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SOME ASPECTS OF THE DYNAMICS OF A HUNTED BOBWHITE POPULATION

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Abstract:

Dynamics of a hunted bobwhite population have been investigated on a 1,450-acre study area near Carbondale, Illinois since 1952. Habitat conditions have not changed greatly during the study, and November densities have oscillated regularly about a rather stable long-term mean. Most of the variance of annual rates of population change is due to variation in net productivity from spring to fall rather than to variation in net losses from fall to spring. Population declines from November to April averaged 66% (range 36 to 81%); about 0.66 of this resulted from hunting. Post-hunting mortality, which was slightly density-related, partially compensated for hunting losses. Spring densities were correlated with ($r = +0.75$) and almost as variable as preceding fall populations. Net increases from spring to fall varied from 17 to 383 and averaged 235% of the breeding population. Multiple regression analysis showed that annual rates of productivity were significantly influenced by the combined effect of breeding density, length of snow cover during the previous 2 winters, and amounts of prenesting rainfall. Annual rates of population change were inversely related to the preceding fall density, but strong correlations between successive seasonal population levels caused periods of change as well as highs and lows to persist for several years. Major highs and lows each occurred at 8- to 10-year intervals. It was not clear whether 2 severe winters caused the apparent cyclic regularity or merely accentuated the lows.

Introduction and Methods

In 1952, the Cooperative Wildlife Research Laboratory (CWRL) of Southern Illinois University and the Illinois Natural History Survey initiated a long-term investigation of the dynamics of a hunted bobwhite population on 1,450 acres of privately owned, unmanaged farmland (Carbondale Research Area) in southern Illinois. From 1953 to the present, seasonal population levels have been censused by crews of 6-12 men using trained bird dogs. Counts are made in early November (prehunting), early January (posthunting), mid February and late March prior to covey breakup. During the hunting season, each hunter is interviewed and his quail checked to determine size and composition of the harvest and total hunting pressure. Land-use and cover conditions have been recorded continuously since the project began. From 1953 through 1963 field crews attempted to locate and study all nests on the area.

Maximum census error is estimated at $\pm 10\%$ and average deviations $\leq 5\%$. Hunting pressure and harvest estimates (which include known cripples) are minimal but thought to be at least 95% accurate. Annual trends in quail abundance in southern Illinois, as determined from

wing collections and hunter questionnaires (unpublished data, CWRL), have been similar to those on the Carbondale Research Area (CRA) with 1 exception. The 1960 decline was apparently much less severe on our study area than throughout the entire region of southern Illinois.

The research area is located about 5 miles northeast of Carbondale at 37° 46' N latitude. Topography is gently rolling, and unimproved soils are of low to very low permeability and productivity. The climate is characterized by relatively hot, humid summers and mild to occasionally cold winters. Annual precipitation averages 44.8 inches with 54% occurring from April through September (3). Maximum daily temperatures average 89.8 F during the period June through August. January is the coldest month with daily lows averaging 25.4 F. Temperatures of 0 F or less occur, on the average, only 1 day a year. During the study, the number of days with ground snow cover $\geq$ 1 inch averaged 12.6 and ranged from 3 to 36.

Land use has averaged about 30% intertilled crops, 30% forage, 8% small grains, 21% idle and fallow, 10% woods, and 1% miscellaneous. Seventeen lots averaging 8.6 acres in size (range 2 to 32 acres) constitute most of the wooded acreage. These lots have remained essentially stable, but fencerow and roadside cover had declined. Idle, fallow, and forage acreages have increased slightly, primarily at the expense of small grains and to a lesser extent of intertilled crops. From 1953 through 1958, corn was the principal crop, with only 27% of the intertilled acreage planted to soybeans. During the next 9 yr, soybean acreage increased to 57% and since 1968 has constituted over 70% of the intertilled acreage. Subjectively, it appears that secondary plant succession has caused some deterioration of nesting habitat in several fields formerly utilized heavily for nesting. Conversely, some prime habitat has been developed by land use and secondary succession in other parts of the area.

Of the many past and present graduate and undergraduate workers of the Laboratory and the long hours they spent in the field collecting data, we are deeply appreciative. We also thank Tony J. Peterle, Ohio State University, William R. Edwards, Illinois Natural History Survey, and Samuel R. Jewell, Southern Illinois University, for their helpful criticisms of the manuscript.

Population Levels and Fluctuations

Although there has been considerable annual variation in November and March population levels on the CRA (Fig. 1), a degree of long-term stability is evident. Net population changes between November censuses (i.e. annual population changes) have exceeded 15% in 12 of the 18 years of study. Six of these changes have been increases averaging almost 41% and 6 have been declines averaging just over 30%. The net population change for the 18-yr period is +4.3%. The maximum November density was 1 bird per 2.2 acres and the minimum 1 bird per 8.2 acres.

Most populations are likely to fluctuate annually even under

conditions of relatively stable habitat (24), but the level about which these fluctuations occur is a function of habitat quality among other things. Wagner et al. (36) stressed the importance of maintaining the distinction between population balance and density determination when attempting to explain population behavior. We believe that overall habitat conditions on the Carbondale Research Area during these investigations have been sufficiently stable to permit a discussion of factors other than habitat that may be influencing annual fluctuations. We realize, however, that subtle, short-term changes in habitat quality may have caused some of the variance in seasonal population levels and thus in estimated rates of productivity and mortality.

Fig. 2 represents a simplified compartmental model of some of the more important components and interactions contributing to annual population change on the study area. Except for sampling error, these annual changes and their variance are accounted for by the 2 major components of the model, i.e. net losses from fall to spring and net gains from spring to fall. The relative importance or input of recognizable components of any system should be understood before attempting to interpret the subcomponents (22). Thus, we attempted to determine how much of the variation in annual population change was attributable to variation in net rates of gain from spring to fall as opposed to rates of loss from fall to spring. Initially, we cast rates of gain and loss as independent variables in a multiple regression model which predicted annual population change, then examined the several indicators of relative "importance" (4). However, Tukey (33) and Darlington (4) have warned that any attempt to quantify exactly the relative importance or contribution of each individual predictor variable in a set is probably not advisable when there is intercorrelation among these predictors. Consequently, we will merely state that differences in rates of productivity from spring to fall have contributed substantially more to the variance of annual population change than have rates of loss from fall to spring.

Net Losses from Fall to Spring

Population decline from November to April is the cumulative result of hunter harvest, natural mortality, and the effect of differential ingress-egress. No attempt will be made here to distinguish between losses due to mortality and egress. We have observed that while some covey movement across study area boundaries does occur during this time, the net result is not great. Thus, most nonhunting losses actually reflect mortality, most of which are believed due to predation.

November to April losses have averaged 66.2%. During the seasons of 1970-71 and 1971-72, low fall populations declined only 36 and 37%, respectively. Prior to these years, winter losses varied only from 60 to 81% (Table 1). Of the total number of birds lost each year from November to April, hunting takes an average of 67% while natural mortality during the hunting season and from January through March accounts for 11 and 22%, respectively.

The percentage of birds removed from the fall population by hunters has averaged 43.9% (range 22.3 to 67.1). Annual rates of harvest have not been strongly correlated with fall densities ($r = +0.33$). However, the harvest rate is correlated with the amount of hunting pressure ($r = +0.84$), which has varied from 162 to 457 and averaged 321 gun hours per season. No strong correlation exists between fall densities and hunting pressure even though late-season declines in effort were often noticeable during years of low populations. Kill per unit effort averaged 0.61 bird per gun hour (range 0.25 to 1.16) and, as would be expected, was strongly correlated with fall population size ($r = +0.90$).

Percent population decline from November to April is definitely related to hunter harvest rates ($r = +0.60$) but the correlation does not seem particularly strong because harvested birds usually constitute 0.66 of all losses during this period. Apparently, rates of harvest and total winter loss are not more closely correlated because posthunt mortality from January through March is somewhat dependent ($r = +0.32$) on January densities which in turn depend partially on harvest rates. The slight density-related nature of these posthunt losses may reflect Errington's contention (5,6,7) that predation varies directly with population density in relation to habitat quality. The fact that populations are lowered by hunting on our study area may reduce the effect of density on late-winter mortality.

While some compensation to hunting is effected by the slight density-related nature of posthunt losses, hunting does increase total winter loss to some degree. On a nearby nonhunted study area, we found winter losses to average about 54% which may not be an unrealistic approximation of what they would be on the CRA if it were not hunted. There is prima facie evidence that the CRA population is maintaining equilibrium in spite of annual harvests which average 44%. However, stabilization of an exploited population does not necessarily mean that it exists at natural equilibrium density (35). We will pursue this question in a later paper.

As shown in Fig. 3, annual breeding densities are quite dependent on ($r = +0.75$), and almost as variable as, preceding fall densities (coefficients of variation = 31.4 and 34.3%, respectively). The strong correlation between these 2 seasonal levels implies that fall to spring mortality rates are mostly independent of fall densities. Actually, a moderate correlation ($r = +0.54$) exists between November densities and percent declines from November to April. However, this correlation is due almost entirely to the seasons of 1970-71 and 1971-72, when both variates were quite low. Prior to 1970, the small variations in rates of winter loss appeared to be independent of fall densities, possibly because (A) harvest rates, which contribute substantially to total losses, are apparently not density-related and (B) the relatively heavy annual harvests may tend to keep posthunt populations below the area's late-winter carrying capacity. This latter possibility is further suggested by the apparent lack of a relationship between winter weather and rates of nonhunting losses.

Latham and Studholme (19) said that of all the environmental factors affecting the bobwhite, snow caused the greatest hardship. Studies of lightly or nonhunted populations in Wisconsin (12), Iowa (16), and Virginia (21) all demonstrated a positive correlation between length of snow cover and winter losses. The detrimental effect of snow on bobwhite survival has been noted also in Missouri (32). Using multiple linear regression (MLR), we tested the effects of length of snow cover and low temperatures on posthunting survival, but no relationship was evident at any level of population density. The fact that weather has not had a measurable influence on survival over the entire range of our data does not mean that losses, either directly or indirectly attributable to weather, have not occurred. Mortality amounting to 18% of the mid-February population accompanied a 23-day period of severe weather in late winter, 1960 (26). Field observations suggested that these losses, which mainly resulted from increased vulnerability to predation, would have been considerably higher if most coveys had not had access to standing corn and soybeans left unharvested the previous fall.

Net Productivity From Spring to Fall

Net population increases from March to November expressed as percentages of March populations are referred to in subsequent discussion as percent summer gains. These gains, which have ranged from 17 to 383 and averaged 235%, are strongly correlated with corresponding rates of annual population change ($r = +0.74$; Fig. 4). Variations in percent summer gains could be influenced by differences in reproductive rates or survival of chicks or both. Mortality of adult hens could also be involved although most of such losses are thought to occur after hatching (12,27) and thus would not influence reproduction. Lack (17,18) believed that density-related variation in rates of summer gain reflected differences in survival of young rather than reproductive rates; Hickey (9) agreed with this assumption. Conversely, we feel that variation in annual summer gains on the CRA is influenced more by differences in the number of chicks that hatch than by variation in rates of survival.

We have no direct data on chick mortality, estimated at 2 to 4% per week in other areas (12,14,28). However, from 1954 to 1963, there was a correlation of +0.85 between the ratio of the known number of chicks hatching to the estimated breeding population and the percent summer gain. This implies that 72% of the variation in gains was attributable to variation in the number of chicks hatching versus the estimated breeding population, thus leaving only 28% of the variance to be associated with other factors such as survival rates of chicks.

Our nesting studies indicated that total and relative productivity were not influenced by annual differences in mean clutch size or hatchability rates of eggs, but did correlate directly with the number of successful nests found in relation to the estimated breeding population. Further, differences in annual rates of successful nests per breeding bird were due not so much to differences in the proportion of total nests that hatched as in the total number of nests built.

In an attempt to interpret the influence of weather on productivity, we calculated average maximum, minimum, and mean daily temperatures and total rainfall for 10-day intervals throughout the year. These data were tested, by simple correlations against the corresponding percent of gains during summer to select biologically meaningful parameters of temperature and moisture conditions during the periods of winter, prenesting, egg laying, and hatching. The following predictor variables were thus selected and tested by step-wise multiple linear regression in an IBM 360 computer for their combined and individual contribution to the variance of yearly rates of summer gain from 1954 through 1971 (criterion variance):

- (1) breeding density
- (2) number of days of snow cover ≥ 1 inch during the previous winter
- (3) number of days of snow cover ≥ 1 inch during 2 winters previous
- (4) average minimum daily temperature during the previous 1 February to 21 March
- (5) average mean daily temperature from 22 March to 30 April
- (6) total rainfall from 22 March to 30 April
- (7) average maximum daily temperature from 1 May to 19 July
- (8) total rainfall from 1 May to 19 July
- (9) average maximum daily temperature from 1 July to 28 August
- (10) total rainfall from 1 July to 28 August

When considered in the presence of (with knowledge of) the other predictors, breeding density, snow cover during the previous 2 winters, and rainfall from 22 March to 30 April, were each found to account individually for a significant ($P < 0.001$) portion of the criterion variance. Collectively, these predictors accounted for almost 75% of the variance in annual rates of summer gain ($R^2 = 0.747$; $P < 0.01$). None of the remaining variables contributed significantly ($P > 0.05$) to the predictability of rates of summer gain. Although the mechanism by which the variables influence productivity is not revealed by the MLR analysis, the extent and form of this influence is indicated. First high breeding density and snow cover during the previous 2 winters tended to depress gains while prenesting rainfall increased productivity. Secondly, breeding density and snow cover during the previous winter had a greater effect on rates of gain than did prenesting rainfall or snow cover 2 winters previously. Thirdly, the negative regression of productivity on snow cover in the previous winter was significantly ($P < 0.001$) curvilinear with the detrimental effect becoming relatively greater as length of snow cover increased.

Several previous studies of bobwhites (5,6,12,16) have shown a

tendency for percents of summer gain to be correlated negatively with breeding density. This relationship is the well-known "inversivity principle" (6). Annual rates of summer gain on the CRA are plotted against corresponding breeding densities in Fig. 5. The negative correlation is not particularly strong ($r = -0.44$) which is not unexpected because productivity is also significantly affected by other factors (weather) besides density. Notwithstanding the negative influence of density on rates of gain, total production has varied directly with breeding densities resulting in an essentially linear relationship between spring and subsequent fall populations (Fig. 6).

The possibility that duration of snow cover may adversely influence productivity in the following summer is made tenable by numerous studies of penned ring-necked pheasants (Phasianus colchicus) demonstrating that malnutrition or other stress prior to the breeding season can impair reproductive performance. A common response to artificially induced stress is delayed egg laying (1,2,8). Stanford (32) reported a marked delay in nesting of wild bobwhites in Missouri following the severe winter of 1960. We did not observe this delay on the CRA although, as mentioned earlier, unusually favorable food supplies may have lessened the impact of the weather. But in southern Illinois as a whole, the 1960 hatch was quite late as judged by analysis of a large sample of wings. In fact, these data have shown a positive correlation between duration of snow cover and subsequent lateness of hatch from 1951 through 1970. Also, late hatches have usually been associated with poor reproductive years based on fall age ratios and hunter questionnaires (unpublished data, CWRL). Similar findings have been reported in Missouri (30).

A possible explanation for the decline in productivity with increased duration of snow cover may be that bobwhite hens stressed by snow or high density or both have reduced vigor which delays nesting and decreases the probability of renesting. This would also explain why a low number of nests per breeding bird and late hatches are commonly associated with poor reproductive seasons.

During years of high densities, some coveys winter in marginal ranges that are normally unoccupied during years of lower populations (31). This phenomenon, coupled with the possibility that good habitat quality may buffer the influence of winter stress on the birds, suggests that the adverse effect of winter weather on productivity may not be constant over all levels of population density. We investigated this hypothesis, which is contrary to the concept that the effects of weather are essentially density-independent (9,23), by adding interaction terms to the MLR model allowing the expression of different regressions of productivity on snow cover at different levels of population density. When tested by the F statistic, this interaction was not significant at the 0.05 level. However, the probability of the amount of additional criterion variance thus accounted for being due to chance was only about 10%. Further, a model plot of this interaction simulated from computer-determined regression coefficients fit the hypothesized concept. That is, the adverse effect of snow on productivity was greater at higher than at lower densities. Or stated

another way, the negative influence of breeding density on productivity was less after mild winters than after severe ones.

Latham and Studholme (19) wrote that in Pennsylvania: ". . . reproduction of bobwhite quail is adversely affected for at least 2 seasons following severe winters." We presently consider this hypothesis tenable but not proven on the CRA, based on the MLR analysis which showed a slight but significant ($P < 0.001$) portion of the variance in rates of summer gain to be accounted for by knowledge of length of snow cover 2 winters previous (when breeding density, snow cover the previous winter, and prenesting rainfall are also known). If the influence of snow does extend for 2 seasons, it suggests that the adverse effect of stress is somehow transmitted from parents to their offspring. Lower survival rates have been reported for Hungarian partridge (Perdix perdix) chicks whose parents had been stressed previously by crowding (11).

As noted earlier, total rainfall during the 6 weeks prior to egg-laying exerted a statistically significant, though not particularly strong, positive effect on productivity. The mechanism of this influence is unknown but may operate through nutritional or cover characteristics of the vegetation. Jackson (10) believed that the effect of rainfall deviations on vegetation contributed to oscillations of bobwhite densities in marginal ranges of Texas. Lehmann (20) linked rainfall and corresponding vegetative growth to initiation of nesting in the same state. Interrelationships between rainfall, vegetation, and nesting would conceivably be more pronounced in arid regions of the bobwhite's range than in southern Illinois where extremes of early season rainfall and corresponding vegetative response are not so great.

Many workers contend that cool, moist summers are more conducive to good reproduction than hot, dry summers (25,28,29,32). However, several long-term studies (12,16), including ours, have failed to demonstrate a significant relationship between summer weather and productivity. The absence of a correlation between these variables on our study area does not negate the potential importance of summer weather to reproduction. It simply means that during the years 1954 through 1971, variations in rates of productivity did not seem attributable to variations in temperature and moisture conditions as we measured them. This is not surprising considering that each year of the study, except 1954, had a mean maximum daily temperature for the period June-August that was cooler than the 1910-53 long-term mean (3,34). Furthermore, nesting studies from 1954 through 1963 indicated that individual nests and eggs were affected only rarely by heat, drought, or heavy rains although maximum July-August temperatures may have influenced termination dates of egg-laying (15). Extremely hot weather during peak egg laying in June of 1952 and 1953 may have abbreviated the nesting season and increased nest abandonment, but the effect on total productivity was not clear.

The Pattern of Population Change Between Years

Three characteristics of long-term population behavior on the CRA are evident from Fig. 1. First, there is a tendency for between-year

changes to be negatively related to previous densities. Secondly, periods of increase, decline, highs, and lows each generally persist for several years. Finally, there is an apparent regularity of oscillation with 8-10 year intervals between major highs and lows, respectively.

The negative relationship between population change and density is clearly seen in Fig. 7 which plots annual rates of change as a function of previous fall densities ($r = -0.49$). This population characteristic, which is implicit in the concept of balance, is apparently a manifestation of the previously described density-related nature of both mortality and productivity and possibly of the interaction between density and weather. However, response to deviations from mean density is usually not immediate. Instead, increases or declines tend to overshoot the mean by a considerable margin then persist for several years at more stable densities well above or well below the mean. This population momentum, which apparently results from the strong correlations between successive seasonal levels (Figs. 3 and 6), seems able to persist for several years before other pressures, presumably density related, finally stabilize the population or impel it in another direction.

Serial correlations between seasonal densities may not be the only cause of momentum. It has been observed that some populations tend to remain at low levels for a time following declines even when apparent causes of the decline (e.g. weather, high density) are no longer operating directly on the individuals. When this occurs in short-lived species, it suggests that the offspring of parents which originally suffered the decline are somehow "disadvantaged" in terms of their own survival or reproduction or both. Errington (6) termed this period a "depression phase" while others (12,36) have mentioned the possibility of stress-induced weakness being transmitted nongenetically from parents to young. Obviously, further research is needed regarding the effects of various kinds of stress on bobwhite population behavior and the possibility that these effects may be delayed as well as direct.

Whether "cyclic" population tendencies are due entirely to intrinsic mechanisms or are the result of periodically occurring extrinsic factors has long been a subject of great interest among population ecologists (9,13). At least some of the regularity observed in our data seems attributable to the combined effects of momentum and density-related changes operating in tandem. Complicating the picture, however, is the effect of weather, especially snow cover, which our study and others have shown to be considerable. It would seem that randomly occurring years of severe weather would tend to mask or dampen any intrinsic tendencies toward regularity of oscillations. However, both winters of heavy snows occurring on the CRA in 1960 and 1970 came immediately after periods of high densities, just as the population appeared to be beginning a decline. In addition, it is likely that the adverse effects of these winters were at least somewhat intensified by the high densities. Thus, it is not entirely clear whether the winters of 1960 and 1970 actually caused or merely accentuated the population lows which followed. We anticipate that information from our study will ultimately provide valuable new insight into the phenomenon of population cycling. However, in order to clarify the role of weather, it will be necessary to quantify

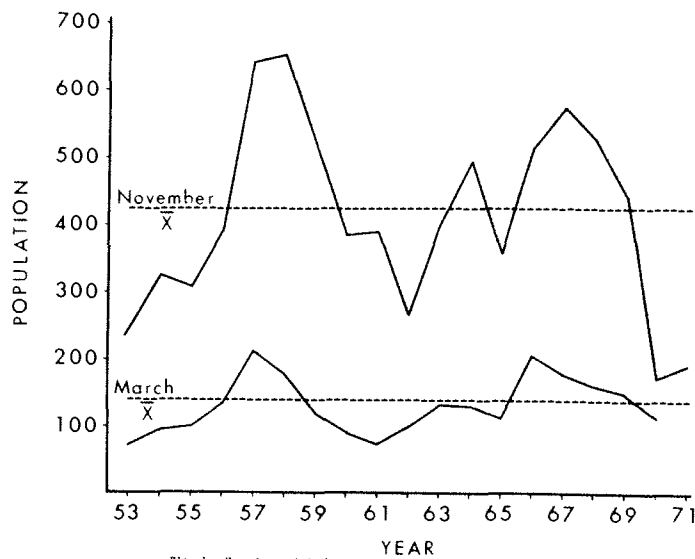


Fig. 1. November and following March population levels, Carbondale Research Area, 1953-1971.

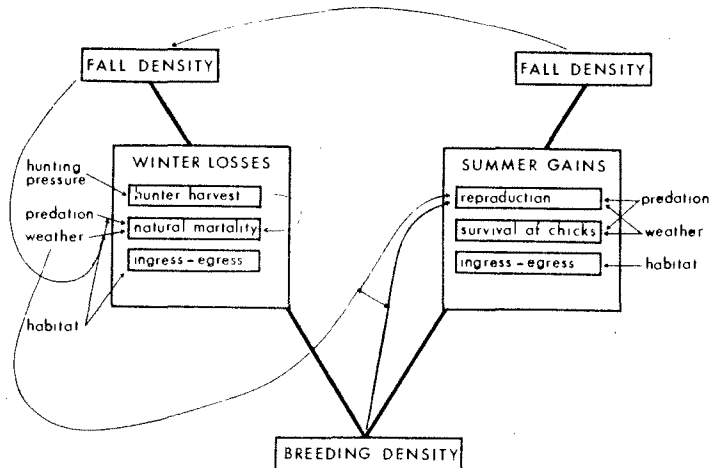


Fig. 2. A simplified model of November to November population change on the Carbondale Research Area.

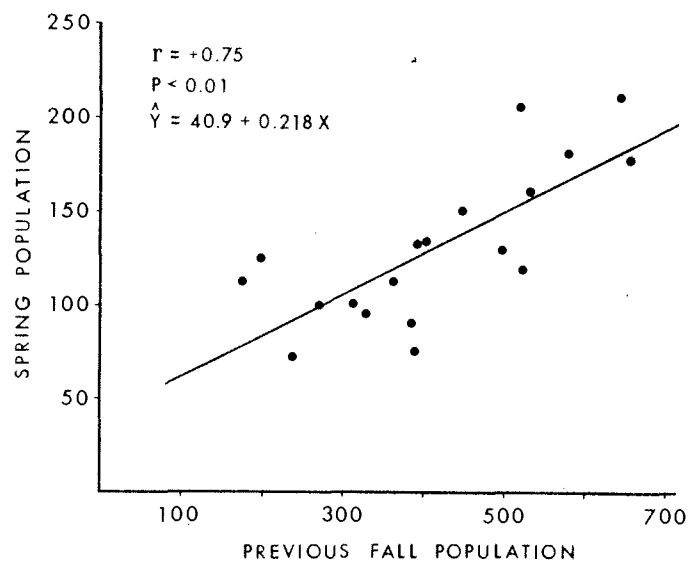


Fig. 3. Relationship of fall to following spring population levels, Carbondale Research Area, 1953-1972. Line fitted by method

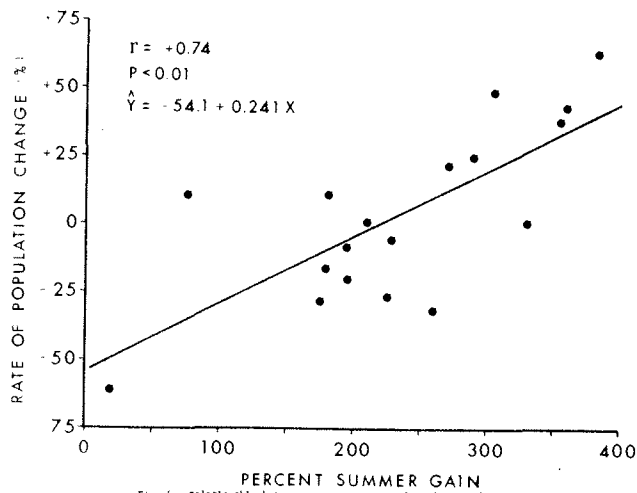


Fig. 4. Relationship between percent summer gain and rate of population change, Carbondale Research Area, 1950-1971. Line fitted by method of least squares.

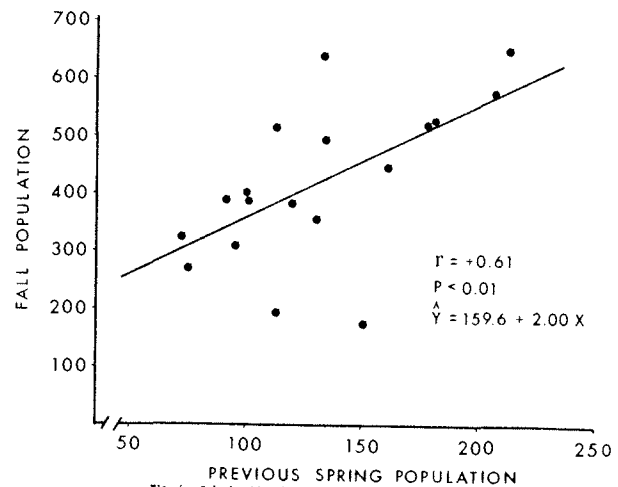


Fig. 6. Relationship of spring to following fall population levels, Carbondale Research Area, 1954-1971. Line fitted by method of least squares.

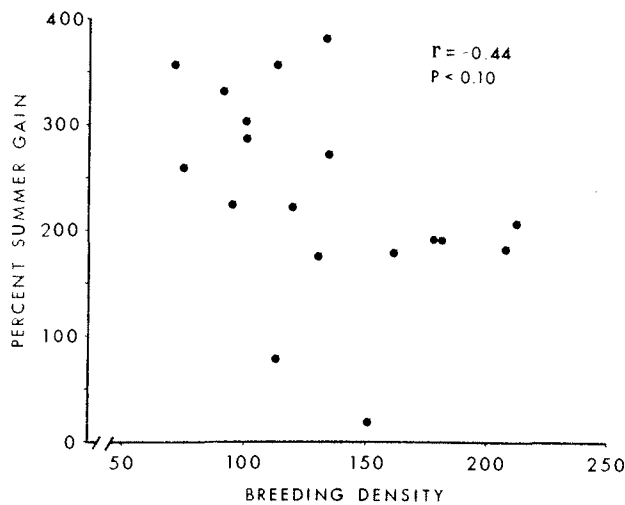


Fig. 5. Relationship between breeding density and percent summer gain, Carbondale Research Area, 1954-1971.

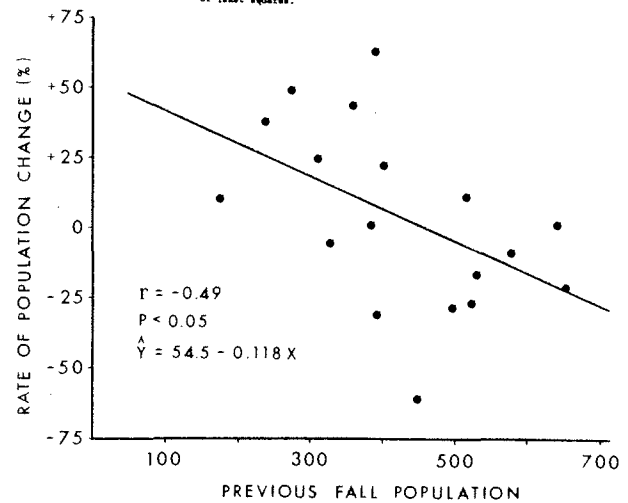


Fig. 7. Relationship between fall densities and rate of population change the following year, Carbondale Research Area, 1954-1971. Line fitted by method of least squares.

Table 1. Some bobwhite population data, Carbondale Research Area, 1953-1972.

Year	Estimated population as of:			% Gain previous summer	Hunter harvest		% Loss Jan. to Apr. (of Jan. level)	% Loss Nov. to Apr. (of Nov. level)
	Nov. 10	Jan. 1	Mar. 20		#	%		
1953-54	237	139	72	-	-	-	48.2	69.6
1954-55	328	199	95	356	119	36.3	52.3	71.0
1955-56	311	151	101	227	130	41.8	33.1	67.5
1956-57	392	228	133	288	210	53.6	41.7	66.1
1957-58	643	240	212	383	357	55.5	11.7	67.0
1958-59	655	285	178	209	273	41.7	37.5	72.8
1959-60	523	197	119	194	198	37.9	39.6	77.2
1960-61	386	110	91	224	259	67.1	17.3	76.4
1961-62	392	132	75	331	222	56.6	43.2	80.9
1962-63	270	189	100	260	82	30.4	47.1	63.0
1963-64	404	143	134	304	258	63.9	6.3	66.8
1964-65	497	136	130	271	224	45.1	4.4	73.8
1965-66	359	171	113	176	163	45.4	33.9	68.5
1966-67	518	272	207	358	198	38.2	23.9	60.0
1967-68	579	303	181	180	217	37.5	40.3	68.7
1968-69	531	192	161	193	233	43.9	16.1	69.7
1969-70	449	256	151	179	190	42.2	41.0	66.4
1970-71	176	129	113	17	54	30.7	12.4	35.8
1971-72	197	144	125	74	44	22.3	13.2	36.5

its effects during other phases of the "cycle".

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BOBWHITE WHISTLING ACTIVITY AND POPULATION DENSITY ON TWO PUBLIC HUNTING AREAS IN ILLINOIS

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Abstract:

Eight years of data from 2 public hunting areas in southern Illinois demonstrate high multiple correlations ($r = 0.97$ and 0.84) for prebreeding densities and call indices with the prehunt densities of bobwhites (Colinus virginianus). Models derived from multiple correlation analyses produced satisfactory predictions of prehunt densities. The average number of calls per stop was the key element in the predicting model. The number of whistling cocks heard per stop is of limited value as an index because of difficulty in determining numbers when more

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