wausau

CONSERVATION DEPARTMENT

L. P. Voigt
Director

GEORGE SPRECHER
Assistant Director

C. A. BONTLY
Finance

W. T. CALHOUN (on leave)
Information and Education

G. S. HADLAND
Law Enforcement

ROMAN H. KOENINGS
Forests and Parks

LULU M. KORN
Clerical

JOHN A. BEALE
Chief State Forester

NEIL LeMAY
Forest Protection

WILLIAM A. MATSON
Personnel

LAURENCE F. MOTL
Engineering

EDW. SCHNEBERGER
Fish Management

J. R. SMITH
Game Management

S. W. WELSH
Forest Management

RELATION OF WEATHER, PARASITIC DISEASE AND HUNTING TO WISCONSIN RUFFED GROUSE POPULATIONS

by

Robert S. Dorney and Cyril Kabat

TECHNICAL BULLETIN NUMBER 20

Wisconsin Conservation Department
Madison 1, Wisconsin

1960

ACKNOWLEDGEMENTS

Frederick Holzer, Russell Mattison and Helmer Mattison worked full time on banding and hunting-season checks. Raymond Kyro, John Berkhahn, Ronald Melville, David Cash and Dan Bernhardt assisted part time in trapping ruffed grouse. Donald Thompson provided statistical advice. George Halazon, Daniel Thompson and Bruce Stollberg collected fall specimens in 1948. James Hale and Robert Wendt supervised the early years of the study. Banner Bill Morgan, Geoffrey Lord and Kenneth Flakas provided technical help on the parasite surveys conducted. The field personnel of the Game Management, Fish Management, Forest Management, Forest Protection and Law Enforcement Divisions contributed hunting-season specimens and valuable field observations.

Joseph Hickey, Arlie Todd, Gordon Gullion, Ruth L. Hine and James Hale provided critical advice in the preparation of this report.

This study was financed with Federal Aid to Wildlife Restoration funds under P-R projects W-13R and W-79R.

CONTENTS

INTRODUCTION

Population fluctuations of both mammals and birds in the northern hemisphere have attracted the attention of many animal ecologists, particularly since many of these fluctuations are supposedly "cyclic" or rhythmic in nature. According to many observers (Leopold, 1929; Schorger, 1945; Grange, 1948) ruffed grouse (*Bonasa umbellus*) in Wisconsin exhibit a similar cyclic fluctuation. A 10-year population research study was started in 1949 in northern Wisconsin to collect data on some of the potential underlying factors, and evaluate the relationship of these to drastic changes in numbers. In particular, we concentrated on measuring population density, yearly reproductive success, annual mortality, movement, and parasitic-disease relationships.

Extensive data were gathered in a 24-county area in the northern half of Wisconsin; intensive data, from three study areas. The initial work was started by George Halazon in 1948. James B. Hale and Robert F. Wendt directed the project from 1949 to 1952. Dorney was assigned to the project from 1952 to 1958. From 1948 to 1952, the project emphasized population-inventory techniques and reproduction studies. From 1953 to 1958, an increase in personnel and the development of new trapping techniques made it possible to study spring age structure, mortality, and movement of ruffed grouse. Parasitic disease investigations were carried on throughout the entire period.

We will first discuss numerical density and sex and age structure of the grouse populations studied. The effects of weather, parasitic diseases and hunting on these fluctuations will then be considered. A comparison of the results of this study with others made on "cyclic" populations will conclude this report.

AREAS STUDIED

Inventories and fall sex and age studies were undertaken in 24 counties in northeastern and northwestern Wisconsin (Fig. 1). A more-detailed examination of population mortality and movements was conducted on three smaller areas—Cedar Rapids, Otter Creek and Highway 27 (Figs. 1, 2 and 3). A brief sketch of these three areas follows.

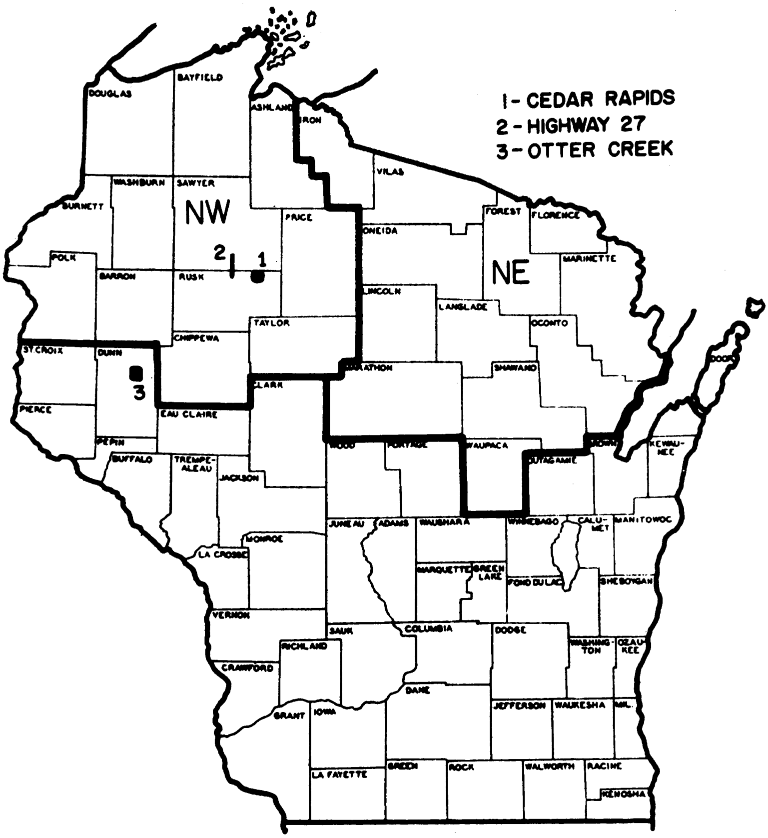

Figure 1. Counties included in the northwestern and northeastern portion of Wisconsin and locations of three study areas, Cedar Rapids, Highway 27 and Otter Creek.

Cedar Rapids. Characterized by solid stands of aspen (*Populus tremuloides*) and northern hardwoods (*Acer saccharum, A. rubrum, Tilia americana*), this area of 4,006 acres has a topography that is level to gently rolling, with few natural openings. For a more detailed breakdown of cover types, see Dorney (1959). Only one road serves the area. The grouse populations are generally low to medium in density and are primarily hunted along the road. This area appears to be representative in topography and cover type of millions of acres in our federal, state and county forests in northern Wisconsin.

Highway 27. Although cover types are similar to Cedar Rapids, this area has more farm-field openings, logging and woodland pasturing. These land practices result in better interspersion of edge and, consequently, in excellent grouse populations. Most of the hunting is done on foot in the woods, as contrasted to road-hunting in Cedar Rapids. Six to eight circular 132-acre plots arbitrarily selected were studied along 15 miles of this road. The description of the plot centers is as follows:

Plot 1. NE Corner SE¼ Sec. 33 T36N R6W
Plot 4. NE Corner Sec. 16 T36N R6W
Plot 5. NE Corner Sec. 9 T36N R6W
Plot 6. NE Corner SE¼NE¼ Sec. 4 T36N R6W
Plot 8. ⅜ Mile South NE Corner Sec. 21 T37N R6W
Plot 11. NE Corner SE¼NE¼ Sec. 9 T37N R6W
Plot 12. 2/10 Mile North NE Corner Sec. 4 T37N R6W
Plot 15. NE Corner SE¼NE¼ Sec. 16 T38N R6W

In 1954 drumming cocks were trapped on plots 1 to 11, and in 1955 and 1956 cocks were trapped on all plots.

Otter Creek. Primarily agricultural, with young scrub oak on steep hills and jack pine-aspen-alder on poorly drained bottomland, this tract of 16.9 square miles has a wooded area that is highly interspersed with fields and pastures and makes for excellent grouse populations. Hunting is mostly done in the woods on foot.

METHODS

Fall Age Ratios

Techniques developed by Bump, Darrow, Edminster and Crissey (1947:84,92), Ammann (1948), and Hale, Wendt and Halazon (1954) make it possible to sex and age ruffed grouse shot in fall, by the use of wing tips and tails. During the course of the present study, both wings and the tail of individual birds were submitted each fall by cooperating hunters, and in addition, departmental field men sent in similar specimens collected during routine field checks. The number of samples annually varied from 216 to 4,533, totalling 26,317 in the 10-year period. Hunters recorded for each specimen the date shot, location (county and township), and (from 1953 to 1957) whether the bird was shot while the hunter was on foot in the woods (brush-hunting) or shot along a driveable road (road-hunting).

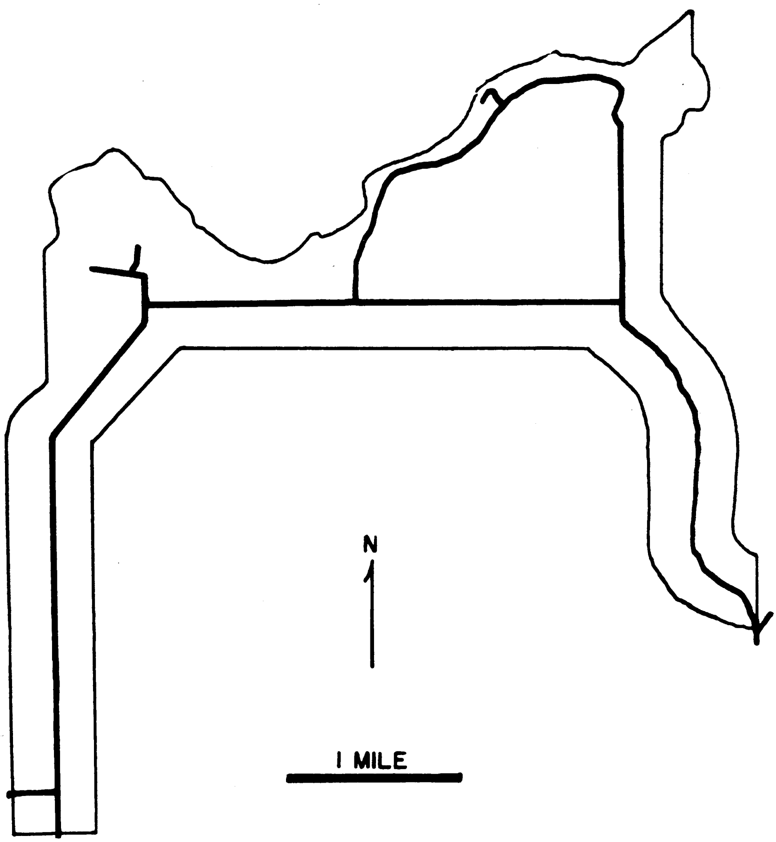

Figure 2. Map of Cedar Rapids study area, Rusk County, showing fire-lane network (solid dark lines) and study area boundaries (light lines) within which all territorial cocks were counted in spring.

Sex and Age Differentiation

Sex in the fall-shot sample was determined by measuring the length of the plucked central tail feather. Tails 15.0 cm. or more in length were recorded as males; less than 15.0 cm., as females. Only juveniles 16 weeks or older could be sexed, since the tails of younger birds are only partially grown. Where tail growth was incomplete in adults, sex was arbitrarily based on color pattern and width of the central tail feather. This adult sexing procedure avoided an adult sex bias due to adult females molting later than males.

Age separation in fall was established by examining the sheathing on the shafts of wing primaries number 7 to 10 and by noting the

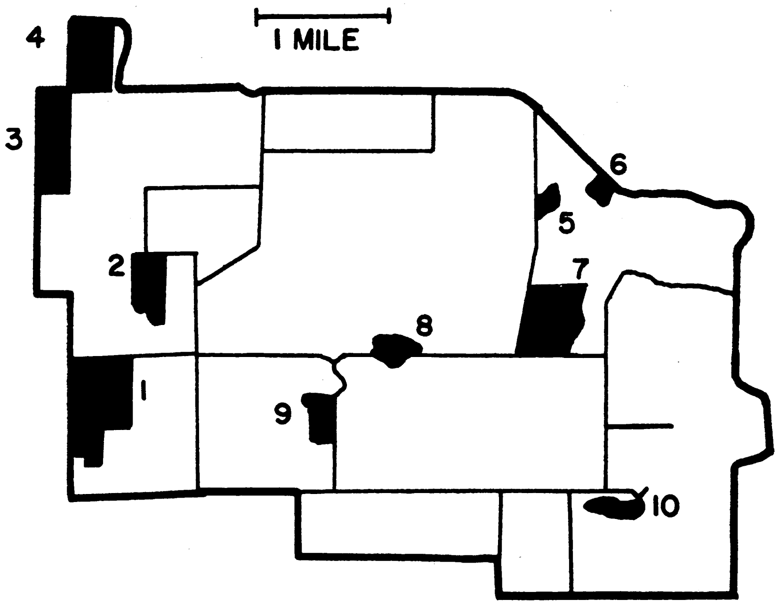

Figure 3. Map of Otter Creek study area, Dunn County, showing road network (solid lines) and ten sample plots.

contour on the tip of primaries 9 and 10. Juveniles have a pointed ninth and tenth primary; adults, rounded. Adults have sheathing on primaries 7 to 10; juveniles, sheathing on 8 but not 9 and 10. Hale, Wendt and Halazon (1954) have established the reliability of these sex and age criteria for fall-shot Wisconsin grouse. In the present study, juveniles were separated by week classes based on criteria given by Bump *et al.* (1947:87).

Male grouse trapped in spring were classified as 1-year-olds or 2-years-plus by measuring the ninth-primary-shaft diameter, central-tail shaft diameter and length, primary contour and its sheathing, and bursal depth. The details and reliability of this spring-aging technique have been published previously (Dorney and Holzer, 1957).

Trapping Methods

Techniques used in the present study for trapping ruffed grouse in spring, fall, and winter have been described by Liscinsky and Bailey (1955) and Dorney and Mattison (1956). Ruffed grouse of all ages and sexes were caught in fall in clover-leaf traps usually located near roads for convenience. In spring, cocks only were taken by the use of mirror traps on the entire Cedar Rapids study area, the six to eight plots on Highway 27, and the 10 sample plots in Otter Creek. Over 80 per cent of the drumming cocks on these areas were caught each spring. In winter, smaller numbers of birds were taken using a bob-trap, a clover-leaf trap, and a tip-top trap. The design for the tip-top trap was adapted from Farmes (1955).

Population Measurement

Breeding populations for all of northern Wisconsin were measured by use of a winter-flush-count index (February and March) and a spring-drumming-cock index (April and May). Details on methodology and the comparative reliability of these techniques have been presented by Dorney, Thompson, Hale and Wendt (1958).

A fall-population index for the entire north was established by mailing a questionnaire on hunting success to grouse hunters cooperating in the wing and tail collection. Since some hunters hunt many different areas of the state, a small portion of questionnaire data represented non-northern areas. Total-kill data for the 24 northern counties (Fig. 1) were compiled from Conservation Department kill reports to furnish another fall-population index.

Population densities in the three study areas were measured in the following manner.

Highway 27. Counts were made of the number of drumming or territorial cocks on the plots described, in April and May. All active drumming logs were located on these plots by direct searching and by following the sound of drumming birds. Each plot was visited three or more times at intervals of 1–3 weeks.

Cedar Rapids. Spring density of breeding cocks was determined in the same manner as on Highway 27. In September, the trapping and release of leg-banded birds furnished two estimates of fall population density by use of the Lincoln Index Method (Lincoln, 1930). First, by using binoculars, direct observations were made on the ratio of banded to unbanded birds feeding on clover along the fire-lane just prior to the gun season. From these observations, a preseason estimate of the percentage of the population with leg-bands was calculated. Secondly, a sample of birds shot by hunters on the area and checked by Conservation Department personnel in October and November supplemented this preseason banded ratio. In 1953 only 6.7 miles of fire-lane were sampled by trapping and hunter checks, while from 1954 to 1957, 10.0

miles of fire-lane were checked between the two road junctions (see Fig. 2) on either end of the area.

Otter Creek. Spring cock density was determined on 10 plots, varying in size from 17 to 162 acres and selected so as to be representative of the entire study area (see Fig. 3). Using the same methodology as on Highway 27, active male territories were located and cocks trapped in spring. Grouse were also trapped and leg-banded in August and September prior to the hunting season. The percentage of the population banded could be estimated from a sample of birds shot during the hunting season in October, November and December; and, in addition, from roadside observations during and after the hunting season. By use of the Lincoln Index technique, the total preseason population could then be calculated.

Harvest Measurement

Quantitative measurement of the hunting harvest was achieved on the Cedar Rapids and Otter Creek study areas using the following methods. The inscription "$1 Reward for Return to Wisconsin Conservation Department" was stamped on all leg bands placed on birds; and, in addition, newspapers in the surrounding communities carried short notices requesting band returns. A field check by one or two men conducted on all hunting week ends and a partial check during the week insured a high likelihood of contact between hunters and checkers. Because of the intensive field check and the monetary reward, we feel that between 95 and 100 per cent of the bands were returned.

Parasitic Disease Studies

Project personnel obtained intestinal tracts by shooting grouse in August, September, and October in the years 1948 to 1952. From 1953 to 1955, project personnel removed viscera from birds freshly shot by hunters in early October. The gastrointestinal tracts for all years came mainly from Rusk, Sawyer, Price and Bayfield Counties with smaller numbers from about seven counties in northeastern and central Wisconsin. All viscera were preserved in FAA (formalin, alcohol, acetic acid) and examined grossly for endoparasites by spreading the intestinal contents thinly on a sheet of paper or placing the opened intestines in a pan of water. The horny lining of the gizzard had to be removed to locate gizzard worms. Trachea were examined in some years for gapeworms. The following people examined the specimens for endoparasites: George Halazon, 1948; Kenneth Flakas, 1949–51; Geoffrey Lord, 1952; Dorney, 1953–58.

By the use of a sugar flotation technique Dorney checked in fecal samples the quantity of nematode eggs present in 1957 and 1958. Spring feces taken from drumming logs in May and winter samples collected from fresh snow roosts in early January were frozen until analyzed. The use of plastic bags prevented desiccation of the collected material.

POPULATION DENSITY AND AGE AND SEX STRUCTURE

Changes in Grouse Abundance

The numbers of territorial cocks located on the three study areas (Fig. 4) varied widely, presumably due to a fundamental difference in "carrying capacity." As indicated by all indices and direct counts, late-winter and spring populations were generally high in 1950, decreased to a low level in 1954, and then increased, with a small drop in 1958. Fluctuation of the Otter Creek (a semi-agricultural area) spring cock population (1956–58) was, however, inverse to that of northern Wisconsin and Cedar Rapids.

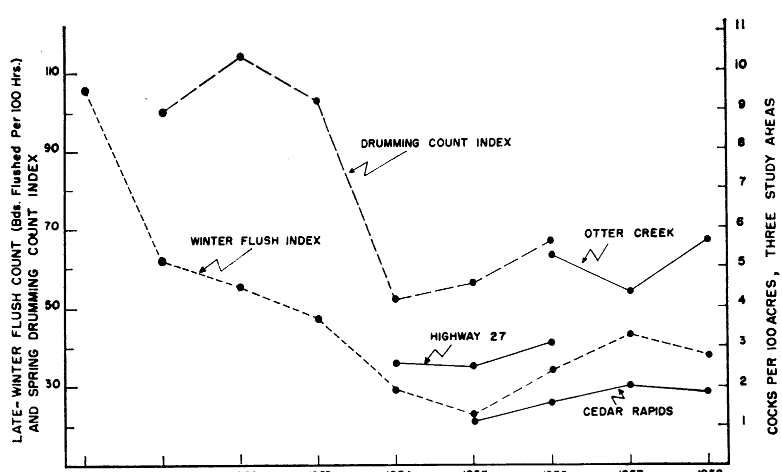

Figure 4. Late-winter flush index in northern Wisconsin (February and March), spring drumming-count index in northern Wisconsin, and spring territorial-cock counts (solid lines) on three study areas, 1950-58.

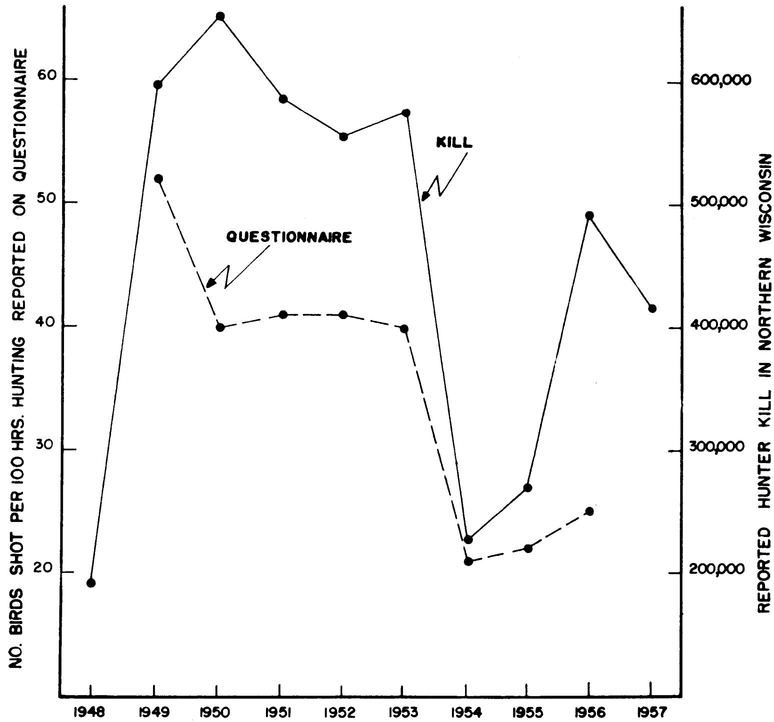

Figure 5. Indices of fall ruffed grouse populations based on hunter kill in northern Wisconsin and hunter questionnaire for entire state.

Fall populations measured by a hunter-postcard questionnaire and total kill data (northern Wisconsin) were high in the period 1949 to 1953, dropped sharply in 1954, and generally recovered from 1955 to 1957 (Fig. 5).

Figure 6 presents the calculated Lincoln Index preseason populations for the Cedar Rapids study area and the number of birds flushed per hour by "brush hunters" (hunting on foot in woods). Due to movement of juveniles to the fire-lane in fall in Cedar Rapids, primarily juveniles were banded there; consequently, the Lincoln Index calculations deal almost exclusively with juveniles. For this reason, all adults were omitted from the Lincoln Index data graphed in Figure 6. Because of the smaller road area checked in Cedar Rapids in 1953, the data from this sample were arbitrarily expanded to compare with the population estimates from 1954 to 1957.

In both Otter Creek and Cedar Rapids, the movement of banded juveniles away from the study area, as indicated by total band returns,

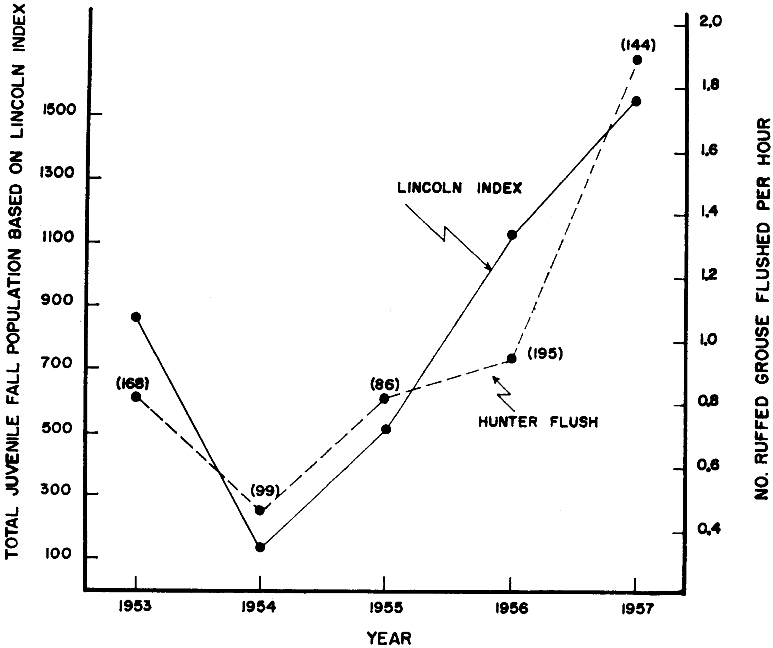

Figure 6. Indices of the fall population of ruffed grouse in the Cedar Rapids area. Numbers in parentheses are the total hours of hunting effort of hunters in the woods (brush-hunting). Lincoln Index calculations are based on banded juvenile birds only and corrected for egress.

made it desirable to subtract the estimated number that left the area from the total number of birds banded. For example, if 100 birds were banded and 30 per cent were shot away from the area, it would be assumed that 70 birds remained on the area. This appeared to give a more realistic (minimal) estimate of the total preseason population of juveniles. In Otter Creek the following percentage of juveniles left the study area: 1956, 3 out of 14 (21 per cent); 1957, 1 of 4 (25 per cent). In Cedar Rapids the ratios and percentages were as follows: 1953, 5 of 21 (24 per cent); 1955, 4 of 10 (40 per cent); 1956, 5 of 25 (20 per cent); 1957, 5 of 15 (33 per cent). No adults left the Otter Creek area. From all indications, hunting pressure was about the same on as off the two study areas.

The banding data used to calculate population levels in Cedar Rapids by the Lincoln Index Method (Fig. 6) appear in Table 1. Similar data (Table 2) from Cedar Rapids were derived from preseason observations of banded and unbanded birds feeding along the

TABLE 1

Sample Sizes from Hunter Returns Used in Calculating Total Preseason Populations of Juvenile Ruffed Grouse at Cedar Rapids by the Lincoln Index Method

Year	Total No. Juveniles Banded*	No. Banded Juveniles Shot by Hunters	Total Number Juveniles Examined	Per Cent Total Population Banded	Calculated Total Juvenile Population	95 Per Cent Confidence Limits
1953	65	18	161	11	581**	409–1,066
1954	9	1	15	7	135	43–∝
1955	35	3	43	7	502	236–∝
1956	80	13	183	7	1,126	748–2,424
1957	62	7	173	4	1,532	899–5,636

*Corrected for movement from area.
**Only 6.7 miles of 10.0 miles on Study Area (Fig. 2) were trapped; hence total comparative number of birds is 867.

road. The preseason data were collected after the bulk of the birds had been banded, usually 5 days prior to the opening of the season. Because there is no way of telling at what date the birds moved off the area, these preseason sight records cannot be corrected for this movement. The primary usefulness of the preseason observations is to show that the statistic on percentage of the population banded from hunter bag checks (Table 1) has more restricted confidence limits than indicated, since the statistics on percentage of population banded in Tables 1 and 2 are similar. In addition, there is a significant correlation ($r = 0.89$, 3 d.f.) between the calculated total juvenile population and hunter flush counts (Fig. 6) in Cedar Rapids.

For the Otter Creek area (Fig. 7), the absence of differential juvenile vulnerability (described later), as well as the unimportance of road hunting, made it possible to calculate total preseason popula-

TABLE 2

Percentage of Birds Banded, as Observed Along Road Prior to Hunting Season, Cedar Rapids (No Correction for Movement Off Study Area)

Year	Total Birds Observed	Per Cent Banded
1953	84	14
1954	0	--
1955	67	4
1956	108	8
1957	352	4

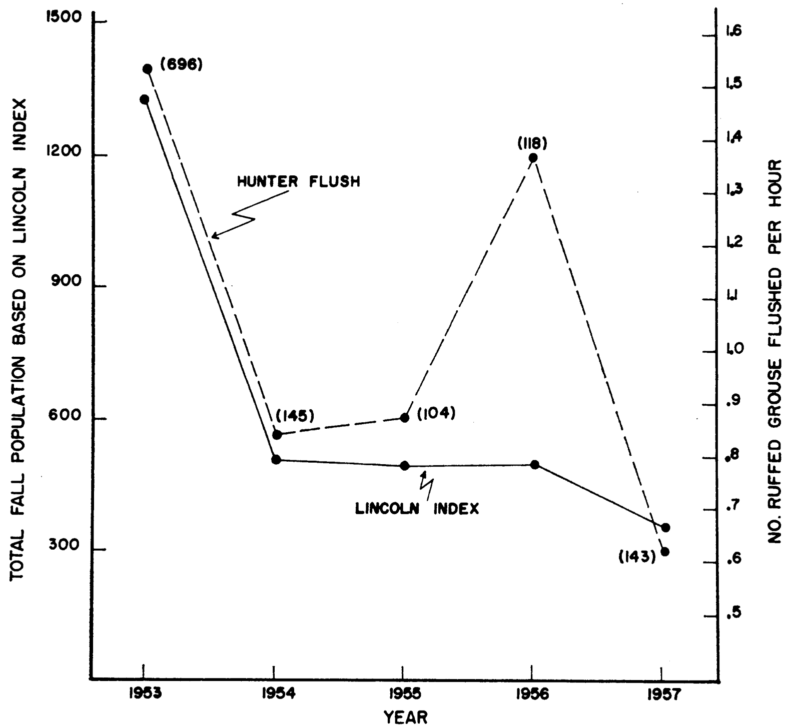

Figure 7. Indices of the fall population of ruffed grouse in the Otter Creek area, which are based on birds flushed by hunters in woods (brush-hunting), and Lincoln Index calculations from banded birds. Numbers in parentheses are total hours of hunting effort sampled in each year. Lincoln Index calculations are based on both juvenile and adult grouse.

tions of adults and juveniles combined. Cocks trapped in spring, and all sex and age components trapped in fall were added together to give the total number banded (Table 3). The percentage of the population banded was then based on a ratio of banded to unbanded birds shot by hunters and checked in the field by research personnel (Table 3). Comparative data (Table 4) are presented on the percentage of the population banded based on roadside observations of live birds during and after the hunting season. Although the samples on which Table 3 are based are small, the data in Table 4 again help to confirm the statistics in Table 3 used to calculate total fall populations.

Population trends based on subjective observation agreed with that shown by the total populations calculated in Table 3. In addition, the correlation coefficient of 0.77 (tab. 0.05 = 0.88, 3 d.f.) between

TABLE 3

Sample Sizes from Hunter Bag Checks Used in Calculating Total Preseason Populations of Ruffed Grouse at Otter Creek by the Lincoln Index Method

Year	Total Number Banded	No. Banded Shot by Hunters	Total Number Examined in the Bag	Per Cent Population Banded	Calculated Total Population	95 Per Cent Confidence Limits
1953	76	17	295	6	1,319	874–2,303
1954	61	3	25	12	508	238–∝
1955	128	6	23	26	490	283–1,910
1956	124*	9	34	26	468	302–1,127
1957	82*	5	21	24	344	188–1,822

*Corrected for the movement of juveniles off study area.

number of birds flushed by brush-hunters (Fig. 7) and calculated total fall population from banding ratios suggests a close relationship between these two statistics. In view of the small samples of banded birds and hunting hours (Table 3, Fig. 7), the disparity shown in Figure 7 for the year 1956 is not surprising. As indicated, fall populations in Otter Creek (Fig. 7) did not fluctuate in synchrony with those in northern Wisconsin (Figs. 5 and 6).

TABLE 4

Percentage of Birds Banded, as Observed Along Roads During and After Hunting Season, Otter Creek, 1955–57

Year	Total Number	Per Cent Banded
1955	104	20
1956	92	10
1957	32	16

Age and Sex Structure of the Population

Spring Age Ratios

The ages of spring-trapped males for the three study areas (Table 5) show in the spring of 1955 a ratio heavily in favor of birds 2 years or more in age. In 1954, and 1956 to 1958, the ratio was either favorable to young birds or was about equal.

In Table 6, data from Table 5 are combined with the total number of spring territorial males located on each area to make possible an estimate of the annual mortality rate. As shown by the data from

TABLE 5

Age of Drumming Males Trapped in Spring on Drumming Logs

Year	Highway 27		Cedar Rapids		Otter Creek		Total	
	1-Year-Olds	2 Years or over	1-Year-Olds	2 Years or over	1-Year-Olds	2 Years or over	1-Year-Olds	2 Years or over
1954	15	13	--	--	2	3	17	16
1955	7	20	13	28	18	24	38	72
1956	21	16	37	19	33	33	91	68
1957	--	--	44	22	23	26	67	48
1958	--	--	43	16	14	19	57	35
Totals	43	49	137	85	90	105	270	239

Highway 27 and Cedar Rapids, the period from the spring of 1954 to the spring of 1955 had the lowest annual loss, 24 per cent. In the years that followed, the mortality increased.

Next, an attempt was made to explore spring age biases resulting from cocks failing to set up territories as 1-year-olds. One method for estimating this bias is to leg-band juvenile cocks in the fall. Then as spring trapping takes place year after year on the same area, tabulate the number of banded 2-year-old cocks caught on logs in spring that were missed as 1-year-olds. This number can then be compared to those known-age cocks caught on territories as both 1- and 2-year-olds.

In the springs of 1955 and 1956, of a total of 6 cocks caught as 2-year-olds, only 4 had been caught as 1-year-olds. These data, although dealing with small samples, suggest about one-third of the young cocks failed to set up recognizable territories in their first year of life. Although considerable time was expended checking the area at least three times for drumming cocks, a sizable proportion of young cocks appear to have been missed, even with this supposedly thorough coverage.

A further indication that all 1-year-olds are not strongly territorial is shown by the sequence of events following the accidental death of a cock in a mirror trap. In about six cases where this happened, a new cock usurped the same drumming log in a few days. In each case the new cock was a 1-year-old bird. Although this is not necessarily proof that these particular cocks would not have set up a territory sometime later in the spring, the circumstantial evidence suggested that these cocks were part of what might be considered a nonbreeding reserve.

In the spring of 1958 in Cedar Rapids, an additional experiment on nonterritorial cocks was conducted by trapping and removing all cocks on a 360-acre area. When 10 territorial birds were removed, 9 of which were 1-year-olds, new 1-year-old cocks appeared in two of the territories. After these two replacements were removed, no other cocks appeared.

TABLE 6

Annual Mortality Rate of Spring Territorial Males Based on Total Population (Both Trapped and Untrapped) and Spring Age Ratio of Trapped Cocks

	Observed Age Structure		Total Number Males on Plots	Computed Age Structure		Calculated** Annual Mortality Rate
	1-year-olds	2 Years or Over		1-year-olds	2 Years or Over	
Highway 27						
1954	15	13	25	13	12	
1955	7	20	25	6	19	24%
1956	21	16	30	17	13	48%
Cedar Rapids						
1955	13	28	43	13	28	
1956	37	19	65	43	22	46%
1957	44	22	79	53	26	60%
1958	43	16	74	54	20	75%
Otter Creek						
1956	33	33	36	18	18	
1957	23	26	30	14	16	56%
1958	14	19	39	17	22	27%
Total and Average	250	212	446*	248	196	56%

*Does not always equal total of 1- and 2-year-olds or older, since in some years—when time permitted—birds adjacent to plots were caught, while in other years all birds on plots were not trapped.

**Calculated from the computed age structure, by dividing the number of 2-year-olds in any subsequent year by the total number of 1- and 2-year-olds from the previous year, and then taking the reciprocal.

Taber (1949) and Collias and Taber (1951) have shown that in ring-necked pheasants (*Phasianus colchicus*), submissive cocks are nonterritorial and do not crow. Indirect evidence from the present study indicates that the situation in ruffed grouse is similar, with some 1-year-old cocks making up a reservoir of nonterritorial males. In isolated cases, a 1-year-old cock apparently can usurp a territory from an older bird. This was noticed once, when an old cock was replaced one spring by a 1-year-old, and then the original cock was retrapped the following year on the same drumming log.

As a result of this tendency to underestimate the 1-year-old segment

TABLE 7

Ruffed Grouse Hunting-season Sex and Age Ratios, Northern Wisconsin

Year	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	Mean and Total
No. birds sampled	216	1,344	2,687	2,909	2,939	4,072	1,999	2,830	4,533	2,788	26,317
Per cent males in juvenile sample	47	55*	48	51	49	50	52	52*	51	49	50
Per cent males in adult sample	57	57*	53	53	56*	54*	58*	52	53	52	54*
Per cent juveniles	87	80	77	79	77	77	75	84	81	81	80
No. juveniles per adult female	15.7	9.1	7.4	8.2	7.9	7.4	7.1	10.9	9.2	9.1	9.2
No. juveniles per adult male	11.8	6.9	6.4	7.3	6.1	6.4	5.2	10.0	8.2	8.3	7.7
No. juveniles per adult	6.7	3.9	3.4	3.9	3.5	3.4	3.0	5.2	4.3	4.3	4.2

*Differ significantly at 95 per cent level from a 50:50 ratio.

of the population in spring, we believe that the age ratios in Table 5 show too few juveniles. Similarly, the mortality calculations (Table 6) would be minimal, especially if population density is directly related to number of nonterritorial cocks. Adjustment of the average implied mortality rate (Table 6) of 56 per cent by addition of one-third more juveniles would result in a theoretical annual average adult male mortality of 66 per cent. The age-ratio and mortality data (Tables 5 and 6) should be useful, nevertheless, for indicating major differences and trends between years.

Fall Age and Sex Ratios

The ten-year study on sex and age structure of the population (Table 7) showed a juvenile sex ratio each year closely approaching equality, with the over-all average ratio, 50:50. The adult sex ratio on the other hand, each year strongly favored males, with the over-all ratio significantly different from 50:50. The juvenile percentage fluctuated from 75 to 87 per cent throughout the 10-year span. This percentage can be better understood when it is expressed as a ratio of juveniles per adult male or adult female. We prefer the statistic juveniles per adult male if a juvenile-adult ratio is to be used, since it provides a better yardstick for comparing productivity between years. For example, a look at juvenile production in 1954 and 1955 shows a ratio of 5.2 and 10.0 juveniles per adult male. The juveniles per adult female statistic only shows a 7.1 to 10.9 difference for these same years. This difference is due solely to a change in adult sex ratio, 58 and 52 per cent, for these same years.

Factors Biasing Fall Age and Sex Ratios

The fall age ratios compared (Table 8) for birds shot on foot in the woods (brush hunting) and shot on roads, indicate a much higher percentage of juveniles shot on roads (highly significant difference). It is only possible to segregate the fall wing and tail samples into these two road and brush groups from 1953 to 1957, since in previous years hunters were not asked to record their method of hunting.

A comparison of the sex ratios between road- and brush-shot samples (Table 9) indicates no difference ($\chi^2 = 2.0$) between the adults, but a highly significant difference ($\chi^2 = 8.6$, $P < 0.01$) between the results obtained in the two methods of sampling juveniles. In comparisons of the adult brush- and road-shot samples, the data from each year consistently favor males. Perhaps a larger adult sample would also show a significant preponderance of males in the brush-shot samples.

TABLE 8

Comparison of Age Ratios Between Ruffed Grouse Shot in Woods (Brush Hunting) and on Roads (Road Hunting), Northern Wisconsin, 1953 to 1957

Year	Brush Hunting			Road Hunting		
	Total Sample	Per Cent Juveniles	Ratio Adult to Juvenile	Total Sample	Per Cent Juveniles	Ratio Adult to Juvenile
1953	2,482	74	1:2.9	1,051	83	1:5.0
1954	1,451	72	1:2.6	482	83	1:4.8
1955	1,841	82	1:4.4	872	89	1:8.4
1956	2,848	79	1:3.7	1,493	86	1:6.0
1957	1,774	79	1:3.8	913	85	1:5.5
Totals	10,396			4,811		
Means		77	1:3.5		85	1:5.9

TABLE 9

Comparison of Sex Ratios of Juvenile and Adult Ruffed Grouse Shot in Woods and on Roads, Northern Wisconsin, 1953 to 1957

Year	Brush Hunting				Road Hunting			
	Adult		Juvenile		Adult		Juvenile	
	No.	Per Cent Male	No.	Per Cent Male	No.	Per Cent Male	No.	Per Cent Male
1953	619	57	1,721	52	173	44	815	46
1954	396	57	968	51	82	60	375	53
1955	336	52	1,390	54	92	55	720	50
1956	570	53	2,037	53	198	50	1,163	48
1957	368	51	1,307	48	141	54	711	50
Totals	2,289		7,423		686		3,784	
Means		54		52		51		49

Another approach for quantitative evaluation of differential sex and age vulnerability is possible by comparing the band returns for each sex and age group. In Table 10, these differential returns for birds banded and shot in the same year are compared for Otter Creek. Since very few birds were shot on the road in this study area, this sample can be considered a brush-shot sample. Unfortunately, the small number of band returns makes it impossible to compare male and female returns within the adult and juvenile groups. However, a chi-square comparison between all juveniles and all adults indicates no difference in the recovery rate. It appears, therefore, that age ratios in the bag in Otter Creek (brush hunting) should be without age bias.

Tables 11 and 12 show differential band returns between age classes for road- and brush-shot samples in Cedar Rapids for birds banded and shot in the same year. A chi-square comparison of all adults and all

TABLE 10

Number of Ruffed Grouse Banded and Shot (Both Road- and Brush-hunting) in Same Year for All Sex and Age Groups, 1953 to 1957, Otter Creek Area

Year	Adult Males		Adult Females		Juvenile Males		Juvenile Females		Juveniles Unsexed		Total All Groups		
	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Per Cent Shot
1953	19	6	10	4	9	5	10	0	14	3	62*	18	29*
1954	36	2	5	1	4	0	--	--	16	1	61	4	7
1955	58	5	5	0	29	3	15	1	21	1	128	10	8
1956	69	7	8	2	12	4	10	2	38	8	137	23	17
1957	53	5	2	0	7	1	8	2	21	1	91	9	10
Totals	235	25	30	7	61	13	43	5	110	14	479	64	13
Mean Per Cent by Groups	11	:	23	:	21	:	12	:	13				
		12		:		15				:			

*Only 62 of 76 birds were aged, hence total does not agree with Table 3.

TABLE 11

Number Ruffed Grouse Banded and Shot on Roads in Same Year, All Sex–Age Groups, 1953 to 1957, Cedar Rapids Area

Year	Adult Males		Adult Females		Juvenile Males		Juvenile Females		Juveniles Unsexed		Total All Groups		
	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Per Cent Shot
1953	--	--	2	--	35	8	35	6	15	3	87	17	20
1954	--	--	2	--	1	--	7	--	1	--	11	--	0
1955	40	--	3	--	17	1	21	2	20	3	101	6	6
1956	56	1	9	1	57	11	38	8	5	3	165	24	14
1957	69	2	6	--	38	8	18	1	36	2	167	13	8
Totals	165	3	22	1	148	28	119	17	77	11	531	60	11
Mean Per Cent by Groups		2 :		4 :		19 :		14 :		14			
			2	:		16					:		

TABLE 12

Number Ruffed Grouse Banded and Shot in Same Year in Woods, All Sex and Age Groups, 1953 to 1957, Cedar Rapids Area

Year	Adult Males		Adult Females		Juvenile Males		Juvenile Females		Juveniles Unsexed		Total All Groups		
	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Banded	Shot	Per Cent Shot
1953	--	--	2	2	35	6	35	2	15	1	87	11	13
1954	--	--	2	--	1	1	7	--	1	--	11	1	9
1955	40	1	3	--	17	1	21	2	20	--	101	4	4
1956	56	2	9	1	57	2	38	1	5	--	165	6	4
1957	69	5	6	--	38	2	18	--	36	2	167	9	5
Totals	165	8	22	3	148	12	119	5	77	3	531	31	6
Mean Per Cent by Groups	5	: 6	14	: :	8	: 6	4	:	4		:		

juveniles (1955–57) indicates a highly significant difference ($\chi^2 = 19.5$, $P < 0.01$) between the recovery rates for those age groups shot on the road (Table 11) and no difference for those shot in the woods (Table 12). In computing the chi-square values, the 1953 and 1954 samples were not used because no adult males were banded in these years. Therefore, on the basis of band returns, juvenile birds in Cedar Rapids are more vulnerable to road hunting but not to brush hunting. This substantiates the results found in the hunting season sex and age analysis (Table 8). Brush-shot age samples thus appear to provide a reasonable measure of productivity while road samples do not.

The marked scarcity of adult males in road-hunting samples (Table 11) suggests that fall mobility of juveniles and adult males may be involved. The distances the various age and sex groups have moved are given for Otter Creek and Cedar Rapids, 1953 to 1957 (Table 13), for birds shot in the same year as banded. As indicated, adult males are less mobile than juveniles. A chi-square value of 8.5 ($P < 0.01$) for adult males and juveniles moving less than or more than one-half mile indicates that a real difference in mobility does occur. The small sample of adult female returns makes any conclusion hazardous for this age and sex group. Chambers and Sharp (1958) also found juveniles more mobile than adult males in Pennsylvania.

On a theoretical basis, increased mobility of juveniles, by itself, should not result in a higher recovery of juvenile bands. This is borne out by the juvenile-adult band returns in brush-shot samples from both

TABLE 13

Distance Ruffed Grouse Moved from Trapping to Shot Location in Same Year as Banded, 1953 to 1957, in Miles or Fractions of Miles

Where Banded	Age Group	Distance Moved 0–½	½–1	1–2	2+	Mean
Cedar Rapids	Adult male	6	2	2	1	0.8
	Adult female	3	--	--	1	1.4
	Juvenile	35	14	12	13	1.0
Otter Creek	Adult male	22	3	--	--	0.2
	Adult female	7	--	--	--	0.2
	Juvenile	15	5	6	7	1.4
Totals	Adult male	28	5	2	1	0.4
	Adult female	10	--	--	1	0.6
	Juvenile	50	19	18	20	1.1

Otter Creek and Cedar Rapids, which show no differential juvenile vulnerability (Tables 10 and 12). Possible explanations for the heavy kill of juveniles along roads in the north will be discussed in the next section of this paper.

A further check on hunting-season age-ratio biases is possible by comparing these ratios with the number of young observed in summer broods. Only broods judged by trained field men to be completely counted were used. However, these counts remain as minimal estimates of brood size, since a few chicks can be missed in heavy cover. In Table 14, the brood and age-ratio data are compared for the years 1953 to 1957. Although the extent of summer mortality of juveniles and adult females is unknown, the brush-hunting ratio of juveniles per adult female is similar to actual sight records of brood size, strengthening the belief that brush-shot samples give a realistic age ratio while road-shot samples do not.

One more difficulty in the use of fall age-ratios is shown in Table 15. The age ratios for brush-shot birds in northern Wisconsin appear to decrease in some years throughout the 6-week hunting season (October 1 to mid-November). The correlation coefficients for each of the years are as follows (arc sine transformations used for the percentages): 1953, -0.86; 1954, -0.64; 1955, -0.42; 1956, -0.04; 1957, -0.76; with an overall, -0.78 (tab. 0.05 = 0.81), with 1953 showing significance, and 1957 and the overall approaching significance. The specific factor(s) responsible for this apparent shrinkage are unknown, although the lack of differential band returns of age groups in brush-shot samples suggests that this shrinkage should not be due to a differential harvest of juveniles in the brush but rather a reflection of other natural mortality factors. A similar age ratio shrinkage has also been shown for California quail (*Lophortyx californica*) by Emlen (1940) and for pheasants (*Phasianus colchicus*) by Kimball (1948) and Eberhardt and Blouch (1955).

Securing Unbiased Age and Sex Ratios

To trap a representative spring age sample of territorial cocks appears to be extremely difficult due to the large proportion of apparently non-breeding males. Trapping and removal of all territorial cocks on a large block of range might make it possible to obtain a reasonable age sample, since the nonbreeders appear to establish territories once competition is removed. However, this saturation trapping and removal would involve considerable time and manpower.

TABLE 14

Comparison Between July—August Brood-size Observations and October—November Brush- and Road-shot Age Samples, Northern Wisconsin

Year	Broods		Brush-Shot			Road-Shot		
	No. Counted	Av. No. Chicks	No. Adult Females	Number Juveniles	Juveniles/ Ad. Female	No. Adults Females	Number Juveniles	Juveniles/ Ad. Female
1953	171	6.7	273	1,846	6.8	97	875	9.0
1954	62	6.7	170	1,052	6.2	33	399	12.1
1955	55	8.4	162	1,502	9.3	41	779	19.0
1956	96	7.8	280	2,249	8.0	106	1,279	12.1
1957	74	8.6	179	1,406	7.9	65	772	11.9
Unweighted means		7.6			7.6			12.8

Unbiased fall age ratios in northern Wisconsin can only be secured by sampling birds shot away from roads (brush-hunting), see Tables 8, 10, 11, 12 and 14. This is due to the habit of juveniles concentrating along roads and fire-lanes which is characteristic of only this area. Since one-third to one-half of all birds are shot on roads in this part of Wisconsin, any comparison of age ratios between our southern and northern range must be made with only brush-shot samples. The same situation may well apply to other states or provinces in this region.

Field observations indicate that road-shot samples are predominantly juvenile for the following reasons:

1. Presence of succulent green food (esp. clover) along road edges, tending to hold young birds when they find these areas in their fall wanderings.

2. Presence of gravel and dusting spots on or along the road or shoulder of road.

3. Adult males in fall remain attached to previously established drumming sites, resulting in their widespread distribution, as contrasted to the unattached juvenile male.

4. There is a possibility that adults are more wary along roads. However, this seems unlikely since adults are properly represented in brush-shot samples.

Sharp differences in ruffed grouse age ratios apparently can be expected in different geographic areas. Bump *et al.* (1947:513) consider a 1.0–1.4:1 juvenile-adult ratio in late August as typical for New York. As shown in Table 8, a 3.5 to 1 juvenile-adult ratio in the hunting season (October–November) was indicated for birds shot in the brush in northern Wisconsin. This difference (discussed more fully later) between Wisconsin and New York must be the result of severe summer brood mortality (60–65 per cent) suffered in New York (Bump *et al.* 1947:527) compared to low losses (20 per cent) in Wisconsin (Table 17). Unfortunately, age data collected on ruffed grouse in many other states and provinces remain unpublished to date, making a more comprehensive comparison impossible.

An explanation of the differences in fall sex ratios for both age classes between road-and brush-shot birds presents more of a problem. The reason for the observed significant difference in juveniles is unknown. However, for the adults the difference could be due to fall territoriality, restricting adult male movement.

Bump *et al.* (1947:514–515) based on direct observation of flushed birds, considered the summer sex ratio of adult grouse to lie between 42.5 and 49.7 per cent males. In contradiction to this, they showed

TABLE 15

Shrinkage in Percentage of Juveniles Throughout Six Weeks of Hunting Season, Northern Wisconsin, Brush Hunting Only, 1953 to 1957

Year	Sample Size by Weeks						Per Cent Juveniles by Weeks						Unweighted Average
	1	2	3	4	5	6	1	2	3	4	5	6	
1953	937	618	367	206	178	176	78	75	71	74	67	69	72
1954	447	201	321	190	121	171	74	80	74	69	60	71	71
1955	638	421	392	204	71	115	83	83	81	78	70	83	80
1956	1,225	594	400	286	200	138	79	80	80	77	77	81	79
1957	586	450	280	259	145	54	80	80	84	76	74	72	78
Totals	3,833	2,284	1,760	1,145	715	654							
Means							79	80	78	75	70	75	76

winter-shot samples to comprise 55 and 58 per cent males. Based on our data (Table 7) these summer adult sex ratios appear to be biased, while the winter sex ratios of their samples agree with those found in this study.

FACTORS AFFECTING POPULATION LEVELS

Weather

The effects of weather on ruffed grouse populations in northern Minnesota have been studied recently with orthogonal polynomials by Larsen and Lahey (1958). They concluded that above-average winter temperatures tend to be associated with a decreasing population in the following April, while warm spring and summer weather tends to be associated with increasing populations in the following April. Bump *et al.* (1947:304) also noted that cold, rainy spring weather adversely affected the survival of grouse chicks. Siivonen (1957) in Finland has also related population fluctuation of European tetraonids to spring temperatures.

By using fall sex and age ratios, winter flush counts, and summer brood counts, we endeavored to determine the influence of weather at these various times of year.

Spring

The effect of spring weather on production was explored by computing an average of the maximum and minimum spring temperatures from weather records at Weyerhauser and Antigo in northwestern and northeastern Wisconsin. In a few cases where Weyerhauser data were lacking, temperatures from Ladysmith (20 miles east) were used. Next, the spring was arbitrarily divided into a pre-laying period (April 1–27), laying period (April 28–May 12) and incubation period (May 13–June 5) based on observed ages of broods (see Hale and Wendt, 1951). The number of juveniles per adult male from hunter-bag checks was used as a yardstick of productivity (Table 16) and compared with the average temperatures for each of these reproductive periods. The correlation coefficient for both the April 1–27 and April 28–May 12 groups was 0.41, and for the May 13–June 5, 0.43. All were short of significance (tab. 0.05 at 16 d.f. = 0.47).

A second trial was then made using the temperature (average of minimum-maximum) for each of the months of April, May, and June. Only the correlation coefficient for the May data (0.57) was significant,

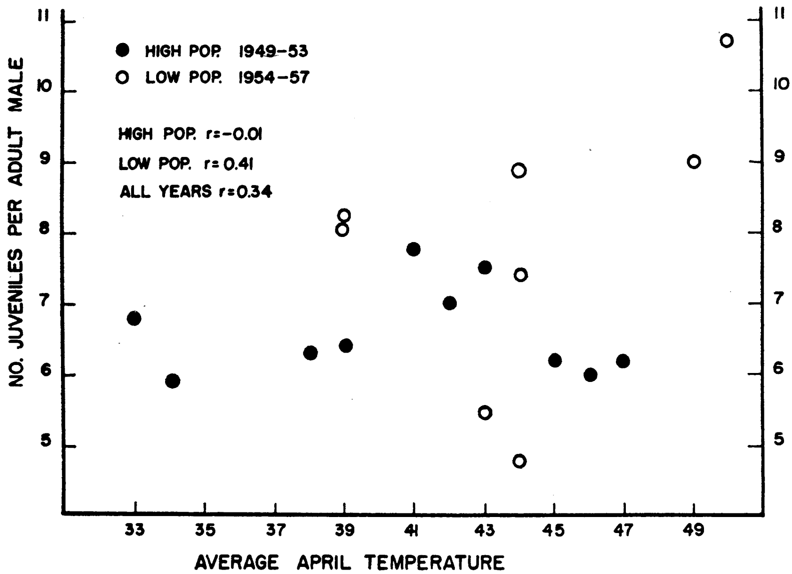

Figure 8. Relationship between April temperatures (°F.) and fall age ratios, 1949-57, northwestern and northeastern Wisconsin.

with coefficients of 0.34 for April and -0.34 for June. In Figures 8 and 9 the April and May data are graphed, and in addition, are arbitrarily segregated into high populations (1949–1953) and low populations (1954–57). Because of their negative relationship (-0.34), June data are not plotted. The correlation between temperature and productivity is better for the years of low populations, with $r = 0.41$ (low) and -0.01 (high) in April (both not significant), and in May $r = 0.88$ for low populations (highly significant) and 0.68 for high populations (significant). Thus the reproduction of low populations appears to be more strongly related to April and May temperatures than is true of high populations.

Percentages of adult males in the fall population (Table 16) were then compared to average May temperatures (Fig. 10). The data for May showed an inverse relationship with an over-all correlation coefficient of -0.41 (not significant). When partitioned into low and high populations, the correlation coefficient for the low density was -0.83 (significant) and -0.10 (not significant) for the high. Again, there was a better relationship between adult male sex ratios and May temperatures for low than for high populations. This sex-ratio shift to favor adult males we presume is due to heavy differential adult female

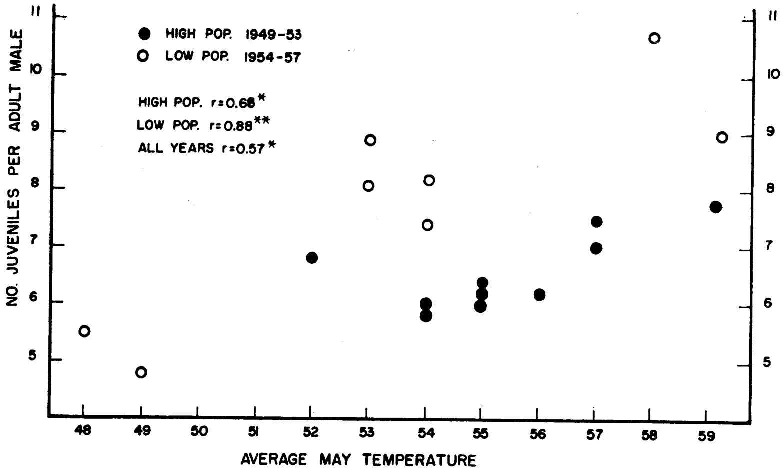

Figure 9. Relationship between May temperatures (°F.) and fall age ratios, 1949-57, northwestern and northeastern Wisconsin.

mortality in cold springs. Visual examination of April and June temperatures plotted against adult sex ratios indicated no relationship.

In summation, it appears that ruffed grouse respond to warm spring temperatures by having higher fall age ratios and more equal adult sex ratios; conversely, cold May weather results in low production and high differential adult female loss. Laying and incubation temperatures (May) appear to be more important than pre-laying (April) or hatching (June) temperatures. Low populations respond to favorable May temperatures better than do high populations (Fig. 9) since summer chick loss (discussed later) is about 12 per cent in "low" years compared to 23 per cent in "high" years (see Table 17).

Winter

The depressing effect of above-average winter temperatures on populations, as inferred by Larsen and Lahey (1958), strongly suggested that warm temperatures were reacting adversely on the birds through crusted snow. Over the past 4 years all our attempts have failed to devise a temperature-snowfall relationship to make possible computation of snow-crust conditions in wooded terrain. For example, a lightly crusted snow that ruffed grouse cannot penetrate, in cold weather can again become "soft", allowing birds to burrow under it. Exposure, cloud cover and wind as well as temperature all affect the crusting of

TABLE 16

Fall Sex and Age Data for Northwestern and Northeastern Wisconsin, 1949–1957, from Hunting-season Samples

	Northwest				Northeast			
Year	Total Juveniles	Total Adults	Per Cent Ad. Males	No. Juv./ Ad. Male	Total Juveniles	Total Adults	Per Cent Ad. Males	No. Juv./ Ad. Male
1949	676	162	56	7.5	396	110	58	6.2
1950	1,307	363	53	6.8	774	243	54	5.9
1951	1,322	351	54	7.0	989	247	51	7.8
1952	1,382	394	56	6.2	898	265	56	6.0
1953	1,895	526	57	6.3	1,255	396	49	6.4
1954	861	262	59	5.5	637	239	56	4.8
1955	1,472	259	53	10.7	904	195	51	9.0
1956	2,340	547	52	8.2	1,342	304	54	8.1
1957	1,456	315	52	8.9	809	208	52	7.4

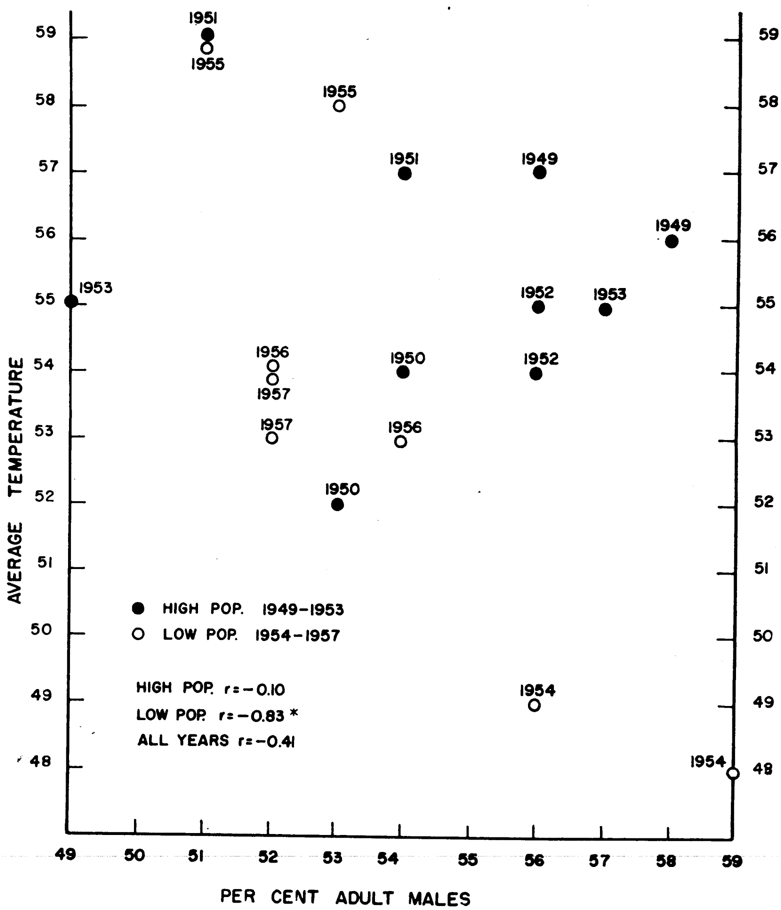

Figure 10. Relationship between adult sex ratios measured during hunting season and average May temperatures (°F.), 1949-57, northwestern and northeastern Wisconsin.

snow. Since detailed snow-crust data were lacking only a crude analysis could be made to relate weather and winter mortality.

Comparative fall and winter mortality rates were estimated from computed fall populations (Table 26) and the shrinkage to the next year's February–March flush count (Fig. 4). The computed fall populations, as later explained, were calculated in this paper from the over-all fall age ratios (Table 7) multiplied by the February–March flush count and added to the respective flush count. The flush statistic was assumed to represent the relative spring population level, since

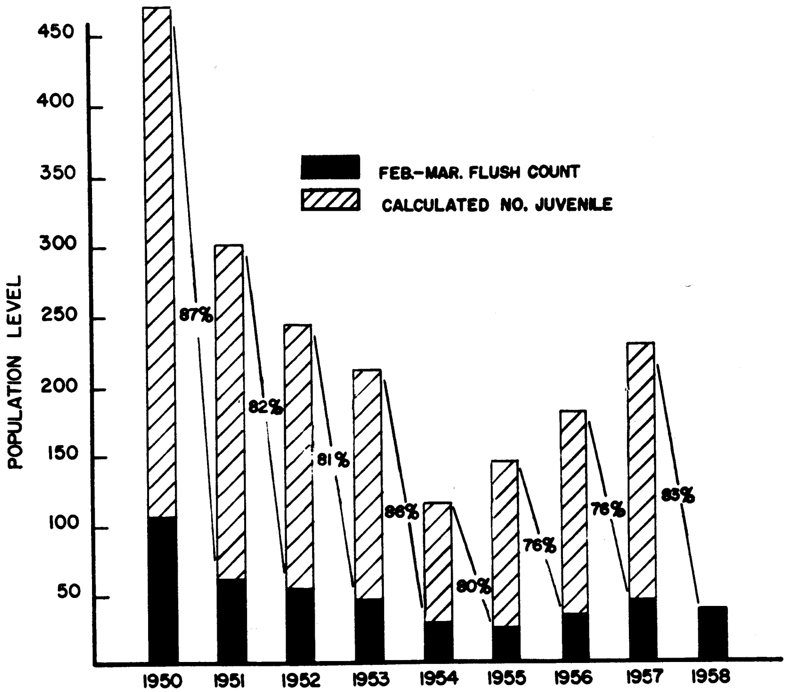

Figure 11. Comparative late-winter and fall-population levels, 1950-58, based on February-March flush counts and fall age ratios, with indicated percentage fall and winter mortality.

it correlated well with spring-drumming counts (Dorney *et al.* 1958). Figure 11 shows these computed fall and winter mortality rates. Since these mortalities are based on age ratios derived from both road- and brush-shot birds, it is necessary to assume that this age bias is constant from year to year, and that adults had a fairly constant summer mortality rate. The mortalities observed are hence not exact statistics. If these assumptions are all valid, then the heaviest losses occurred in the fall and winters of 1950–51, 1953–54, and to a lesser extent, 1957–58.

Weather during these three winters, according to Dahlberg and Guettinger (1956:176–178) and Wisconsin Conservation Department grouse project field notes, was generally more mild and open than the intervening winters. These mild and open conditions in northern Wisconsin typically lead to crusted snow, with little or no bare ground present. General snow conditions in the north, therefore, appeared to be correlated with above-average fall and winter mortalities computed from flush counts and age ratios.

One exception to the above observations must be mentioned. In Otter Creek in the winter 1957–58, with little snow present, total annual mortality measured by spring age ratios and territorial cock counts was very low (Table 6). Apparently, some compensatory factor or factors must have been present to counteract any unfavorable influence from warm winter weather.

When a correlation between calculated overwinter losses (Fig. 11) and average December to March temperatures was made, a coefficient of 0.25 (not significant) was found. This might be explainable, since Larsen and Lahey (1958) were working with about 25 years of data, whereas this study had only 8 years. In addition, fall-harvest levels could influence these computed fall-winter mortality statistics.

The possibility that density-related factors may be involved in overwinter loss cannot be excluded. The mortalities shown in Figure 11 suggest that losses were above average during the decline from high population levels. Annual mortality of territorial males (Table 6) also suggested that as populations recovered, mortality increased.

In summation it therefore appears that above average winter temperatures may be unfavorable to grouse in northern Wisconsin. The exact mechanism of this relationship must await more detailed ecological research.

Summer

As far as we could ascertain, summer weather (June 15–August) exerts little influence on chick survival. Brood observations from 1950 to 1957 showed a slight decline in average size from June to August, with heavier losses of 23 per cent in the high population years compared to 12 per cent in low years (Table 17). In none of the separate years of this study was a die-off or heavy summer mortality indicated.

TABLE 17

Comparison of Average Monthly Brood Sizes for High (1950–53) and Low Populations (1954–57), Northern Wisconsin

	High Populations			Low Populations		
Month	No. Broods	Ave. Size	2 S.E.	No. Broods	Ave. Size	2 S.E.
June	99	8.8	0.61	51	9.0	0.98
July	204	7.4	0.44	125	7.9	0.44
August	211	6.8	0.46	163	7.9	0.42
Per cent loss June–August		23			12	

From this we concluded that, during the years studied, summer weather was generally suitable for chick survival. Bump *et al* (1947:303) concluded that unfavorable June weather did affect the survival of young grouse in late summer (July 16–August 31). However, the summer mortality of New York ruffed grouse (about 60–65 per cent, compared to our 20 per cent) is consistently more severe. For example, Bump *et al.* (1947:527) stated, "by late August, broods comprising more than a hen and four chicks have been uncommon and those with fewer chicks frequent." The two situations are, therefore, not comparable. Losses due to cold and rainy weather immediately following hatching might logically be expected. However, this detailed type of analysis was not possible since hatching curves were not calculated during the course of this study.

Parasitic Disease

Incidence of Parasitism

The incidence of parasitism (Table 18) for the five most common intestinal helminths throughout the period 1948–55 shows *Ascaridia* to be the most abundant. Specific determination as *Ascaridia bonasae* and *Cheilospirura spinosa* was established for these two parasites by Dorney. Speciation of *Heterakis, Capillaria, Raillietina* and *Oxyspirura* in ruffed grouse could not be determined since no specimens were saved by earlier workers.

The infection rate, July to October, 1949–1952, for juvenile ruffed grouse (Table 19) indicates that both *Ascaridia* and *Raillietina* infections were contracted very early in the summer, with the latter apparently decreasing by October. The incidence of gizzard worm (*Cheilospirura*) increased from July to October. Bump *et al.* (1947:412), with larger samples, have shown a similar decrease in *Raillietina* and an increase in *Cheilospirura* from summer to fall.

When the parasitic rates were compared by sex and age groups (Table 20), it appeared that adult males were less commonly parasitized. The difference between the adult male and juvenile incidence for one or more parasites was highly significant. The solitary and nonmobile nature of the adult male may account for this decreased parasitism. The adult female and juvenile infestations did not differ significantly.

Kenneth Flakas, from 1950 to 1952, examined the respiratory tracts of 51 ruffed grouse for gapeworm, *Syngamus sp.* No gapeworms were saved from the 10 infected birds for specific identification. Flakas found

TABLE 18

Incidence Ruffed Grouse Intestinal Parasites, 1948–1955

Year	Number Examined	Per Cent Negative	Per Cent Infected				
			Ascaridia	*Heterakis*	*Cheilospirura*	*Capillaria*	*Raillietina*
1948	96	45	42	8	15	Not taken	1
1949	91	42	49	9	2	3	0
1950	99	32	58	4	6	5	9
1951	87	40	55	1	3	7	5
1952	103	47	52	1	0	0	5
1953	99	47	47	2	5	0	0
1954	78	56	40	0	9	0	1
1955	96	51	45	0	6	0	0
Total	749						
Means		45	48	3	6	2	3

TABLE 19

Monthly Infection of Juvenile Ruffed Grouse with 3 Genera of Helminths, 1949–1952

Month Sampled	Number Examined	Per Cent Infected		
		Ascaridia	*Raillietina*	*Cheilospirura*
July	12	50	50	0
August	70	57	10	3
September	196	57	2	6
October	27	56	0	5

gapeworms in March and April as well as during the summer (Table 21). Seventy-four road-killed birds (1956–58) were examined for gapeworm by Dorney; all were negative. The data in Table 21 superficially suggest that gapeworms were much more common during the high-population years (1950–52), but a statistical comparison is invalid since the winter specimens from 1956 to 1958 were not collected in the same manner, at the same season, nor from the same geographic area as the earlier samples.

Fecal sugar-flotation methods used on winter and spring fecal droppings made it possible to get quantitative comparisons between the number of eggs shed at these two seasons as well as a check on nematode genera present (Table 22). With a few exceptions, 5-gm. fecal samples were analyzed. Since no cecal droppings were examined, the incidence of *Heterakis* sp. could not be determined.

TABLE 20

Relationship Between Parasitic Infection and Ruffed Grouse Sex and Age, 1948–1955

	Number Sampled	Per Cent Infected		
		Ascaridia	*Cheilospirura*	One or More Parasites
Adult males	23	17	9	26
Adult females	69	39	6	48
All adults combined	124	33	6	40
Juvenile male	181	55	3	61
Juvenile female	204	55	7	63
All juveniles combined	616	51	6	58

TABLE 21

Comparative Infection of Adult and Juvenile Ruffed Grouse with Gapeworms (*Syngamus* sp.) Based on Tracheal Examination

Year	Time of Year	Area of State	Adults*			Juveniles**		
			Number Studied	Number Positive	Per Cent Positive	Number Studied	Number Positive	Per Cent Positive
1950	March–April	Rusk, Sawyer	12	4		--	-	
1950	Summer	Northwestern	14	2		72	2	
1951	March–April	Rusk, Sawyer	12	1		--	-	
1952	March	Dunn	13	3		--	-	
1956–57	Winter	Entire state	33	0		10	0	
1957–58	Winter	Entire state	27	0		4	0	
Total and means			111	10	9	86	2	2

*Hatched in a previous calendar year.
**Hatched in current calendar year.

TABLE 22

Incidence of Nematode Eggs Counted Using Sugar Flotation, from Spring and Winter Ruffed Grouse Droppings in Cedar Rapids and Otter Creek Areas, Spring 1957, Winter 1957–58

Season	Spring		Winter	
Sample Size	48		68	
Parasite	Per Cent Infected	EPG*	Per Cent Infected	EPG*
Ascaridia	77	43	53	27
Cheilospirura	2	1	12	1
Oxyspirura	--	--	6	2
Syngamus	--	--	4	10
Capillaria	--	--	3	<1

*Eggs per gm. of feces.

The results from the fecal flotation (Table 22) agree well with those shown in Tables 18 and 21 on intestinal and respiratory helminths. It is of special interest that the number of eggs per gram shed in winter and spring are not greatly different, when one takes into consideration the probably larger fecal volumes passed in winter when grouse are on a fibrous diet.

It can be hypothesized that these nematode eggs spread over the range in winter and spring might be the cause of juvenile infection during the next summer and fall, particularly for those parasites having a direct life cycle (*Ascaridia, Heterakis*). This hypothesis is tested in Figure 12 by graphing February–March flush counts from the same calendar year (Fig. 4) and the preceding fall-population level based on the hunter questionnaire (Fig. 5), against the abundance of ascarids in juveniles. An index of ascarid infection (per cent infected x no. ascarids per infected bird) was computed (Table 23) and used in this figure since this statistic presents a better picture of infection than either value separately. The parasite *Ascaridia* was used in Figure 12 because of its high incidence and because of its uniform occurrence in juvenile grouse from July to October (Table 19). The correlation coefficient for the flush counts is 0.94, (tab. 0.05, 0.88, 3 d.f.) and is significant; for the preceding fall population, $r = 0.82$, and is just short of significance.

To give the entire population-infection data additional meaning, it should be mentioned that the relatively low ascarid index for 1948 and 1949 compared to 1950 (Table 23), corresponds to low wintering

TABLE 23

Data Used to Compute Juvenile *Ascaridia* Index

Year	No. Birds	(A) Per Cent Infected	(B) No. *Ascaridia* per Infected Bird	A X B X 100
1948	80	48	3.3	158
1949	63	52	4.9	255
1950	82	61	7.6	464
1951	74	58	4.4	255
1952	86	55	Not taken	---
1953	81	50	3.0	150
1954	60	45	4.6	207
1955	90	44	2.6	114

populations in 1947–48 and 1948–49, based on subjective field observations. If quantitative fall population and February–March flush counts had been available for 1947–49, the correlation would have been improved.

Ascarid eggs collected in spring from about ten winter droppings were successfully embryonated in the laboratory at room temperature. This showed that eggs could overwinter and develop in spring. Levine (1937) showed similarly that unembryonated *Ascaridia lineata* ova could overwinter. All the objective plus subjective evidence, therefore, points to a very strong relationship between wintering population density and incidence of *Ascaridia* in the young hatched the following year.

Blood smears taken from 1948 to 1955 were examined by different workers; hence comparisons between years were not feasible. However, the 1952 series comprised 85 birds shot primarily in August and September and was examined by Dr. Lord using high-dry and oil-immersion objectives. These birds had an incidence of 81 per cent *Leucocytozoon,* 14 per cent *Haemoproteus,* 6 per cent *Plasmodium* and 5 per cent *Trypanosoma.* These values are similar to those found by Fallis (1945) in Ontario and Erickson (1953) in Minnesota. Blood smears taken from drumming cocks in this study also had heavier infections with blood protozoans than comparable fall smears.

When the incidence of intestinal parasites found in this study is compared with that of similar studies (Table 24), some striking differences are apparent. *Dispharynx* sp. appears to be largely confined to eastern ruffed grouse and blue grouse (*Dendragapus obscurus*) in British Columbia. This parasite causes severe pathology to both ruffed grouse and blue grouse, according to Bump *et al.* (1947:421) and Bendell (1955). The gizzard worm (*Cheilospirura spinosa*) was very

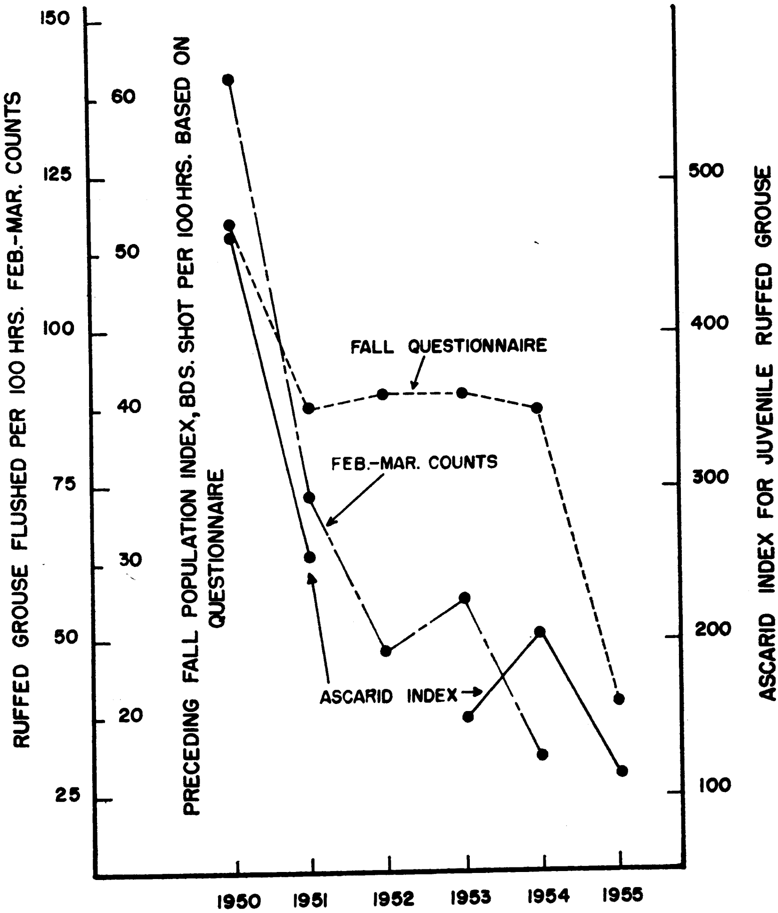

Figure 12. Comparison between index of *Ascaridia bonasae* abundance in late-summer and fall juveniles, and preceding fall and late-winter (February-March) population levels of ruffed grouse. February-March counts include observations in northwestern Wisconsin only.

abundant (19–45 per cent) in all three of the Lake States in the 1930's, but rapidly decreased to about 5 per cent in Minnesota and Wisconsin during the period 1941–1955. *Ascaridia bonasae* was considerably lower in New York and Ontario than in Wisconsin, Minnesota and Michigan. Surprisingly, only trematodes and cestodes were found in 64 ruffed grouse from Labrador (Cram, 1931), nematodes being completely absent. Possible explanations for these chronological and geographic parasitic variations in ruffed grouse will be presented later in this report.

TABLE 24

Comparative Infection Rates for Various Portions of North America for Ruffed and Blue Grouse, All Ages and Sexes Combined

Species and Region	Time Period Studied	Number Specimens Examined	Per Cent Occurrence			Observer
			Ascaridia	*Cheilospirura*	*Dispharynx*	
Ruffed Grouse						
Minnesota	1931–35	431–475	37	19	0	Boughton (1937)
Minnesota	1941–47	231	38	5	0	Erickson *et al.* (1949)
Wisconsin	1928–29	82	?	21	2	Gross (Pers. comm. and 1930)
Wisconsin	1948–55	749	48	6	0	This study
Michigan	1933–36	239	30	45	½	Fisher (1939)
Ontario	1931–35	120–124	21	9	0	Clarke (1936)
New York	1931–41	2,847	16	5	10	Bump *et al.* (1947)
Labrador	1931	64	0	0	0	Cram (1931)
Blue Grouse*						
British Columbia	1950–52	210	9	16	34	Bendell (1955)

**Dendragapus obscurus.*

Importance of Parasitic Disease

In evaluating the role of disease in population fluctuations, it is necessary to revert to indirect types of evidence. The following data support the hypothesis that parasitism plays a role in grouse fluctuations:

1. Parasitic incidence (*Ascaridia,* and probably other species) is related to population density (Fig. 12). The frequent occurrence of parasites in young birds in July (Table 19) suggests an early and continued contact with parasitic-disease agents.

2. Juvenile summer chick loss was twice as high during the period 1950–53 (high populations) than during the "low" years, 1954–57 (Table 17). The greater loss of chicks in the high years is not likely due to predation, since alder (*Alnus* sp.) cover types are used almost exclusively by Wisconsin grouse in summer. These alder areas are extremely dense; hence it is hard to visualize winged predators effectively capturing young grouse there. Mammalian predators, with the exception of weasels (*Mustela* sp.), are too uncommon in most of northern Wisconsin to be important summer grouse predators.

3. As evidenced by adult sex ratios (Table 7), adult females experience greater mortality than adult males. For example, a change from a 50:50 to a 56:44 male: female sex ratio would be produced by a differential female mortality of 21 per cent. Adult females are more heavily parasitized (Table 20). Furthermore, adult female mortality is closely related to May temperatures (Fig. 10) for the low populations ($r = -0.83$) only. The poor correlation ($r = -0.10$) for high populations suggests that additional density-dependent factors must be involved in this adult female loss. The high incidence of gapeworm in breeding birds noted from 1950 to 1952 (high population years) by Flakas (Table 21) suggests that this parasite could be one density-dependent factor involved, since this nematode has a known devitalizing effect on penned galliformes (Morgan and Hawkins, 1949:279). Various intestinal nematodes in adult females are probably also related to density as was true in juveniles (Fig. 12), although too few adults were examined to establish this relationship in the present study. This increased parasitism could interact with the physiological stresses of egg laying and incubation to accelerate female losses under nesting temperatures that would not ordinarily cause mortality in low populations.

4. Accelerated overwinter losses that are apparently density related (Fig. 11) suggest disease, predation, or lack of food as causal agents.

However, the relative importance of these possible density-dependent factors is still unknown.

Many general lines of evidence from this study, therefore, suggest that parasitic disease may elevate mortality rates as populations increase. Parasitism may act as a brake or damper on numbers. As density increases, parasitism could be more and more involved in adult female, juvenile, and overwinter losses, thereby increasing the probability of a population decrease when other factors, e.g. weather, are unfavorable.

By using anthelmintics, experimentally trapped populations could be partially relieved of their parasitic burdens. A better understanding of the role of parasites in population mechanics could thereby be determined. Another approach, suggested by Michigan workers (W. L. Palmer, pers. comm.), is to stock "parasite-free" pen-raised stock on grouse-free islands and compare their population fluctuations with those of adjacent islands where parasitized grouse are present. These two experimental approaches would be helpful in showing whether parasitism plays a major or a minor role in grouse "cycles."

The role of ticks in grouse summer mortality deserves some mention also. These ectoparasites (assumed to be *Haemaphysalis leporis-palustris*) were noted to be abundant on summer birds. Since snowshoe hares are the primary host of these ticks (Green, Evans, and Larson, 1943), the presence of young grouse in alder swamps where hares also concentrate provides a parasitic link between grouse and hares. Snowshoe populations did show a decline around 1950 similar to that shown for ruffed grouse (Figs. 4, 5 and 11).

The enzootiology of gapeworm in ruffed grouse is not clear. Goble and Kutz (1945) in New York found the genus *Syngamus* present in the crow (*Corvus brachyrhynchos*), robin (*Turdus migratorius*), meadowlark (*Sturnella magna*), grackle (*Quiscalus versicolor*), ruffed grouse and pheasant (*Phasianus colchicus*). The cross transmission of gapeworm from robins to chickens appears to be possible in the laboratory (Ripple, 1941), but has not been studied in the field. Since robins and crows are common summer residents in northern Wisconsin, they may have been involved in the gapeworm infestations noted in ruffed grouse by this study.

Geographical Differences and Historical Changes in Parasitism

The spectacular decrease in the incidence of *Cheilospirura* (Table 24) in the last 25 years in the Lake States (Minnesota, Michigan, Wisconsin) may be due to two factors, grasshoppers and sharp-tailed grouse (*Pedioecetes phasianellus*). In the 1930's, high populations of grasshoppers, the intermediate host, were common in Wisconsin (E. L. Chambers, pers. comm.). The better interspersion of grassy openings as a result of logging and uncontrolled fires also may have increased contact between ruffed grouse and grasshoppers. Boughton (1937) and Morgan and Hamerstrom (1941) have further shown that sharp-tailed grouse are also infected with *Cheilospirura spinosa.* Since sharptails were abundant in the 1930's and consume large numbers of grasshoppers (Grange, 1948:158), they could have constituted a primary host for the gizzard worm. Fisher (1939) noted considerable evidence of tissue destruction associated with heavy infestations of gizzard worm in ruffed grouse he encountered. Perhaps this parasite in the 1930's may have been a limiting factor for ruffed grouse. The present incidental status of this nematode then is likely due to the decrease in both grassy openings and sharptails.

The low *Ascaridia* incidence of 16 per cent in New York ruffed grouse (Table 24) is perhaps the result of an annual shift of these birds to coniferous areas in fall and winter (Bump *et al.* 1947:819), and the absence of birds in conifers in summer. This summer to winter range shift would effectively reduce contamination of juveniles with fall and winter droppings. In northern Wisconsin, however, no seasonal alternation of forest types occurs (Dorney, 1959), hence greater contact with infective larvae would exist in Wisconsin, explaining our high incidence (48 per cent).

Dispharynx in both ruffed grouse (Bump *et al.* 1947:411) and blue grouse (Bendell, 1955) is considered to be a very pathogenic parasite. It is almost absent in ruffed grouse from the Lake States and Canada (Table 24). Bendell (1955) has shown heavy chick mortality associated with this pathogen in conjunction with another acanthocephalan parasite in blue grouse. Grouse broods in New York are known to suffer a similar severe summer mortality of about 60–65 per cent (Bump *et al.* 1947:527) of unknown cause, as contrasted to about 20 per cent in Wisconsin (Table 17). If helminth parasitism is responsible for these severe summer losses in New York, then *Dispharynx* is the most probable agent, since this parasite is rare in the Lake States (Table 24). Perhaps the pathogenic role of this parasite in juvenile ruffed grouse should be re-examined in the eastern states.

The high survival of grouse chicks in Wisconsin (Table 17) plays down the role of blood protozoans, e.g. *Leucocytozoon,* as pathogenic agents for juveniles as suggested by Clarke (1936). Erickson (1953) in Minnesota also has concluded that blood protozoa are probably not important pathogens. However, the role of these protozoans in the mortality of adult females during the breeding season is deserving of further research.

Hunting

Harvest Pressure

The hunter harvest calculated from band returns is shown in Table 25 for birds shot in the same year as banded. The Cedar Rapids sample is segregated into juveniles and adults because of the differential age vulnerability previously shown for these birds in the Cedar Rapids area (see Table 11). For both Otter Creek and Cedar Rapids, harvest was heavy in 1953, dropped off in 1954 and 1955, and increased in 1956 and 1957. When the harvest percentages for both Cedar Rapids and Otter Creek were plotted (Fig. 13) against estimated fall populations (Tables 1 and 3), the correlation coefficient was 0.47 (tab. 0.05 = 0.63, 8 d.f.) and was short of significance.

An annual hunting-pressure index for all of the north was calculated by the following procedure. The February–March flush index was assumed to represent breeding-population levels. Dorney *et al.* (1958) have presented evidence showing a strong correlation between these flush counts and spring drumming-cock counts. Then the over-all fall ratio of juveniles per adult (Table 7) was multiplied by the flush index and added to this flush index to give a theoretical fall-population level. Using total kill data for the north, it was then possible to calculate a ratio between this computed fall population and the total kill (Table 26) to arrive at a comparative harvest index for the various years.

As shown in Table 26, this harvest index increased steadily from 1950 to 1953, dropped sharply in 1954 and 1955, recovered in 1956, and dropped again in 1957. This index closely parallels the actual harvest from band recoveries in Cedar Rapids and Otter Creek (Table 25) with correlation coefficients of 0.78 and 0.88 respectively (tab. 0.05 = 0.88, 3 d.f.). The steady increase in harvest pressure from 1950 to 1953 (Table 26) in spite of a declining fall population is perhaps most easily explained by increased hunting effort, since the opening dates, length of hunting season, and bag limits were roughly similar throughout the period 1950–57. There was, however, a steady decline in voluntary reports by hunters of game killed during this period, introducing a potential upward bias of unknown magnitude in the kill since the hunters not reporting may have experienced lower success.

TABLE 25

Hunter Harvest Shown by Band Recoveries

	Otter Creek			Cedar Rapids					
	Adults and Juveniles			Adults			Juveniles		
Year	No. Banded	Per Cent Shot	95 Per Cent Limits	No. Banded	Per Cent Shot	95 Per Cent Limits	No. Banded	Per Cent Shot	95 Per Cent Limits
1953	76	25	15–35	2	100	----	85	34	24–44
1954	61	7	1–13	2	0	----	9	11	0–32
1955	128	8	3–13	43	2	0–6	58	16	7–25
1956	137	17	11–23	65	8	1–15	100	25	16–34
1957	91	10	4–16	75	9	2–16	92	16	8–24
Totals	493			187			344		
Means		13			8			22	

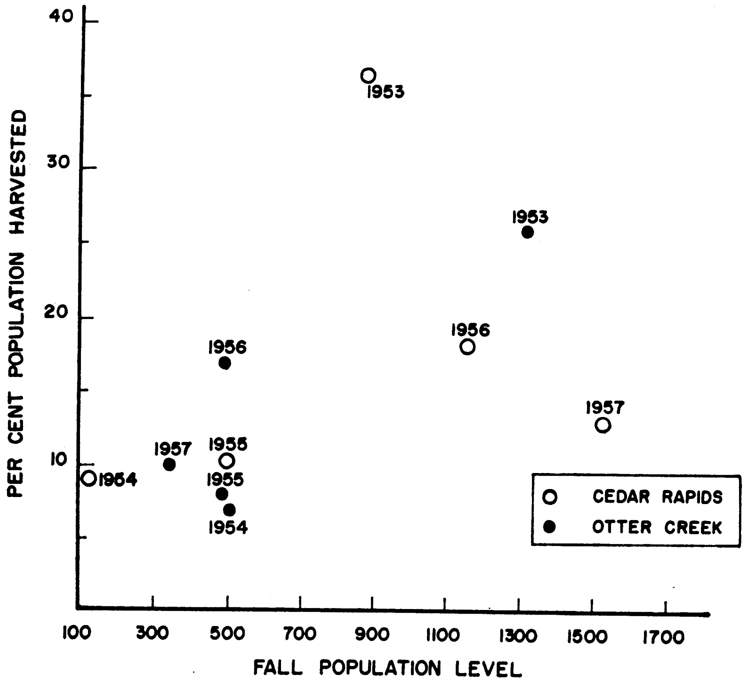

Figure 13. Relationship between harvest based on band returns, and fall population level from Lincoln Index calculations for Otter Creek (Fig. 7) and Cedar Rapids (Fig. 6) study areas.

Effect of Hunting on Populations

The steady increase in harvest pressure indicated from 1950 to 1953 (Table 26) and the decrease in population level (Fig. 11) certainly raise the question as to a possible relationship. Opening dates of the hunting season, length of the season, and bag limits were quite constant from 1950 to 1957 and can be ignored. Palmer (1956), by the use of unhunted control areas, has presented evidence in Michigan that hunting losses there do not affect ruffed grouse population fluctuations on small units of range (4,000–5,000 acres). Edminster (1937) also showed that winter populations on a refuge and a hunted area (each about 2,000 acres) were approximately the same over a 3-year period. Ammann (1949) was able to show no adverse effect of continued state-wide open-hunting seasons during low years.

If hunting depresses or increases spring populations, there should be a relationship between harvest and spring-population levels on large blocks of range. This was tested by correlating the harvest index

TABLE 26

Hunting–Pressure Ratio Derived from Theoretical Fall-population Levels (Calculated from February–March Flush Counts and Fall Age Ratios) and Hunting Kill, Northern Wisconsin

Year	(A) Total Kill*	(B) Theoretical Fall Level**	A/B
1950	652	470	1.4
1951	584	301	1.9
1952	556	245	2.3
1953	578	211	2.7
1954	227	116	2.0
1955	270	143	1.9
1956	493	181	2.7
1957	418	229	1.8

*In hundred-thousands, from Wis. Cons. Dept. files.
**From Fig. 13.

(Table 26) and percentage change in February–March flush counts between years. The two sets of data showed no relationship ($r = 0.17$, 6 d.f.). When the percentage change in fall-population level between years was correlated with the hunting index (Table 26), again no relationship was found ($r = 0.10$, 5 d.f.). From these analyses, it appeared that, for the 8 years studied, there was no detectable relationship between hunting and subsequent populations. This conclusion for Wisconsin conditions, however, should be substantiated by replicating Palmer's use of unhunted control areas over a 6–10 year period. In view of the juvenile mobility noted in this study (Table 13), such control areas should be at least 30 square miles in size.

In quantitative terms, what exploitation rate can ruffed grouse sustain? Harvest and population data from our study units are of limited use since no unhunted control areas were censused. Palmer in Michigan (1956), working on the Rifle River area and using an unhunted control area, suggested 40 per cent as a justifiable harvest level. The Rifle River area is similar to the Cedar Rapids area in that both are surrounded by essentially unhunted lands, providing a likely buffering effect on harvest. It is our opinion that on areas in Wisconsin without this buffering effect, harvests of 30–35 per cent (exclusive of crippling losses) should not be exceeded. Edminster in New York (1947:262) concluded that a 25 per cent kill is safe in all but years of scarcity. New York populations, as previously mentioned, have a lower production of young birds and therefore cannot be harvested at levels comparable to those of the Lake States.

As the present study has demonstrated the existence of density-dependent phenomena in production and survival of Wisconsin ruffed grouse, it now seems highly desirable to test the effects of very heavy hunting pressure on this species during peak population years. During such years, the incidence of parasitic disease is higher, overwinter losses and brood mortality are increased, and nonterritorial males are probably present in considerable numbers. It seems to us highly important that we now test on experimental areas the possibility that the importance of these factors in high populations can be lessened by deliberate reduction of overwintering and breeding densities through controlled harvests taking 55–65 per cent of the birds, exclusive of crippling losses.

Such an experimental overharvest of high populations in the north could test the effects of a hunting season starting in mid-September, and with removal of the bag limit. Newspaper publicity would by necessity be an integral part of the experiment.

The repeated low fall harvest of adult males in Cedar Rapids (Table 11) suggests that this segment of the population can sustain more hunting. An experimental spring hunting season in northern Wisconsin could provide such a harvest, similar to the spring hunting of tetraonid cocks in Europe. A spring hunt should be restricted to the last three weeks in May. It would be biologically feasible for the following reasons:

1. A current low fall harvest of adult males in the north is evident.

2. A reservoir of nonterritorial cocks is able to replace lost males.

3. Areas having low population densities would be made huntable in spring since the cock drumming behavior pin-points the quarry.

4. Few hens are seen once incubation has started, almost eliminating the likelihood of their being shot, especially with hunting activity centering around drumming logs.

5. There is an apparently low inclination of ruffed grouse to renest; hence there is a decreased importance of the cock in the last three weeks of May (see Bump *et al.* 1947:526).

Such a season could provide a million recreational hours annually to hunters in northern Wisconsin. The sporting qualities of such a hunt are high, judging by its widespread acceptance in Europe. Bow hunting for drumming cocks might be more acceptable to the general public and reduce accidental hen losses. A pilot experiment on an area at least 30 square miles in size should certainly be the initial step.

GENERAL POPULATION CONSIDERATIONS

In a discussion of population changes, it should be pointed out that the data from this study do not indicate that a dramatic population "crash" occurred after the 1949–50 high population, although Rowan (1948) in Canada and King (1943) in Minnesota used this word to describe fluctuations with which they were familiar. Rowan's observations apparently were based on subjective evaluations of density. An example of how misleading subjective observations can be is clearly demonstrated by comparing numbers of birds seen along roads in the fall in northern Wisconsin with other population indices.

In September 1953 in Cedar Rapids, 2,000 birds were observed by Dorney and Holzer in 25 days on about 10–15 miles of fire-lane. In 1954, we saw about 10 birds in the same area in 25 days, a spectacular decrease, superficially indicating a "crash" of 99.5 per cent. Very few birds were trapped and shot that fall (Table 25), and this same change in numbers seen along roads occurred all over northern Wisconsin. Actually, a substantial stock of birds remained as shown by objective methods of censusing which included late-winter flush counts, spring drumming counts in 1955, and counts of territorial males on the Highway 27 area (Fig. 4). In addition the exceptionally high annual survival (about 75 per cent) of banded cocks on Highway 27 from the spring of 1954 to the spring of 1955 (Table 6) indicated that this low population had considerable resilience. All evidence for the 1954 fall decrease pointed to the compound effect of a reduced 1954 breeding population and poor reproduction because of cold spring temperatures (see Table 7, Fig. 11) rather than a population mysteriously "crashing" and disappearing from the woods. By sustaining very low adult mortality from 1954 to 1955 in addition to excellent reproduction in 1955 (a favorable spring), the population made a noticable, recovery by the fall of 1955 (Fig. 11). Subjective observations, therefore, indicated a crash in 1954, while quantitative observation showed a reduced breeding population well buffered from environmental vicissitudes.

Synchrony of the grouse cycle has been fairly well observed in most of northern Wisconsin. However, southwestern Wisconsin and the Otter Creek area experienced the same 1954 decline without a subsequent recovery in 1955–57 (Fig. 7). The recovery was very pronounced only 80 miles away in Cedar Rapids (Fig. 6). These local differences are very common in Wisconsin and may obscure regional fluctuations considerably. The very cold spring in 1954 probably helped to bring some uniformity to these variations.

In considering the causes of the population changes that took place from 1950 to 1958, it is possible to segregate two component factors —reproduction and overwinter mortality. This separation has already been made in Table 7 and Figure 11. When the population was decreasing from the peak (1950–54), fall age ratios of about 3.5 young per adult were noted as compared to about 4.5 in the years of increasing populations (1955–57, see Table 7). These differences in fall age ratios were apparently brought about by above-average summer brood mortality in high population years (Table 17). Bump *et al.* (1947:531) also noted increased juvenile mortality in summer associated with high breeding levels. Bobwhite quail (*Colinus virginianus*) (Errington, 1945) have also been observed to show an inverse relationship between breeding levels and rate of summer gain. Based on the observed brood sizes in June (Table 17), clutch size appears to be constant regardless of density. Unfortunately, the amount of renesting and the proportion of broodless hens throughout the eight years remain as unknown variables in this picture.

Overwinter losses were also more severe when the population was decreasing (1950–54) than during the period of increase (1955–57), see Figure 11. Bump *et al.* (1947:534) have shown a similar density relationship between fall populations and overwinter losses.

Mortality rates for territorial cocks calculated in Table 6 increased steadily from 1954 to 1957 for Highway 27 and Cedar Rapids. This increase is not matched by winter mortality statistics presented in Figure 11 from spring flush counts and fall age ratios. This difference may have resulted from above-average juvenile mortality during the winter of 1954–55, while in subsequent years more equal losses to both age groups occurred. Perhaps the ability of the chicks to survive in 1954 was reduced by the unusually cold May weather. There are no other sampling biases or errors that would appear to cause this lack of similarity shown in Table 6 and Figure 11.

Siivonen (1957) has hypothesized that food conditions in winter and spring are the major factors predetermining the reproductive success of tetraonids in Finland. Cold spring temperatures presumably slow down the growth of high-quality green herbs necessary for bringing the hen into a satisfactory condition for egg laying. He stated that these "results reached would seem to explain the fluctuations in numbers of the tetraonids in Finland, at least for the period extending about 70 years back" (p. 40). He further indicated that fluctuations are more severe in the north due to a shorter, more critical time span for the hen to rejuvenate herself before the laying period.

Although our data on May temperatures and reproductive success would agree in part with Siivonen's work, certain portions of our work do not fit this hypothesis for the following reasons:

1. Average temperatures considered as a single factor for the pre-laying, laying, or incubation time periods would not produce the over-all population changes noted in the 8 years of this study.

2. The effects of density on young survival would not have been observed if a density-independent variable like spring temperatures were the sole factor affecting reproduction.

3. Increased overwinter mortality shown for these high populations (1950–54) would not appear to be explainable on the basis of critical breeding temperatures of the previous year since both warm and cold springs occurred during the period 1950 to 1954.

4. Grouse population fluctuations in northern Wisconsin, based on general evidence, tend to be more marked than in southern Wisconsin, and presumably also New York, which lies at a more southerly latitude than northern Wisconsin. Graham and Hunt (1958) have recently published census results for southern Michigan ruffed grouse showing reduced population fluctuations in the south as compared to the north. However, this decreased southern fluctuation according to evidence currently available is apparently the result of high juvenile losses during the summer in the south which thereby prevents the possibility of a large increment to the population. These more severe chick losses in New York as contrasted to northern Wisconsin already have been discussed. Age ratios in Wisconsin also decrease in a southerly direction (Dorney, 1955). Work in Kentucky by Hardy (1950) showed small summer broods in contrast to those in northern Wisconsin. All evidence on ruffed grouse, therefore, points to increasing summer chick loss, not spring weather, as the prime factor causing decreased amplitude of population fluctuations in southern latitudes.

For these four reasons, attributing the primary cause of ruffed grouse fluctuations to spring weather will not satisfy all the observed phenomena in Wisconsin. There is no doubt of its importance; however our data clearly show density-dependent factors involved in reproductive success and probably overwinter survival in addition to weather.

Lack (1954) has suggested predator-prey relationships as the primary causal agent in ruffed grouse "cycles." In our opinion, consideration should be given to the possibility that field evidence was too limited to make such conclusions. In our Cedar Rapids study area, predation was always noticeable, especially by horned and barred owls (*Bubo virginianus, Strix varia*). Also, in Otter Creek during the winter of 1953–54, we lost more birds in live-traps to owls than in the previous year or the three subsequent years. This increased predator activity coincided with a decrease in mice. However, without quantitative studies, premature cause and effect conclusions are hazardous. A good example of this is presented by Bump *et al.* (1947:349). They showed no basic change in fall grouse populations on two areas of about 1,300 acres each, when predators were controlled on one area and not on the other. Nest losses were reduced on areas with predator control, but by the end of the summer similar populations were present on the two areas. Multiple factors were apparently controlling the New York populations and providing a compensatory balance.

Lack (1954) further states that no epidemic is known to affect both ruffed grouse and snowshoe hares. Erickson (1944) has clearly shown heavy parasitic infestation related to density in hares, as has this study for ruffed grouse. It is true that no epidemics or die-offs have been observed in this study. Rather, gradual increases in juvenile, adult female, and overwinter mortality—all density related—have accounted for the population changes observed, coupled with the influence of weather. Parasitism, by providing an additional physiological drain on high populations, could well be "the straw that broke the camel's back." Bacterial and viral agents that have not been quantitatively studied as yet could be involved in the same manner. Since helminth parasitism has been shown to be related to density, it cannot be disregarded simply because it does not cause epizootics. Whether it plays a minor or major role in grouse mortality and reproduction will have to await further experimentation with disease-"free" populations.

Christian (1950) has hypothesized and Frank (1957) concluded that stresses of overcrowding may be the basic cause triggering mammalian population declines. Frank (1953) indicated that no diseases have been implicated in these fluctuations. Jellison *et al.* (1958) have shown that an epizootic of tularemia was involved in a die-off of *Microtus montanus* in western United States following irruptive population densities. Since the disease process depends on the interaction of the etiological agent and the host, resistance to disease may be reduced when the ability of the host is impaired by population stresses resulting from overcrowding. Studies on bacterial invasiveness indicate that injections of adrenocortical hormones may hinder the normal host defense (Thomas, 1953). Christian and Davis (1956) have shown adrenal weight to be directly related to population density in wild Norway rats (*Rattus norvegicus*). Disease and crowding stresses may therefore be interrelated through the action of the adrenal gland. The role of crowding stresses on ruffed grouse has not as yet been studied. The application of the hypothesis of Christian and Frank to ruffed grouse therefore must await future evaluation.

In summation, our observations appear to indicate that an interplay of spring weather and parasitic disease are related to population fluctuations while hunting appears to have no effect on subsequent numbers. The effects of bacterial and viral agents, predation, and intraspecific competition were not studied. The high natural survival of juveniles in northern Wisconsin appears to be the prime factor responsible for increased amplitude in fluctuations in contrast to those of more southerly areas. High population densities appear to be characterized by above-average winter mortality, high parasitic incidence, and decreased reproductive success. To maintain a grouse population at peak levels would require optimum environmental conditions. Since probability dictates the eventual occurrence of unfavorable weather patterns, a decline in numbers is a biological certainty.

SUMMARY

Population density of ruffed grouse was studied in northern Wisconsin from 1949 to 1958. The high period was generally 1949 to 1952, a low was reached in 1954 and an increase observed again in 1957. Average sex and age ratios taken in 10 hunting seasons showed a 50:50 juvenile sex ratio, a 54:46 adult male to adult female sex ratio and a population consisting of 80 per cent juveniles. Fall age ratios from road-shot birds were strongly biased in favor of juveniles. Spring age ratios from mirror-trapped cocks appear to be biased in favor of 2-year-old cocks since about one-third of the 1-year-olds failed to set up territories.

High temperatures in May resulted in above-average production and an almost even fall adult sex ratio; a cold May resulted in low production and a loss in adult females. High populations were less responsive to favorable May temperatures than low populations.

Parasitic disease was density-related since the abundance of grouse in late-winter was found to be directly related to the extent of infection with *Ascaridia bonasae* in young birds the following summer. Parasitic nematodes and cestodes were commonly encountered, the incidence dependent upon the age of the bird and the time of the year.

Fluctuations in numbers did not appear to have been caused by hunting losses. The decline noted was caused by increased winter and summer-brood mortality. Once the population reached a low ebb, high reproductive gain and decreased overwinter losses tended to bring about a recovery. Parasitic disease and May temperatures appear to play a role in these population responses noted.

Hunting, by artificially reducing density, should serve a useful purpose by removing or decreasing some of these density-dependent factors affecting production and survival. A spring hunting season on drumming cocks in northern Wisconsin may be possible because the harvest of this segment of the population during the fall season is disproportionately low.

LITERATURE CITED

AMMANN, G. A. 1948. Aging and sexing ruffed grouse by wing and tail feathers. Mich. Cons. Dept., Lansing. 10pp. mimeo.

————. 1949. Grouse prospects. Mich. Cons., 18(5):14–19.

BENDELL, J. F. 1955. Disease as a control of a population of blue grouse, *Dendragapus obscurus fuliginosus* (Ridgway). Canad. J. Zool., 33:195–223.

BOUGHTON, REX V. 1937. Endoparasitic infestations in grouse, their pathogenicity and correlation with meteoro-topographical conditions. Univ. Minn. Agr. Exp. Sta. Tech. Bull., 121:1–50.

BUMP, GARDINER, ROBERT W. DARROW, FRANK C. EDMINSTER and WALTER F. CRISSEY. 1947. The ruffed grouse—life history, propagation, management. New York State Cons. Dept., Albany. xxxvi+915pp.

CHAMBERS, ROBERT E. and WARD M. SHARP. 1958. Movement and dispersal within a population of ruffed grouse. J. Wildl. Mgmt., 22(3):231–239.

CHRISTIAN, JOHN J. 1950. The adreno-pituitary system and population cycles in mammals. J. Mammal., 31(3):247–259.

———— and DAVID E. DAVIS. 1956. The relationship between adrenal weight and population status of urban Norway rats. J. Mammal., 37(4):475–486.

CLARKE, C. H. DOUGLAS. 1936. Fluctuations in numbers of ruffed grouse, *Bonasa umbellus* (Linne), with special reference to Ontario. Univ. Toronto Biol. Series No. 41. 118pp.

COLLIAS, NICHOLAS E. and RICHARD D. TABER. 1951. A field study of some grouping and dominance relations in ring-necked pheasants. Condor, 53(6):265–275.

CRAM, E. B. 1931. A comparison of internal parasites of ruffed grouse of Labrador with those of ruffed grouse in the United States. J. Parasit., 18(1):48.

DAHLBERG, BURTON L. and RALPH C. GUETTINGER. 1956. The white-tailed deer in Wisconsin. Wis. Cons. Dept., Tech. Wildl. Bull. No. 14, 282pp.

DORNEY, ROBERT S. 1955. P–R Job Completion Rpt., Wis. Wildl. Res., 14(1):141–145.

————. 1959. Relationship of ruffed grouse to forest cover types in Wisconsin. Wis. Cons. Dept., Tech. Bull. No. 18. 32pp.

DORNEY, ROBERT S. and HELMER M. MATTISON. 1956. Trapping techniques for ruffed grouse. J. Wildl. Mgmt., 20.(1):47–50.

DORNEY, ROBERT S. and FREDERICK V. HOLZER. 1957. Spring aging methods for ruffed grouse cocks. J. Wildl. Mgmt., 21(3):268–274.

DORNEY, ROBERT S., DONALD R. THOMPSON, JAMES B. HALE and ROBERT F. WENDT. 1958. An evaluation of ruffed grouse drumming counts. J. Wildl. Mgmt., 22(1):35–40.

EBERHARDT, LEE and RALPH I. BLOUCH. 1955. Analysis of pheasant age ratios. Trans. N. Amer. Wildl. Conf., 20:357–367.

EDMINSTER, F. C. 1937. An analysis of the value of refuges for cyclic game species. J. Wildl. Mgmt., 1(1–2):37–41.

————. 1947. The ruffed grouse, its life story, ecology and management. The Macmillan Co., New York. 385pp.

EMLEN, JOHN T., JR. 1940. Sex and age ratios in survival of the California quail. J. Wildl. Mgmt., 4(1):92–99.

ERICKSON, ARNOLD B. 1944. Helminth infections in relation to population fluctuations in snowshoe hares. J. Wildl. Mgmt., 8(2):134–153.

————. 1953. *Leucocytozoon bonasae* in ruffed grouse; its possible relationship to fluctuations in numbers of grouse. J. Wildl. Mgmt., 17(4):536–538.

————, P. R. HIGHBY and C. EDWARD CARLSON. 1949. Ruffed grouse populations in Minnesota in relation to blood and intestinal parasitism. J. Wildl. Mgmt., 13(2):188–194.

ERRINGTON, PAUL L. 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. Ecol. Monogr., 15:1–34.

FALLIS, A. MURRAY. 1945. Population trends and blood parasites of ruffed grouse in Ontario. J. Wildl. Mgmt., 9(3):203–206.

FARMES, ROBERT E. 1955. A new tip-top trap for taking prairie grouse. Flicker, 27(3):123–125.

FISHER, LEE WILLIAM. 1939. Studies of the eastern ruffed grouse in Michigan (*Bonasa umbellus umbellus*). Mich. State Coll. Agr. Exp. Sta. Tech. Bull. 166. 46pp.

FRANK, FRITZ. 1953. Untersuchungen über den Zusammenbruch von Feldmausplagen (*Microtus arvalis* Pallas). Zool. Zahrb. (Systematik), 82:95–136.

————. 1957. The causality of microtine cycles in Germany. J. Wildl. Mgmt., 21(2):113–121.

GOBLE, FRANS C. and H. L. KUTZ. 1945. Notes on the gapeworms (Nematoda: Syngamidae) of galliform and passeriform birds in New York State. J. Parasit., 31(6):394–400.

GRAHAM, SAMUEL A. and GEORGE S. HUNT. 1958. A noncyclic ruffed grouse population near Ann Arbor, Michigan. J. Wildl. Mgmt., 22(4):427–432.

GRANGE, WALLACE B. 1948. Wisconsin grouse problems. Wis. Cons. Dept., Madison. 318pp.

GREEN, R. G., C. A. EVANS and C. L. LARSON. 1943. A ten-year population study of the rabbit tick *Haemaphysalis leporis-palustris.* Amer. J. Hyg., 38(3):260–281.

GROSS, ALFRED O. 1930. Progress report of the Wisconsin prairie chicken investigation. Wis. Cons. Dept., Madison. 112pp.

HALE, JAMES B. and ROBERT F. WENDT. 1951. Ruffed grouse hatching dates in Wisconsin. J. Wildl. Mgmt., 15(2):195–199.

HALE, JAMES B., ROBERT F. WENDT and GEORGE C. HALAZON. 1954. Sex and age criteria for Wisconsin ruffed grouse. Wis. Cons. Dept., Tech. Wildl. Bull. No. 9. 24pp.

HARDY, FREDERICK C. 1950. Ruffed grouse studies in eastern Kentucky. Ky. Div. Fish and Game, Frankfort. 26pp.

JELLISON, WILLIAM L., J. FREDERICK BELL, J. D. VERTREES, M. A. HOLMES, CARL L. LARSON and CORA R. OWEN. 1958. Preliminary observations on diseases in the 1957–58 outbreak of *Microtus* in western United States. Trans. N. Amer. Wildl. Conf., 23:137–145.

KIMBALL, JAMES W. 1948. Pheasant population characteristics and trends in the Dakotas. Trans. N. Amer. Wildl. Conf., 13:291–314.

KING, RALPH T. 1943. Ruffed grouse management. Roosevelt Wildl. Bull. 8(3):60–80.

LACK, DAVID. 1954. Cyclic mortality. J. Wildl. Mgmt., 18(1):25–37.

LARSEN, JAMES A. and JAMES F. LAHEY. 1958. Influence of weather upon a ruffed grouse population. J. Wildl. Mgmt., 22(1):63–70.

LEOPOLD, ALDO. 1929. Report on a game survey of Wisconsin. Sporting Arms and Ammunition Manufacturer's Institute, 167pp. + appendix.

LEVINE, P. P. 1937. The viability of the ova of *Ascaridia lineata* when exposed to various environmental conditions. J. Parasit., 23(4):368–375.

LINCOLN, FREDERICK C. 1930. Calculating waterfowl abundance on the basis of banding returns. U.S.D.A. Circ. No. 118. 4pp.

LISCINSKY, STEPHEN A. and WILLIAM J. BAILEY, JR. 1955. A modified shorebird trap for capturing woodcock and grouse. J. Wildl. Mgmt., 19(3): 405–408.

MORGAN, B. B. and F. N. HAMERSTROM, JR. 1941. Notes on the endoparasites of Wisconsin pinnated and sharp-tailed grouse. J. Wildl. Mgmt., 5(2):194–198.

MORGAN, BANNER BILL and PHILIP A. HAWKINS. 1949. Veterinary helminthology. Burgess Publ. Co., Minneapolis, Minn. 400pp.

PALMER, WALTER L. 1956. Ruffed grouse population studies on hunted and unhunted areas. Trans. N. Amer. Wildl. Conf., 21:338–345.

RIPPLE, RICHARD C. 1941. Studies on the gapeworm *Syngamus trachea* (Montagu, 1811) in robins and chickens. J. Parasit., 27(5):369–374.

ROWAN, WILLIAM. 1948. The ten-year cycle—outstanding problem of Canadian conservation. Dept. Ext., Univ. Alberta, Edmonton. 15pp.

SCHORGER, A. W. 1945. The ruffed grouse in early Wisconsin. Trans. Wis. Acad. Sci. Arts. and Lett., 37:35–90.

SIIVONEN, LAURI. 1957. The problem of the short-term fluctuations in numbers of tetraonids in Europe. Finnish Game Foundation, Papers on Game Res. No. 19. 44pp.

TABER, RICHARD D. 1949. Observations on the breeding behaviour of the ring-necked pheasant. Condor, 51(4):153–175.

THOMAS, LEWIS. 1953. Cortisone and infection. Pp. 799–814 *in* Mechanism of corticosteroid action in disease processes, edited by Roy Waldo Miner, Annals, N.Y. Acad. Sci. 56(4):623–814.

TECHNICAL BULLETINS

Published by

The Wisconsin Conservation Department

*No. 1 A Device for Dating Natural Events in Game Animals.
Cyril Kabat, Donald R. Thompson and Frank M. Kozlik (1950)

*No. 2 Pheasant Weights and Wing Molt in Relation to Reproduction with Survival Implications.
Cyril Kabat, Donald R. Thompson and Frank M. Kozlik (1950)

*No. 3 Improved Rations and Feeding Procedures for Pheasants
Harry Stanz, Jr. (1952)

*No. 4 Food Habit Studies of Ruffed Grouse, Pheasant, Quail and Mink in Wisconsin.
Bruce P. Stollberg and Ruth L. Hine (1952)

*No. 5 Experimental Level Ditching for Muskrat Management.
Harold A. Mathiak (1953)

*No. 6 Wisconsin Fox Populations.
Stephen H. Richards and Ruth L. Hine (1953)

No. 7 Some Winter Habits of White-tailed Deer and the Development of Census Methods in the Flag Yard of Northern Wisconsin.
Cyril Kabat, Nicholas E. Collias and Ralph C. Guettinger (1953)

*No. 8 Muskrat Growth and Litter Production.
Robert S. Dorney and Alan J. Rusch (1953)

No. 9 Sex and Age Criteria for Wisconsin Ruffed Grouse.
James B. Hale, Robert F. Wendt and George C. Halazon (1954)

No. 10 Role of Refuges in Muskrat Management.
Harold A. Mathiak and Arlyn F. Linde (1954)

No. 11 Evaluation of Stocking of Breeder Hen and Immature Cock Pheasants on Wisconsin Public Hunting Grounds.
Cyril Kabat, Frank Kozlik, Donald R. Thompson and Frederick H. Wagner (1955)

No. 12 Studies on Level Ditching for Marsh Management.
Harold A. Mathiak and Arlyn F. Linde (1956)

No. 13 Seasonal Variation in Stress Resistance and Survival in the Hen Pheasant.
Cyril Kabat, R. K. Meyer, Kenneth G. Flakas and Ruth L. Hine (1956)

*No. 14 **The White-tailed Deer in Wisconsin.**
Burton L. Dahlberg and Ralph C. Guettinger (1956)

No. 15 **A Guide to Prairie Chicken Management.**
F. N. Hamerstrom, Jr., Oswald E. Mattson and Frances Hamerstrom (1957)

No. 16 **An Evaluation of Artificial Mallard Propagation in Wisconsin.**
Richard A. Hunt, Laurence R. Jahn, Ralph C. Hopkins and George H. Amelong (1958)

No. 17 **Pond Culture of Muskellunge in Wisconsin.**
Leon D. Johnson (1958)

No. 18 **Relationship of Ruffed Grouse to Forest Cover Types in Wisconsin.**
Robert S. Dorney (1959)

No. 19 **The Hemlock Borer.**
Ali Hussain and R. D. Shenefelt (1959)

The European Pine Shoot Moth and its Relation to Pines in Wisconsin.
Daniel M. Benjamin, Philip W. Smith and Ronald L. Bachman (1959)

---

*Out of print.