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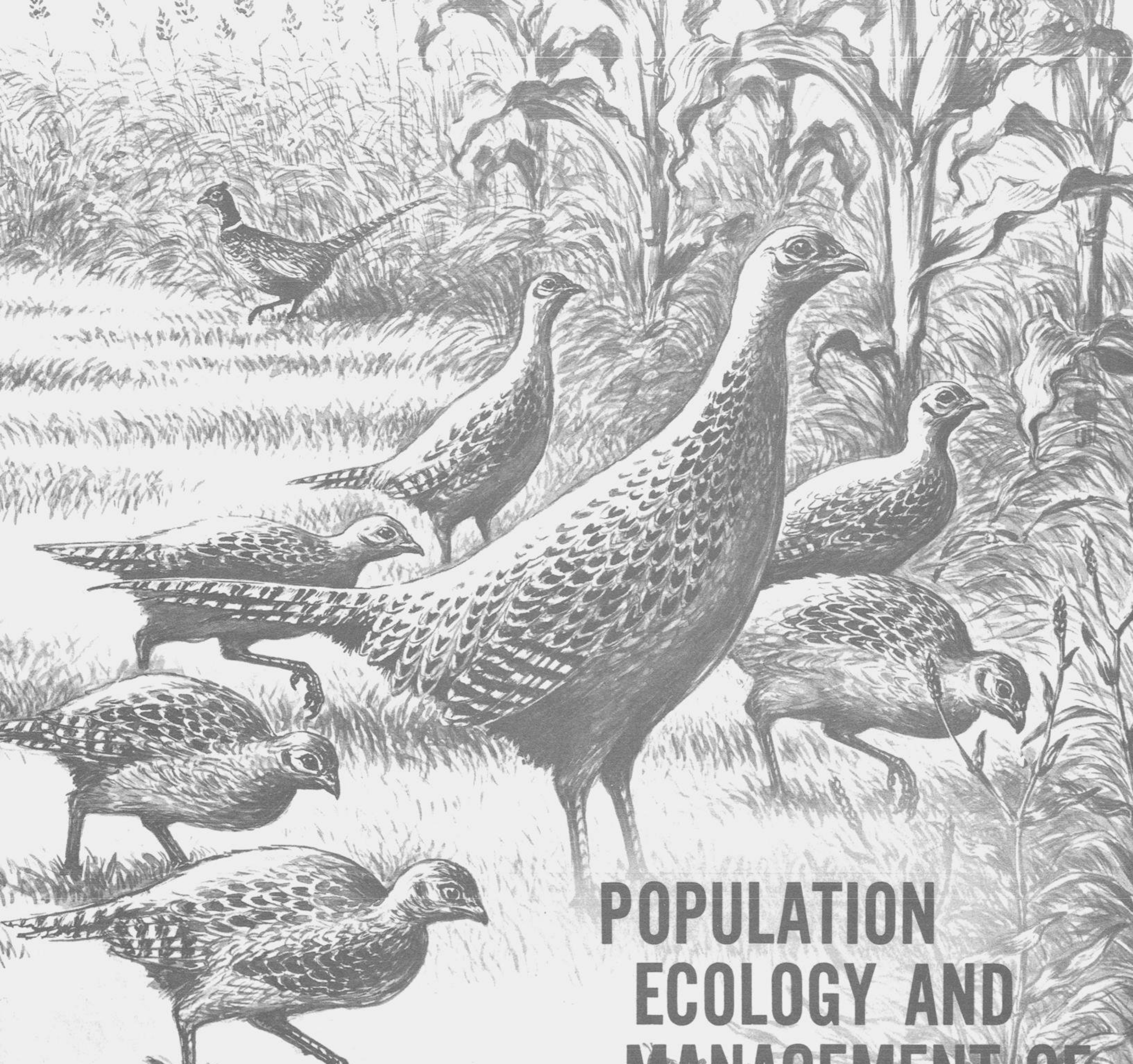

POPULATION ECOLOGY AND MANAGEMENT OF WISCONSIN PHEASANTS

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POPULATION ECOLOGY AND MANAGEMENT OF WISCONSIN PHEASANTS

By

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Since the early 1950's, the majority of the field data have been gathered by Area Game Management personnel of the Wisconsin Conservation Department. These men and other contributors have been acknowledged individually in the quarterly progress reports.

C. W. Lemke and **D. R. Thompson** provided some of the statistical analyses.

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ABSTRACT

Extensive pheasant *(Phasianus colchicus)* population surveys were begun by the Wisconsin Conservation Department in the years following World War II. Among their objectives were the provision of information on: (1) the regional pattern of population distribution and productivity in the state and the relations of these to habitat characteristics; (2) short-term fluctuations and the mechanisms and factors involved; and (3) the extent of hunting take and its effect on the populations.

This report synthesizes the survey data which accrued from 1946 to 1961, integrates these with the existing knowledge of the species and suggests possible mechanisms and causes of: (1) short-term fluctuations, (2) population balance, and (3) determination of long-term mean density in any given area. The management implications which follow from these views are set forth. The focus is on Wisconsin pheasants, but the conclusions may apply more widely over the Midwest and elsewhere.

Quantitative distribution maps of Wisconsin pheasant populations show the highest densities occurring in the southeast quarter of the state. In these areas, between 55–70 percent of the landscape is cultivated and less than 10-12 percent is in woodland; roughly 15-30 percent was in wetlands in 1936-38, approximately three-fourths of these remain today. The cultivated acreage is about evenly divided between hay, oats, and corn. The region has gentle topography, the longest growing seasons in the state and is underlain by dolomitic limestone. Under primeval conditions it was covered by prairies and oak openings. Soils are glaciated silt loams.

Pheasant densities decline progressively where more or less than 55-70 percent of the land is cultivated; where within the 55-70 percent cultivation range progressively fewer wetland acreages occur; where progressively more of the landscape is wooded; where the topography becomes progressively less gentle, the soils are progressively less fertile and the growing season shorter. This distribution pattern appears to have held as long as pheasants have been established in Wisconsin.

Cock population densities were measured in spring (1950-61) with crowing count censuses run by District Game Managers of the Wisconsin Conservation Department, and converted to hen indices with winter sex ratios (1940-42, 1948-61) obtained from roadside counts by game management and research personnel. Reproductive characteristics were measured (1) in summer (1946-60) with roadside brood counts by game management and research personnel to provide average hatching dates, average brood sizes, and percentages of hens with young; and (2) in fall (1953-59) by cock age ratios obtained from hunting-season leg collections and corrected with adult sex ratios. Game Division kill estimates derived from kill report cards voluntarily returned by hunters were used (1937-60) as indices of fall population densities and for calculating annual rates of population change.

Average hatching dates reflect 1947-56 annual variations in nesting phenology in Wisconsin which appear also to have occurred elsewhere in the Midwest and apparently result from variations in the date on which hens begin an incubated clutch. Wisconsin hatching curves appear to be higher and more unimodal in phenologically late years than early years, suggesting concentration of the hatch in a shorter period and perhaps less renesting in late years.

Broods hatched early in the season are larger than late-hatched broods due to a seasonal decline in clutch size, and possibly to a seasonal increase in chick mortality rate. A significant negative correlation exists between annual Wisconsin average brood sizes and average hatching dates. The role of clutch size is unknown in this, but chick mortality rate is evidently higher in late years.

Annual percentages of hens with broods in Wisconsin appear to be higher in early years than in late years. There is no evidence of variation in this statistic between different pheasant density levels in the state.

A significant negative correlation exists between annual young-per-hen ratios derived from hunting season data and average hatching dates in Wisconsin. Similar comparisons are suggestive for other midwestern states.

Reproductive success is significantly correlated with yearly percentage change in Wisconsin kill. Fall populations increase when success is above average, decrease when below, and remain constant when success is average. This suggests that the populations are approximately balanced, i. e., experiencing no pronounced long-term increase or decrease. Annual variations in spring-to-fall hen mortality rates appear to be inversely correlated with reproductive success; while fall-to-spring mortality, at least in the northern Lake States, appears either to be roughly constant between years, or light to moderate if variable. The severe winter of 1958-59 is an exception to this generalization.

Spring densities are closely correlated with levels of previous autumns suggesting that no material winter threshold effect exists. Fall densities are closely correlated with levels of previous springs suggesting that no well-defined summer or fall carrying-capacity effect exists.

Wisconsin average hatching dates are significantly correlated with prenesting temperatures as is yearly percentage change in kill in Wisconsin and other states. Weather, operating directly or indirectly, appears to be one of the principle causes of short-term fluctuation in midwestern pheasants, with prenesting temperatures the dominant in-

fluence in Wisconsin (and perhaps in other parts of the Midwest). No correlation was evident between Wisconsin population trends and June rainfall, May-June temperatures, or mean temperatures and total snowfall for the December-February period.

Whether or not cocks are shot, a pheasant population each year is potentially capable of any "actual rate of population increase" (**r**), within the range +500-600 and −100 percent. Most annual **r** values fall within a limited fraction of this range. Over a period of 10-20 years mean **r** values approach zero in those areas examined except Pelee Island where mean **r** is positive. Equivalence of mean **r** and zero is tantamount to population balance.

In Wisconsin, as in other midwestern states, above- and below-average prenesting temperatures are associated with population increases and decreases, respectively, while mean temperatures (norms) are associated with no population change ($\mathbf{r} = 0$). Hence, the populations are balanced at the local temperature norms. Since the effect of temperatures on populations appears to be direct, any increase or decrease in the prevailing temperatures of an area would apparently be accompanied by a population increase or decrease. Consequently prenesting temperatures per se appear to bring about some limitation on pheasant density, and presumably in a density-independent manner.

Hay mowing phenology, like nesting, may be correlated to some degree with spring temperatures. The percentage of nests in tame hay in different areas reported in the literature is correlated with the percentage of all potential nesting cover in hay. The percentages of all nests and hens destroyed by mowing are closely correlated with the percentage of nests in hay, and hence with the percentage of all nesting cover in hay. The average percentages of nests and hens lost in southeastern Wisconsin may approximate 25-30 and 20, respectively. Those areas on the continent with light hayfield losses tend to have higher pheasant densities. Increase in the severity of mowing loss has been associated with the failure of populations to attain densities of the early 1940's. Mowing losses apparently are density independent.

The main value of the large Wisconsin wetland acreages may be to serve as undisturbed nesting cover and offset the influence of large hay acreages. Population resilience in Wisconsin appears to be a function of the total wetland acreages. An average of 26 percent of these wetlands were drained between the mid-1930's and mid-1950's.

Grain harvests, spring plowing, and livestock grazing all destroy nests and hens. Advances in mowing dates, continued cover loss, changes in livestock practices, and pesticides are all placing increasing pressure on pheasant populations and may be responsible for the generally lower pheasant densities of 1948-60 than in the previous decade.

At least 31 species of mammals, birds, and reptiles occurring in Wisconsin have been reported to prey in varying degrees on pheasant adults, young, or nests. Their collective abundance, with a few exceptions, is probably higher in marginal than good pheasant range.

Frequency of pheasants in the predator diet tends to be roughly correlated with pheasant densities, but is not indicative of the severity of effect on pheasant populations. This effect is determined by the percentage of the pheasant population removed and probably varies with changes in buffer numbers and changes in predator numbers all independent of pheasant density; it may vary negatively with changes in pheasant density. Reported losses to predation in winter ranged from 2 to 26 percent; spring losses perhaps are in the lower part of this range, and summer losses perhaps are on a comparable order of magnitude.

Nest loss due to predation, varying from 3 to 78 percent of all nests in various studies, tends to be inversely correlated with losses due to farming activity and percentage of land under cultivation. Mean nest success is highest in the intermediate cultivation range—60-80 percent—where loss from both factors is light to moderate. Most predator control experiments have been confined to one or a few species, often of short duration, and hence permit few definite generalizations.

Approximately 16 percent of the hens were shot illegally and accidentally in Wisconsin during the 1953-59 seasons as determined by body-shot incidence studies in postseason highway kills. Roughly three fourths of the loss occurs in the first 2 weeks of the season. This loss appears to be a function of hunting pressure and shows no evidence of being related to pheasant density within any given area.

Legal kills exceeding 20-30 percent of the hens in Wisconsin, Minnesota, Indiana, and California appear to have reduced populations. The evidence did not seem to indicate any response to kills below this level. If populations are to absorb hunting kill without influence on their density, they must respond with density-dependent adjustments in the fall-to-spring mortality rate, and/or in the reproductive rate so completely that there is essentially no correlation between fall and subsequent spring densities (threshold phenomenon) in the first case, or between spring and subsequent fall density in the second (inversity). Density dependence can exist and still not compensate completely enough for hunting loss, a situation that seems to prevail in the pheasant. We suspect that the illegal hen loss in Wisconsin does effect some degree of population reduction.

As pheasant densities increase, changes occur in the reproductive behavior of the hen which may reduce mean nesting success, and increase chick and hen mortality rates. Although reproductive measures for a long enough period of time are not available for comparison with density, annual **r** values in Wisconsin, Michigan, Minnesota, Indiana, South Dakota, and Pelee Island are negatively correlated with density. This effect, presumably a function of social strife and representing competition for space, is the one truly density-dependent function we have discerned in pheasant populations. The role of dispersal is unknown but may also play a role.

Population balance—variation within a limited range and about a mean, both of which are relatively constant in time —is effected by the correlation between **r** and density, presumably due to intraspecific intolerance. No natural environment is absolutely constant over a long period of time, and hence absolute balance is somewhat theoretical, though approximately obtained. Short-term fluctuations away from mean or balancing densities result from annual variations in **r**, perhaps most often induced by weather. Recovery toward the mean is effected by the density-dependent relationship, but frequently overshoots the mean in a phenomenon here termed population momentum. Pheasant fluctuations are oscillatory, but not cyclic in the physical or mathematical sense of the term.

With the exception of Pelee Island, all pheasant populations examined have mean **r** values approaching zero at their mean densities. However, extrapolation of their **r**-density regression lines suggests that their **r** values at very low densities are correlated with their ultimate balancing densities, and may reflect differences in density-independent pressure. The level at which a population balances itself depends on its initial **r** value and the space between this value and zero which density dependence must close. We suggest: (1) balance is a function of density dependence; (2) differences in mean density between areas appear to result from differences in density independence; and (3) mean density achieved in any given area is a function of the combined action of both types of factors. Hence, pheasant populations evidently are not self limiting, their density in any given area apparently being a function of the kinds and severity of such density-independent factors as weather, agricultural operations, predation, hen shooting, etc., and of their own density-dependent action. No continental population examined shows evidence of being limited solely by the latter.

In the interests of (1) simplifying regulations, (2) providing a maximum of recreation, (3) minimizing conflict with agricultural operations and other hunting seasons, and (4) achieving a biologically sound harvest, an annual hunting season of 4-5 weeks in length opening on a Saturday in mid-October seems desirable. Daily shooting hours should coincide with waterfowl shooting hours and a daily bag of two cocks seems most appropriate.

Regulations could be formulated which would permit harvesting a restricted fraction of hens, but such harvest would probably increase the total hen kill and, according to the available evidence, result in some population reduction. The occasional suggestion that pheasant hens do not survive in marginal Wisconsin counties and that hens should be made legal game to utilize the annually stocked hens is not valid because a majority of cocks shot even in marginal counties are wild-reared birds.

Wetland drainage is one of the most significant changes occurring in Wisconsin pheasant range. We urgently need intensive research on the exact role of wetlands in pheasant ecology and the socio-economic factors involved in their drainage. An understanding of the broader aspects of pheasant productivity under Wisconsin conditions is needed for evaluating the effects of changing land-use practices on pheasant populations. New types of landowner compensation or wildlife-orientated cropland conversion programs should be developed to provide the large acreages of undisturbed herbaceous cover necessary for successful pheasant nesting.

A statewide winter feeding program is ineffective. However, a winter feeding program may be feasible for an individual landowner interested in managing game on a limited area. Pen-reared birds contribute a small addition to the annual kill. The quality of Wisconsin pheasant hunting is largely a function of wild-reared populations.

An annual pheasant harvest goal of 500,000 cocks has been established and management efforts are being aimed in this direction. The future of pheasant hunting in Wisconsin will depend upon recognition that this species is an integral part of a total land-use program.

CONTENTS

INTRODUCTION

The ring-necked pheasant in Wisconsin has been studied almost continuously since the middle 1930's, primarily by persons in the Wisconsin Conservation Department and the University of Wisconsin. Areas of emphasis have included nesting and population studies, various aspects of physiology, behavior, and problems surrounding artificial propagation and stocking.

Regional and statewide pheasant population studies were begun in the Conservation Department in the early to mid-1940's for the purpose of providing a new dimension to our knowledge of population mechanisms. Previous population studies had largely been confined to study areas of limited size. In addition to the basic need for extending our knowledge of these mechanisms, the studies had the practical objectives of assessing the impact of land-use changes on pheasant populations and of observing the effects of hunting.

This report is centered around findings from these investigations. It explores the mechanisms and causes of population fluctuations, the environmental influences involved in the determination of pheasant densities, and the management implications arising from this knowledge.

While the target of our study has been pheasant population mechanisms in Wisconsin, it became evident early in the analyses and interpretations of our data that findings from this state had to be tested with information from other mid-continental states. Therefore various aspects of the entire body of pheasant knowledge were studied, particularly those relationships that transcend state lines and which become evident only when viewed in the entire perspective.

The mid-continental pheasant range is approximately triangular with angles situated roughly in Ohio, central Alberta, and the Texas panhandle. It is perforated or thinned at points by Lake Michigan, the dissected watersheds of several major rivers, the Wisconsin Driftless Area, and the sandhills of Nebraska and adjacent states. This range coincides fairly well with the mid-continental prairies, bordered on the north by the boreal forests, on the south and east by the deciduous forests of eastern and southern United States, and on the west by the Rocky Mountains. It is an area in North America distinct in its biota, physiography, soils, climate, and land use.

Within this mid-continental pheasant range, there seem to be regional differences in pheasant population ecology that are at least quantitative. But a number of principles also seem to hold throughout large portions of this range.

The first draft of this report was begun in 1956 and largely completed in 1958. Revisions were made in 1961 and 1962. Because of the time between the beginning of writing and completion, and because the research continued during this time, substantial amounts of data accrued in the interim. Where relationships derived from the initial tabulations seemed reasonably well established, we did not feel it necessary to add, nor did time allow the addition of, newly accrued data. Hence the reader will find some analyses based on data gathered up to 1956-57.

However, where results of early analyses were inconclusive, we included more up-to-date findings in an effort to give clearer answers. Data are also more up-to-date in new analyses or questions that occurred to us between first and final drafts. An attempt was made to stay abreast of the literature up to the second writing in 1961-62. During the final editing, a few additional references subsequent to 1962 were inserted.

Although there is a vast amount of material on the pheasant—perhaps more than on any other wild species—it is still insufficient to prove or disprove some of the points we raise in this report. Hence, many of the conclusions we draw must still be considered hypotheses to be proven, modified, or disproven by future, more intensive research.

PART I—SOURCES OF DATA AND METHODS OF STUDY

In this section we discuss various features of the Wisconsin landscape and their gross characteristics which seem to be related to pheasant distribution. Some descriptive material is presented on pheasant range and correlated with population density to develop a perspective for analyzing various factors influencing pheasant populations in the state.

The various sources of basic information used to evaluate Wisconsin pheasant populations and the variables involved in gathering these data are discussed. Since fall kill estimates are used as indices of population levels and yearly trends, we explore the ramifications of using kill estimates in considerable detail.

CHAPTER I. WISCONSIN PHEASANT RANGE

Pheasant Population Distribution

Relative Distribution

A quantitative distribution map of Wisconsin pheasant populations has been prepared which can be used for general comparison with habitat characteristics and distribution of possible limiting factors (Wagner, 1952, 1953; Wagner and Besadny, 1958). This map (Fig. 1), like that published by McCabe *et al.* (1956:275), shows the highest pheasant densities in the southeastern quarter of Wisconsin. As is also shown by McCabe *et al.*, this block does not have uniformly high densities. It is bisected by a north-south strip, roughly one county in width, which is populated with "Fair-Poor" densities.

Except for the nearly pheasantless northern third and central region, the remainder of the state has "Fair-Poor" densities. Several southwestern counties form a coherent block notably poor in pheasants, as do most of the more northern counties bordering the Mississippi River.

Distribution of Kill by Counties

County pheasant-kill estimates were used to depict pheasant distribution on a quantitative basis (Game Management Division Files). This allows a quantitative comparison with some general habitat characteristics.

We used the 1955 pheasant-kill estimates to show distribution of kill by counties (Bersing, 1956). These were divided by the area of the respective counties and then reduced by 25 percent to correct for over-estimation discussed in Chapter III. The result shows the estimated number of cocks shot per square mile in each county in 1955 (Fig. 2). We chose 1955 because the kill in that year reached the highest level during the population changes of the past 20 years. Although pheasant populations have fluctuated throughout this period, the relative distribution within the state has remained similar between years, as the similarity between the 1955 distribution (Fig. 2), that of 1952 (Wag-

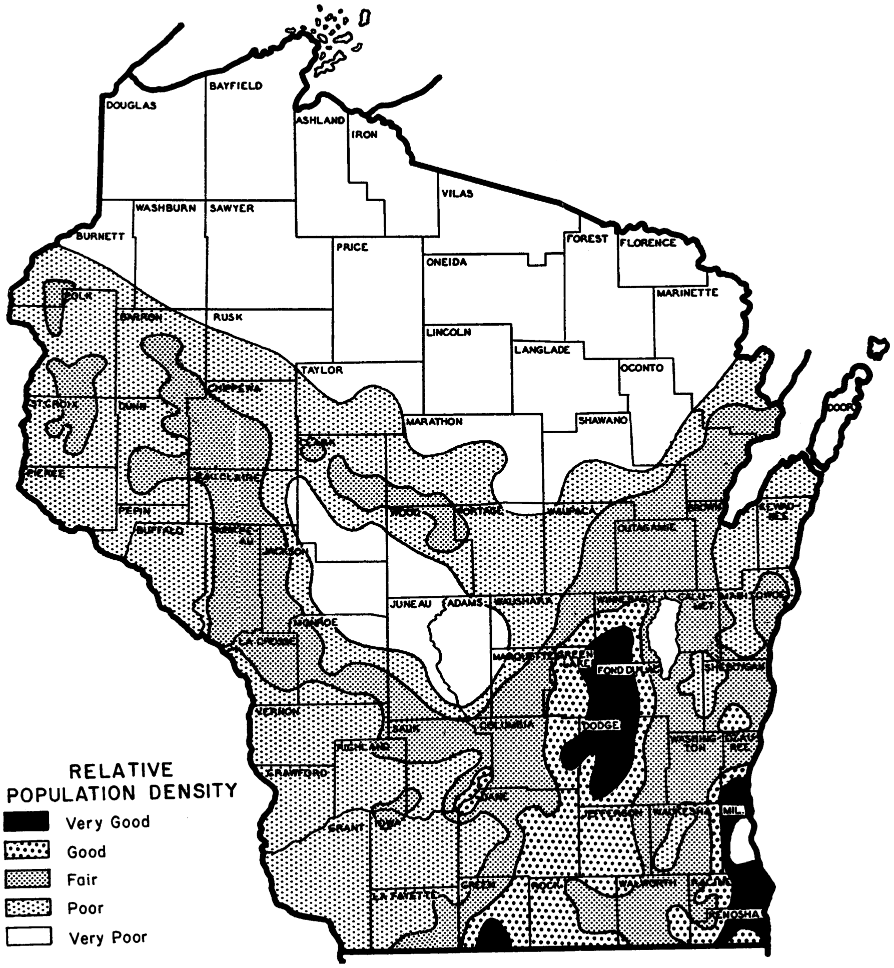


Figure 1. Generalized population distribution of Wisconsin pheasants (after Wagner and Besadny, 1958). For material on which it is based, cf. Wagner (1952, 1953).

ner, 1953), and that of 1942 (Buss, 1946:19) attests.

Hence, the 1955 distribution reflects the approximate, relative distribution during the past two decades—the period in which pheasants have been fully established in their Wisconsin range. This constancy of distribution, also reported for Michigan by MacMullan (1960), contrasts with the pronounced geographic shifts experienced by populations of the Plains States (Kimball *et al.,* 1956:206-211).

Figure 2 shows a distribution similar to that of Figure 1, with the highest pheasant kills occurring in the southeastern quarter of the state. Very poor kills occur in the northern, central, southwestern, and western counties, and mediocre-to-poor kills occur in most of the remaining blocks of counties. As will be shown later, this kill distribution is not an artifact of hunting pressure distribution and thus it reflects actual population differences.

Gross Characteristics of Wisconsin Pheasant Range

Bedrock Geology

Few significant and unequivocal correlations can be drawn between bedrock geology and pheasant distribution. The relationships that exist are probably indirect in many areas, involving topography, native vegetation, soils, and land use.

In general, the best pheasant areas are underlain by dolomitic limestones (Fig. 3), primarily of the Ordovician and Silurian periods (Whitson, 1927:36; Martin, 1932). However, the east central, southwestern, and Mississippi River counties, and the north-south strip bisecting the high southeastern pheasant region are also underlain by these same strata and have "Fair-Poor" pheasant densities.

The nearly pheasantless central area (Fig. 1) is underlain by Cambrian sandstones. These same formations also underlie areas of "Fair-Good" densities in Waupaca, Green Lake, Waushara, and Marquette Counties; and "Fair" densities in Jackson, Trempealeau, Eau Claire, and Dunn Counties.

Pre-Cambrian igneous and metamorphic rocks underlie the surface in the remaining, northern portion of the state where pheasant densities are low or nonexistant.

Influence of Glaciation on Topography

Glaciation has had a dominant influence on the topography of Wisconsin. All of the state, with the exception of portions of the southwest (Fig. 4), was covered by one or more of the Pleistocene ice invasions which largely obliterated the preglacial drainage pattern and moderated the topography (Martin, 1932).

As with the bedrock geology, some generalizations can be made between glacial geology, as indicated by topography, and pheasant densities. All of the good pheasant densities exist in the gently rolling to level regions of the glaciated southeastern quarter of the state. The exception is the dissected Kettle Moraine area which bisects this region and coincides with the pheasant-poor north-south strip in Figure 1.

The unglaciated, severely dissected Driftless Area of southwestern Wisconsin as a whole is poorly populated with pheasants. However, modest densities do occur in western Jackson and Trempealeau Counties.

Soils

In general, the most fertile soils of Wisconsin lie in a U-shaped pattern covering the western, southern, and eastern counties (Fig. 5). These correlate roughly with the distribution of dolomitic limestones (Fig. 3). They undoubtedly owe their fertility to this fact since the parent materials have importantly influenced the nature of the soils even in the glaciated areas (Curtis, 1959:25, 41).

The dark loam soils of the glaciated part of southeastern Wisconsin are the best soils in the state. They have been given mostly "A" agricultural ratings by Hole and Beatty (1957). As a result of the glacial action on underlying limestones, and because of their relative youth and consequent lack of heavy leaching, these soils tend to be well supplied with calcium. Most of the better pheasant densities in the state occur on these soils.

The soils of the unglaciated area are largely residual soils derived from the western limestones. Although they are generally good soils (A and B agricultural ratings), they tend to be leached due to their age, and hence are slightly calcium deficient in spite of their limestone origin (Whitson, 1927:58). Pheasant densities are generally fair to poor on these soils.

A small triangular zone of east central counties is covered largely by reddish or grayish-brown clays (Fig. 5). These are lacustrine soils formed by fluctuations in the shorelines of Lake Michigan. Given "A" agricultural rating by Hole and Beatty (1957), they tend to be quite fertile. Typical of lacustrine soils, they have adequate calcium content. However, they are heavy and poorly drained, warm slowly in spring, and hence must generally be plowed in fall. Pheasant densities on these soils are mostly fair to poor (Fig. 1). Somewhat paradoxically, the best pheasant densities in Michigan occur on these same soil types (MacMullan, 1960:45-46).

The northern third of the state and a block of central counties have poor soils due to the underlying Cambrian sandstones and pre-Cambrian granites and basalts from which they were derived. They are predominately forest soils—sands and gray or brownish-gray loams — and most are "C" and "D" agri-

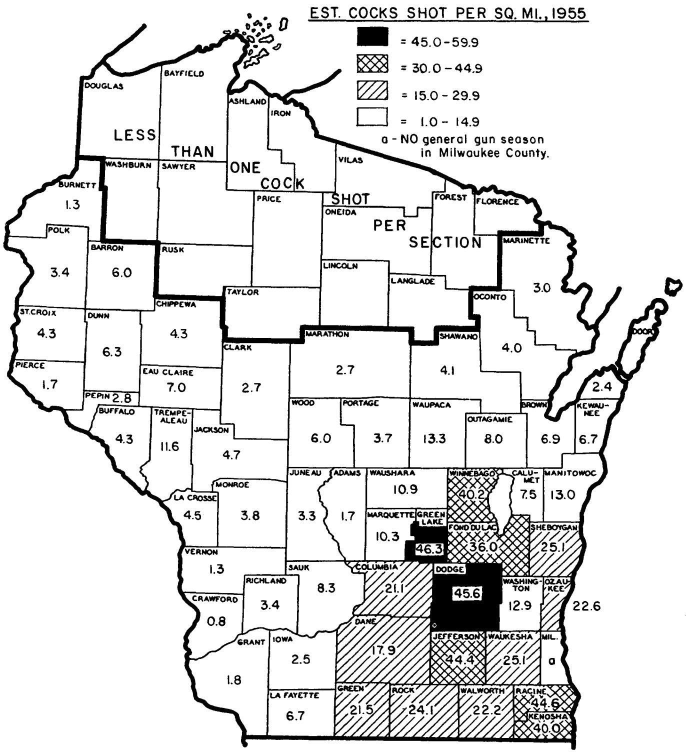


Figure 2. Estimated number of pheasants shot per square mile by counties, 1955 hunting season. The values are based on kill estimates by Bersing (1956) and reduced 25 percent for overestimation.

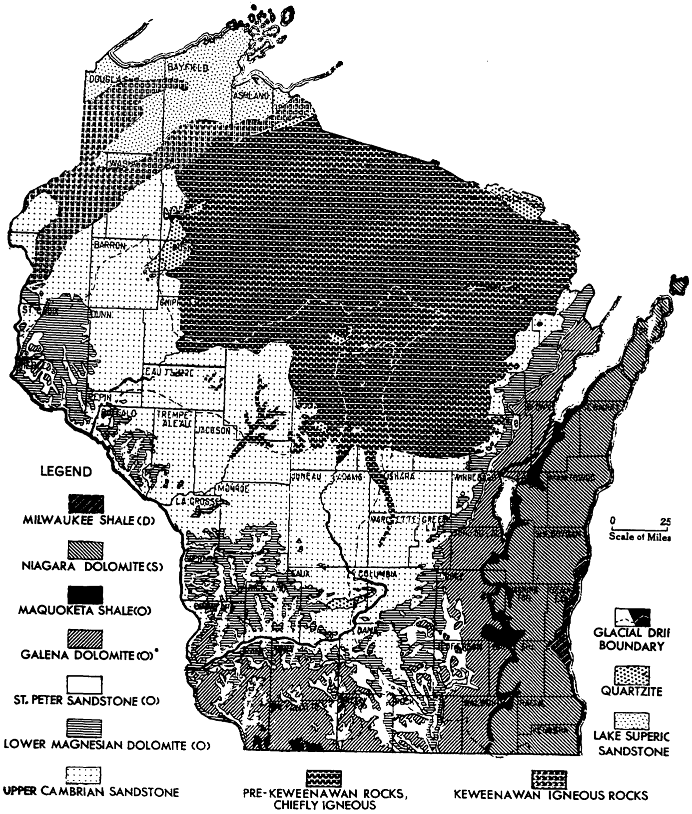


Figure 3. Gross Wisconsin bedrock geology (after Bean, Wis. Geol. and Nat. Hist. Survey).

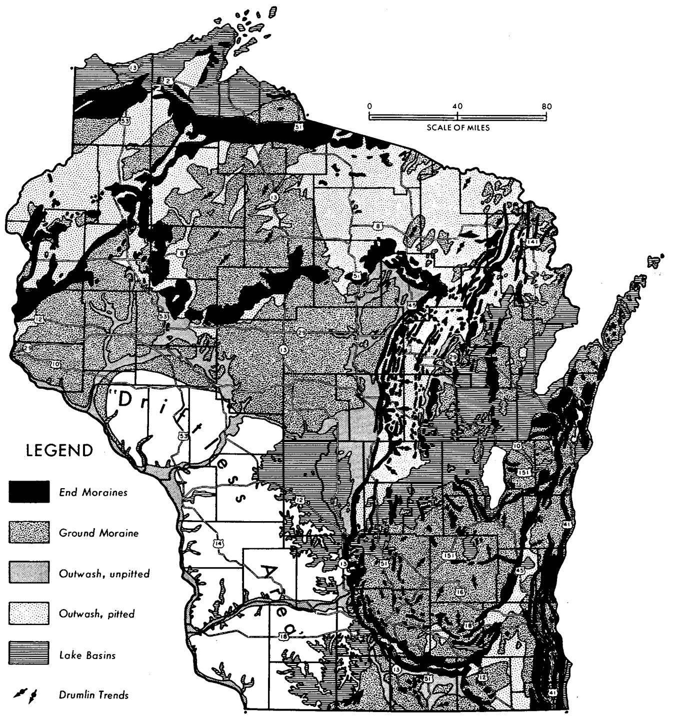


Figure 4. Gross glacial geology in Wisconsin (after Thwaites, Wis. Geol. and Nat. Hist. Survey).

cultural soils. Pheasant populations on these soils generally range from poor to practically no birds in large areas. Minor exceptions are the fair to good densities in sandy areas of Waushara, Green Lake and Marquette Counties. In some years, highly sandy areas in these counties have supported good densities, generally where there is fairly intensive farming and an interspersion of wetlands.

The Wisconsin Vegetation

Native vegetation

Biologically, Wisconsin can be divided into two regions with a line running approximately between the northwestern and southeastern corners of the state (Fig. 6). Northeast of this line the natural vegetation has been termed the northern hardwood floristic province by Curtis and McIntosh (1951). This region was originally covered by mature maple, birch, and pine forests.

The area southwest of this line was originally interspersed with prairie and savannah-like oak woodlands which Curtis and McIntosh (1951) termed the prairie-forest province. It is actually the ecotone between the forests of the north and the continental prairies to the south and west.

The line dividing the two provinces is a narrow zone coinciding with the border between two major climatic zones (Borchert, 1950). It serves as the northern limit of range for many southern plant species and the southern limit for many northern species (Curtis, 1959).

Virtually all of the "Good" and "Very Good" pheasant densities and most of the "Fair" densities occur in the prairie-forest province. This is what might be expected since the pheasant is primarily a prairie or prairie-edge bird east of the Rocky Mountains.

Balance between natural vegetation and cultivation

Today, most of the prairies have been plowed for cropland, and much of the woodland in the southern two-thirds of the state has been cleared for pasture and cultivation. As a result, the percentage of land area under cultivation is highest in the southeastern and eastern counties where the most fertile soils and gentle topography occur (Fig. 7). It is lower in the southwest and west where the topography is more rugged, and in the central and northern counties where soils are less fertile and woodlands abound.

Comparison of the percentage of land under cultivation with pheasant density represented by the county kill shows virtually no pheasants in counties with less than 20 percent of their areas under cultivation (Fig. 8). Densities gradually increase with increasing amounts of cultivation until the best pheasant densities in the state occur in those counties with 55-70 percent of their areas under the plow. However, cultivation of this intensity alone does not insure high densities. Several counties in this range have "Fair-Poor" populations.

In those counties with more than 70 percent of their land areas cultivated, densities fall off suggesting that this 55-70 percent range may be optimum for Wisconsin pheasants. This same approximate range of cultivation is the minimum for

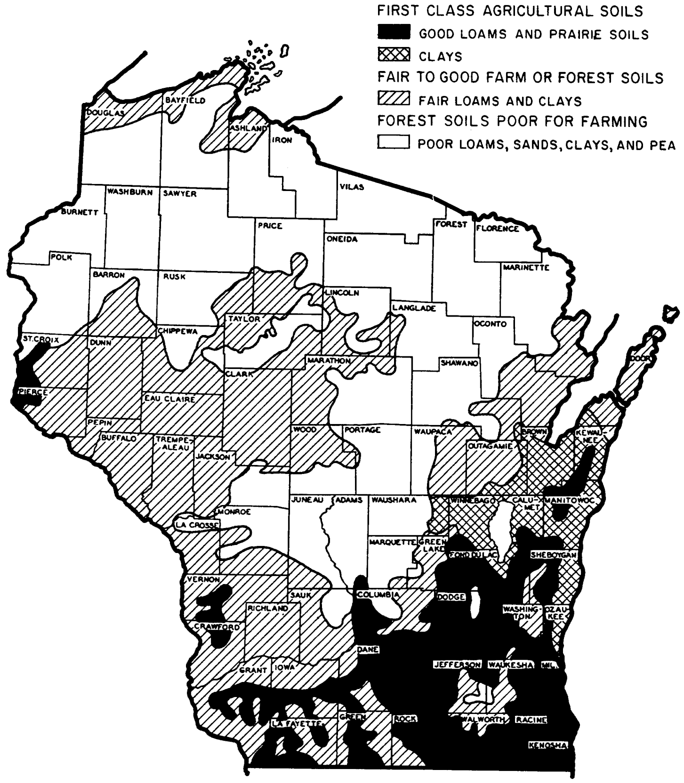


Figure 5. Major Wisconsin soil types (after Hole and Beatty, 1957).

good pheasant habitat in the Plains States (Kimball *et al.*, 1956:213), and may be optimum for South Dakota pheasant areas (Norstog, 1951). Elsewhere in the prairies, high pheasant densities occur in areas more intensively cultivated than the 55-70 percent range (Robertson, 1958:13; Linder *et al.*, 1960). Evidently a substantial amount of disturbance of the landscape is essential for pheasants.

The percentage of land in woodland is approximately the converse of the area under cultivation in each county. The Bordner Land Economic Inventory of 1936-38 showed the lowest percentages of county areas in woodland in southern and eastern Wisconsin (6-17 percent), somewhat higher percentages in the southwest and west (14-43 percent), and highest percentages in the central and northern counties (29-81 percent). Comparison of these values with county pheasant densities shows an inverse correlation (Fig. 9); counties with the least amount of woodland have the highest pheasant densities. Unlike the relationship with cultivation in Figure 8, there is no intermediate optimum range. The correlation is entirely unidirectional.

Wetlands

In Wisconsin, wetlands of varying form constitute an important component of the pheasant range. In order to relate wetland acreages to pheasant distribution we again used the 1936-38 Bordner Land Economic Inventory data although realizing that drainage has continued.

During the 1950's, a detailed wetland survey of 11 southeastern Wisconsin counties showed substantial wetland drainage (Wis. Conservation Dept., 1959-62). While this current information does not allow wetland comparisons with pheasant densities on a statewide basis, it does permit testing the correlation between wetland acreages of 1936-38 and those of the more recent survey. The close correlation (0.967) allows us to use the Bordner figures as indices of present wetland acreages.

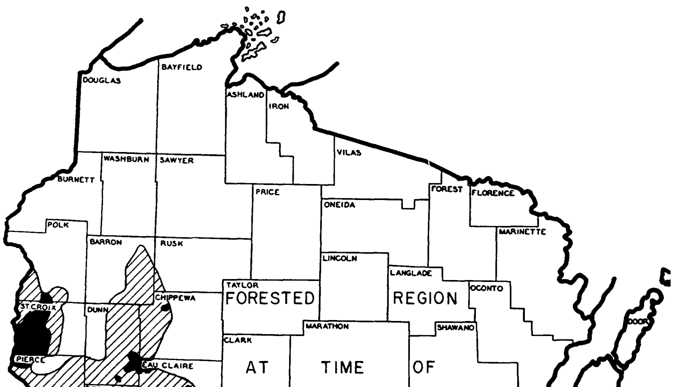


Figure 6. Gross primeval vegetation distribution (after Curtis and McIntosh, 1951).

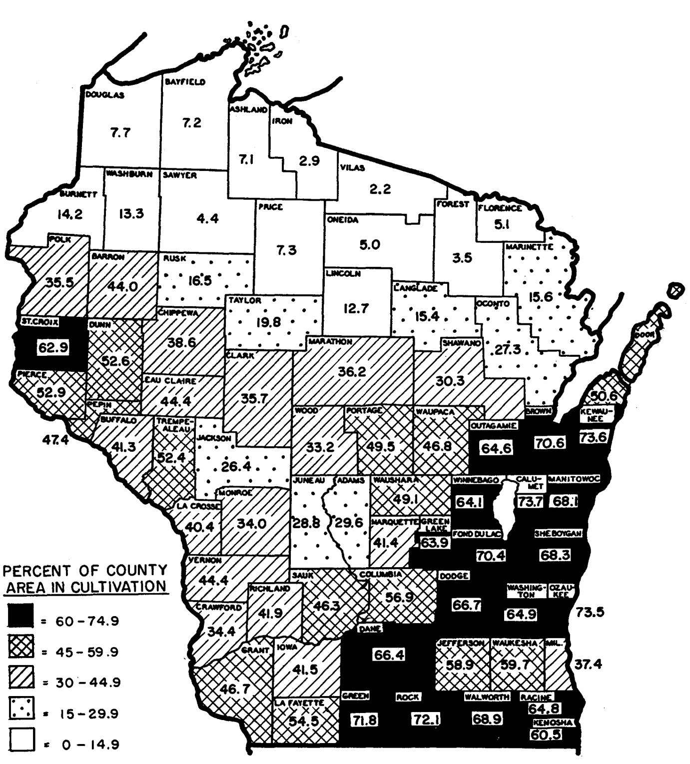


Figure 7. Percentage of county area under cultivation. Data from Ebling, Caparoon, Wilcox and Estes (1948).

Pheasant densities in the western, central, and northern parts of the state seem to be strongly influenced by the low intensity of farming and the large amount of woodland. In these areas, pheasants show some affinity for wetlands, and some correlation appears to exist on a more local level (e. g. township or less) between pheasant distribution and amount of wetland. However, on the county level the woodland-cultivation ratio seems to be such a dominating influence that no wetland-pheasant relationship is evident.

In southern and eastern Wisconsin, where woodland and cultivation acreages fall in the more favorable ranges (Figs. 8 and 9), a strong correlation (0.707, significant at .01 level) is evident between pheasant density and the percentage of each county in wetland (Fig. 10). Some of the highest pheasant densities occur in counties where the percentage of total land area in wetland in 1936-38 fell between 17 and 27 percent. Recent Wisconsin Conservation Department surveys show that many of our better pheasant areas still have 20 percent or more of the land in wetlands.

This is far more cover (grasses, sedges, cattails, brush, etc.) than occurs in most other high-density midwestern pheasant areas. In many of these latter areas, cover occurs only in ves-

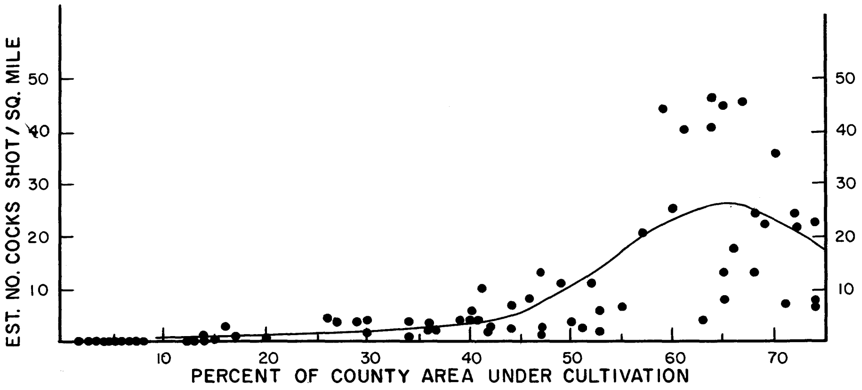


Figure 8. Relationship between county pheasant density (as shown by kill estimate, Fig. 2) and percentage of county under cultivation (Fig. 7). The line is drawn visually from three-point moving averages.

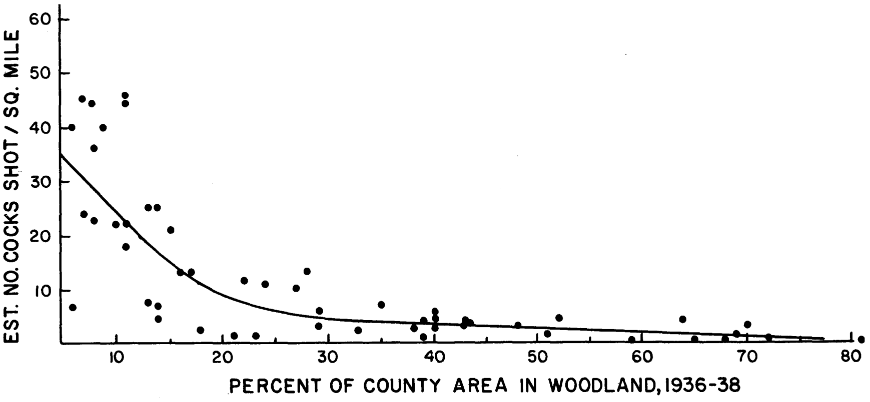


Figure 9. Relationship between county pheasant density (as shown by kill estimate, Fig. 2) and percentage of county area in woodland (as shown by Bordner Land Economic Inventory of 1936-38). The line is drawn from three-point moving averages.

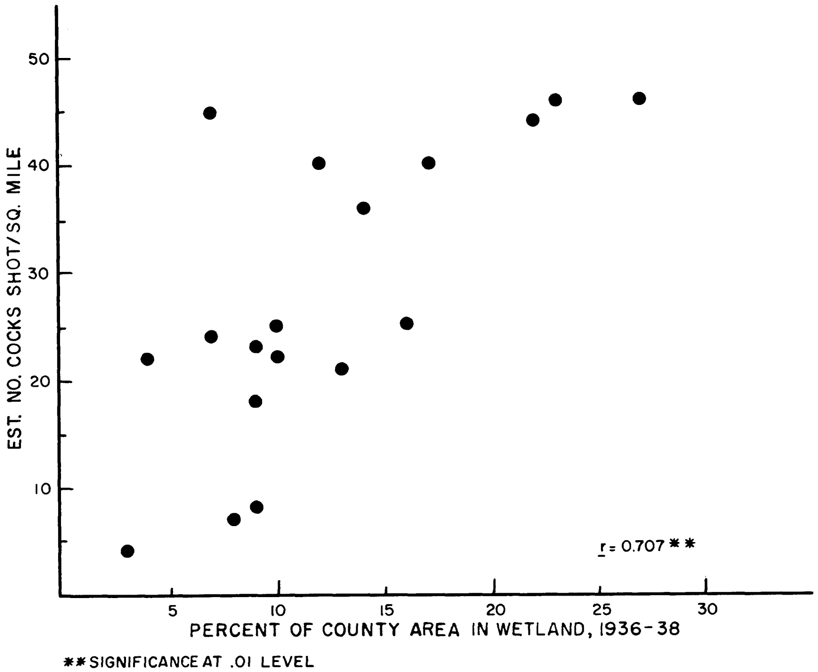


Figure 10. Correlation between county pheasant density (as shown by kill estimate, Fig. 2) and percentage of county area in wetland in 1936-38 (as shown by the Bordner Land Economic Inventory). Comparison is confined to counties with less than 16 percent of their areas in woodland, and more than 55 percent of their areas under cultivation.

tigial parcels and occupies only 1 or 2 percent of the total land area. Where the percentage of land area in wetlands in Wisconsin falls below 5, densities are generally low.

Wisconsin Farming Pattern

Dairying is the major farming enterprise throughout most of Wisconsin. The average farm size is about 133 acres, and the general farming objective is to raise sufficient crops and forage to feed the large dairy herds. Achieving this objective requires three staple crops—corn, oats, and hay—and pastureland. Corn, oats, and hay occupy about 90 percent of the harvested cropland in Wisconsin, and 90 percent of the crops are consumed as forage on the state's farms (Ebling *et al.*, 1948).

The southeastern quarter of the state is the more productive farming area of Wisconsin because of the high soil fertility, fairly level topography, and long growing seasons of 150-170 days (Bordner, 1943). Approximately 60-75 percent of the land area is under cultivation. Permanent pasture makes up 15-20 percent of the farmland acreage; a little less than half of this is grazed woodland, and much of the remainder is grazed wetland.

Corn, oats, and hay are grown in about equal proportions in southeastern Wisconsin usually under a 3-year rotation system. Corn occupies 20-40 percent of the harvested cropland; about two-thirds of this crop is grown for grain and one-third for silage. It is usually planted in May, harvested for silage in September or for grain in the latter half of October and the first half of November.

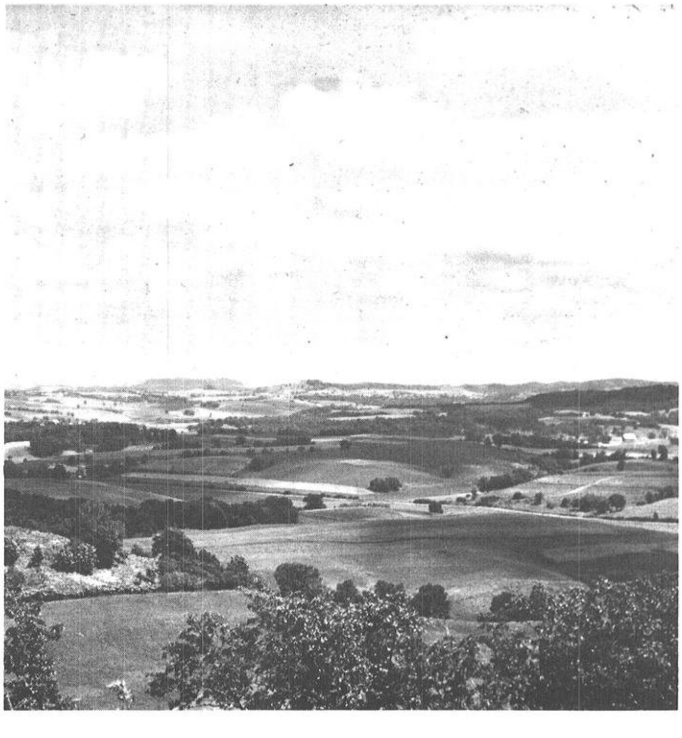
Oats typically occupies 20-35 percent of the southeastern cropland. It is planted in spring as early as possible, often in late March and early April. Harvesting takes place in late July.

Tame hay, predominantly alfalfa, occupies 20-35 percent of the southeastern cropland. In most years, two cuttings are made, usually in mid-June for the first, and July or August for the second.

In other parts of the state one or more of three changes in environmental conditions occur that affects the farming pattern and pheasant densities: shorter growing seasons (northward), lower soil fertility (in all directions), and unfavorable topography (westward). As a result, farmers in these areas have a cropping pattern which differs from that of southeastern Wisconsin.

One of the first cropping variations has already been discussed: a reduction in the percentage of land area under cultivation (Fig. 7); the east central counties are an exception. Hence the total cropland acreage and acreage of each of the three main crops, is less in the western and northern halves of the state than in the southeast quarter. The difference is made up by higher percentages of land in woods, swamp (usually wooded, in contrast to marsh), and other idle lands. Much of this latter group serves as pasture, with permanent pasture often occupying 35-45 percent of the farmland acreage.

Wisconsin's better pheasant range lies in the glaciated southeastern quarter of the state. Here the topography is flat to gently rolling, soils are fertile, and growing seasons long. This is a region of intensive agriculture with between 60 and 70 percent of the land area under cultivation in a corn-oats-hay crop rotation to support Wisconsin's large dairy herds. In other parts of the state, shorter growing seasons (northward), lower soil fertility (in all directions), and unfavorable topography (westward) affects the farming pattern and contributes to lower pheasant densities.



Within the reduced cropland acreages in the western, central, and northern areas, oats tends to occupy about the same percentage of cropland acreage as it does in the southeast. This percentage tends to act as a hub around which the relative proportions of corn and hay change. Westward with more rugged topography and lower soil fertility, and northward with shorter growing seasons and lower fertility, the percentage of cropland in corn decreases while that in hay increases (Fig. 11). In the far northern counties, less than 10 percent of the limited cultivated land is in corn, much of which is grown for silage. Between 70 and 90 percent of the cultivated acreage is devoted to tame hay.

Distribution of Human Population

The human population distribution in both urban and rural Wisconsin coincides closely with pheasant densities. The six most populous counties (Milwaukee, Dane, Racine, Brown, Winnebago, and Rock), with the exception of Brown, lie within the "Good" and "Very Good" pheasant areas (Fig. 1). The remaining counties in these areas are either among the 15 more populous counties in the state, or are adjacent to one or more of them.

The east central counties along Lake Michigan are also among the more populous counties (Manitowoc, Sheboygan, Brown, and inland Outagamie—all in the top 15). These coincide with the rather large area of "Fair" densities.

The cities of La Crosse, Eau Claire, Chippewa Falls, and Menomonie raise the human populations of several western and northwestern counties to coincide with these in areas of "Fair" pheasant densities. Over the remainder of the state, most of the pheasant-poor areas correspond with areas that are sparsely inhabited.

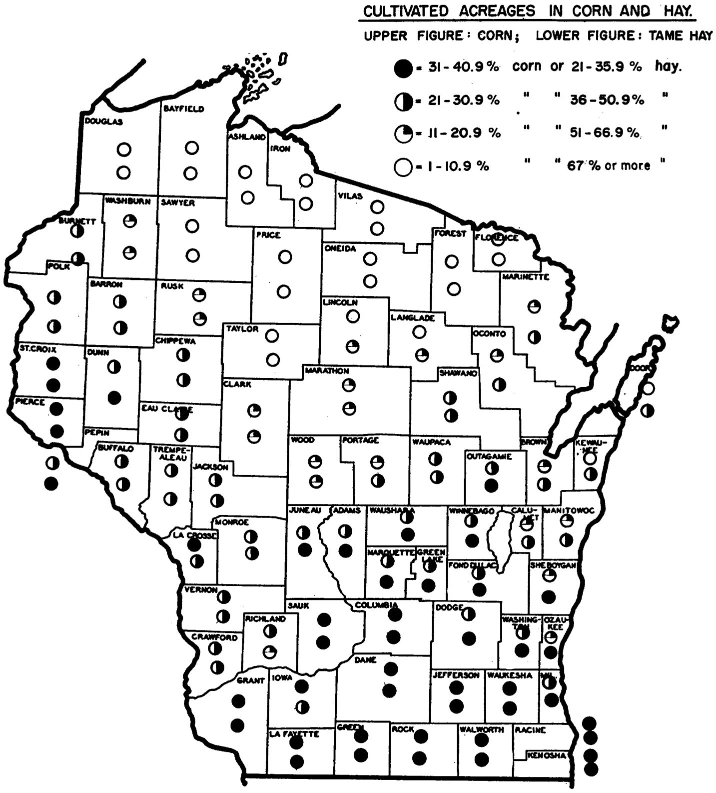


Figure 11. Percentage of cropland in each county planted to corn and tame hay.

Summary

Maps of relative pheasant densities and kill per unit area show "Good" and "Very Good" pheasant densities in southeastern Wisconsin. This region is bisected by a countywide, north-south strip of "Fair-Poor" populations. "Fair" densities occur in most east central counties and a block of west central counties. The southwest, most of the western tier of counties, and the central and northern counties have "Poor-Very Poor" densities.

"Very Good-Fair" density areas are generally underlain by dolomitic limestones and have moderate topography. Lower densities in the southwest and eastern Kettle Moraine area coincide with limestone bedrocks and rugged topography; and in central and northern Wisconsin with sandstones, granites, and basalts.

"Very Good" and "Good" pheasant densities coincide with areas covered by primeval prairies and oak-openings. Most original forest areas have mediocre to poor pheasant populations. Best densities occur on glaciated silt loams. "Fair-Poor" densities exist on lacustrine clays and unglaciated silt loams. "Poor" densities largely occur on sands and gray-loam forest soils.

Pheasant densities are inversely correlated with percentage of land in woodland and positively correlated with percentage of land under cultivation with an optimum range of 55-70 percent cultivated. Above 55 percent cultivation, densities are positively correlated with the percentage of the landscape in wetland.

In the better pheasant areas, corn, oats, and hay occupy about equal proportions of the cultivated lands. In poorer areas, cultivated acreages occupy less and pastureland more of the landscape. Within the lesser cultivated acreage, oats maintains about the same proportion as in the southeast, but corn occupies less and hay more of the remainder. The greatest percentage of corn is grown for grain in the southeast; more is grown for silage elsewhere in the state.

A rough correlation exists between pheasant densities and the distribution of human populations.

CHAPTER II. SOURCES OF POPULATION DATA FROM THE FIELD

Brood Observations

Methods

The brood count techniques used in this study have been similar to those used in other states. An observer cruises roads in pheasant range in early morning or late evening. Morning observations are usually begun about sunrise and continue 2 or 3 hours, or as long as the broods are active and remain visible. When a brood is spotted, the observer stops his car and studies it with binoculars. The age of the brood is estimated according to the criteria given in Appendix A. The number of chicks in the brood is recorded as well as the observer's opinion as to whether or not all chicks were observed. Wherever possible, he flushes the brood in an attempt to obtain a complete count of the chicks. Broods are also considered completely counted when they stand in or walk past openings such as mowed hayfields, road shoulders, plowed fields, etc.

Our brood data come from two principal sources. Intensive observations were begun on four selected study areas by research biologists in 1946 and were continued up to 1957. Observers made repeated trips into the study areas during the brood season, in some cases weekly or oftener. On these mornings, observations were made from random cruising by automobile with an effort made to see as many broods as possible.

Extensive observations, the second source of brood data, have been made yearly by game management personnel of the Conservation Department throughout the state's pheasant range. Roughly three-fourths of these observations have come from the 19 southeastern counties, the state's primary pheasant range. Many of these are random observations made during the regular performance of the game managers' duties. However, many observations from the better pheasant counties have stemmed from early morning trips made expressly for brood observations. Some men have run special brood transects each year.

In the early years of brood observations, the study area data greatly outnumbered the extensive observations. But since about 1950, the extensive data have made up the majority of the observations.

In interpreting the results, we have attempted to set up indices of reproductive success with (1) brood sizes constituting indices of numbers of young raised per successful female; and (2) percentages of hens accompanying broods serving as indices of success in bringing off broods. Ages of broods backdated to date of hatch have provided information on phenology of the hatching seasons for the different years. We have not used the brood data for arriving at indices of population levels by calculating the results on a broods- or birds-per-unit-distance basis.

On the whole, the observations seem to be quite reliable. Average brood sizes for the extensive and intensive observations have followed parallel changes from year to year. Also, brood sizes compare favorably between the two methods with the averages seldom varying more than one- or two-tenths of a chick.

Likewise, brood aging appears to be reasonably accurate. This stems from a combination of supplying the observers with sheets containing the age criteria mentioned above, and from the fact that most of the observers had been involved in the stocking of known-age game-farm birds and/or birds reared by sportsmen's clubs. As with brood sizes, the average hatching dates from both extensive and intensive studies have compared favorably.

Study Areas

In 1946, intensive observations were begun by game research personnel on two areas in the vicinity of Madison. The University Bay area is a portion of the University campus and is a refuge. Its 550 acres of land area consist of mixed agricultural land, marshes, undisturbed weedy fields, and a park and picnic area with brush, woods, and open grass cover. The area is bounded on three sides by residential and business districts and by the University campus, and on a fourth side by Lake Mendota. The pheasant population is fairly well isolated into an island of birds. Between 1940-41 and 1948-49, winter drive-count censuses produced between 100 and 250 pheasant observations on this area (R.A.McCabe, pers.comm.).

The 1,200-acre University Arboretum on the south edge of Madison, also a refuge, is an area of natural vegetation—partly marsh, woodland, and prairie. The Arboretum is not farmed. However, some corn was grown on lands immediately adjacent to the east marsh area until the mid-1950's. Since the natural succession has been allowed to proceed on the Arboretum, the area has grown up to extremely dense cover. Some marsh and brush areas are nearly impenetrable. Although the Arboretum is bounded on the north, east, and west by portions of the city, to the south it is bounded by rural areas which constitute portions of the mediocre pheasant range of south central Dane County. Its population is probably not an entirely self-contained one, and McCabe (1949) surmised that there is an interplay between the Arboretum pheasants and those of adjacent areas. Winter drive counts on this area between 1937 and 1954 produced from 100 to 400 birds.

The University Bay area and Arboretum were considered excellent pheasant areas by Wisconsin standards through the early 1950's. Pheasant populations on both areas have since decreased with increasing urban disturbance and loss of agriculture in the immediate vicinity. Pheasant brood observations were continued on these two areas through 1951.

In 1947, intensive observations were begun in Milwaukee County. Rural and slowly expanding residential areas around the fringes of the city of Milwaukee apparently provided excellent conditions for pheasants. Moderate agriculture, county parks, and idle weedy fields comprised the bulk of the range. The pheasant populations were at high levels in the 1930's and 1940's, began to decrease significantly by the mid-1950's and have since greatly decreased with intensified urbanization. Discharge of firearms is prohibited in the county, but a very light pheasant harvest has been achieved through an annual 2-to-6-month bow and arrow season on either sex. Brood and sex ratio observations were made over most of the range in the county up to 1957. The range here is contiguous with a region of high populations in Racine and Kenosha Counties to the south. Year-to-year population changes in Racine and Kenosha Counties generally follow those of the main portions of the pheasant range. We believe that the Milwaukee County populations coincide with these trends to some extent, although we have had no population indices to measure changes. As will be shown later, changes in reproductive success and phenology in Milwaukee County follow the statewide trends with some consistency.

The southern part of Green County served as a fourth study area. This area contains good pheasant habitat but is bordered on the north, east, and west by mediocre range. Pheasant populations were consistently high until the mid-1950's. It is an area of intensive agriculture. Between 20 and 25 percent of the land area is in corn every year, another 25-40 percent is in pasture. Tame hay and small grains each occupy another 15-20 percent. There is only fragmentary winter cover. Annual changes in population level and reproductive success in this county parallel those in the main pheasant range, although the long-term trends in Green County seem to have been gradually downward. Intensive observations of pheasants in this area were made from 1948 to 1957.

The locations of the various study areas are shown in Figure 12.

Winter Sex Ratio Observations

Methods

The majority of our winter sex ratios were made by tallying cocks and hens seen from cars while the observer cruised through pheasant range. Some data were obtained from drive counts made in pheasant habitat by crews of men systematically "beating out" pockets of cover. As with brood observations, the sex ratio data were compiled both by research personnel and game managers.

Variables in the Data

We used winter sex ratios in this report to estimate population parameters and calculate indices of trend: (1) estimating hens per unit area in spring and percentage of cocks taken during the hunting season and (2) correcting crowing count censuses and cock age ratios for indices of breeding population level and reproductive success.

Because we have made extensive use of these data, it is per-

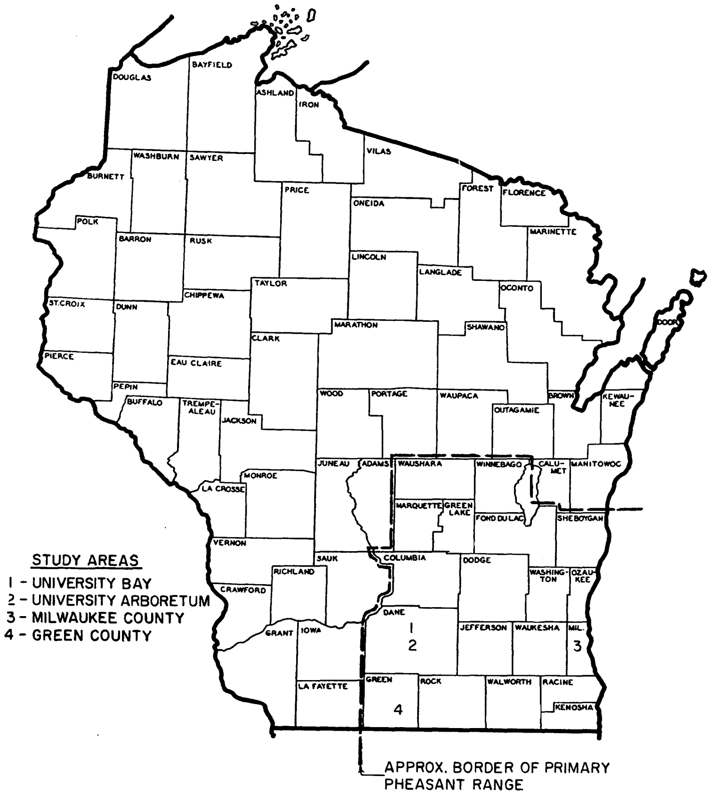


Figure 12. Locations of intensive brood-observation study areas. Also shown is the block of 19 southeastern counties which comprise the primary pheasant range in Wisconsin. The estimated kill in each of 13 of these counties exceeded 15,000 in 1955, and in 8 it exceeded 20,000. This block of counties has produced roughly three-fourths of the statewide or extensive brood-observation data.

tinent to consider the variables involved. Probably the most serious variable besetting accurate estimation of winter sex ratios is the differential behavior of the two sexes. While all degrees of intermixing of the sexes are evident in winter, the cocks tend to segregate, often in small groups or as singles, from the larger, predominantly hen flocks (reported by Wight, 1945:143; Linduska, 1947; Mohler, 1953; not observed by Robertson, 1958:19). The extent to which this tendency influences the data may depend on the method of observation, the weather, and the portion of the winter during which counts are made.

Effect of Method of Observation

The differential behavior of the sexes can influence the relative merits of the methods for obtaining observations in at least two ways. The first way, suggested by Mohler (1953), Stokes (1954:84) and others, depends on how well observations are randomized. Any type of count which tends to seek out concentrations may be biased toward hens because of their prevalence in large flocks. This bias would be most likely to influence the drive counts which frequently are made in larger cover areas known to be frequented by numbers of wintering birds. Such counts may miss the small, upland cover fragments and fencerows which often conceal isolated cocks.

The second way lies in the fact that cocks are more prone to run and hide. Hens are more likely to flush when approached (Leedy and Hicks, 1945:61; Stokes, 1954:83; and others). This behavior would also tend to bias drive counts in favor of the hens.

In Table 1 we have assembled several sets of Wisconsin sex-ratio data wherein results from roadside and drive counts can be compared. These show a higher proportion of hens (significant at .01 probability level by chi-square) in the drive-count results than in the roadside observations, probably due at least in part to the two sources of bias discussed above. Similar results have been reported by Stokes (1954:83) and Mohler (1959:57).

For these reasons, we prefer the roadside counts, and these have been the main source of the Wisconsin data. Cocks, like hens, are forced to move between cover and feeding areas, and are thus susceptible of being seen.

Effect of Weather

Studies by MacMullan (1960) show a strong correlation between pheasant observability and snow depth, a generally recognized relationship. But more important as a sex ratio variable, the increase in observability with snow depth is not proportionate between the sexes. Observability of hens increases more markedly with snow depth than does that of cocks, and the result is an increase in sex ratio (number of hens per cock) with increase in snow depth.

Our data suggest similar results. During the winter of 1953-54 we made observations on a large cornfield at University Bay. The observer circled the field by car and scanned it with binoculars at periodic stopping points. Despite the intensive scrutiny, hens apparently were missed when there was no snow (Table 2).

TABLE 1

Effect of Method of Observation on Observed Sex Ratios

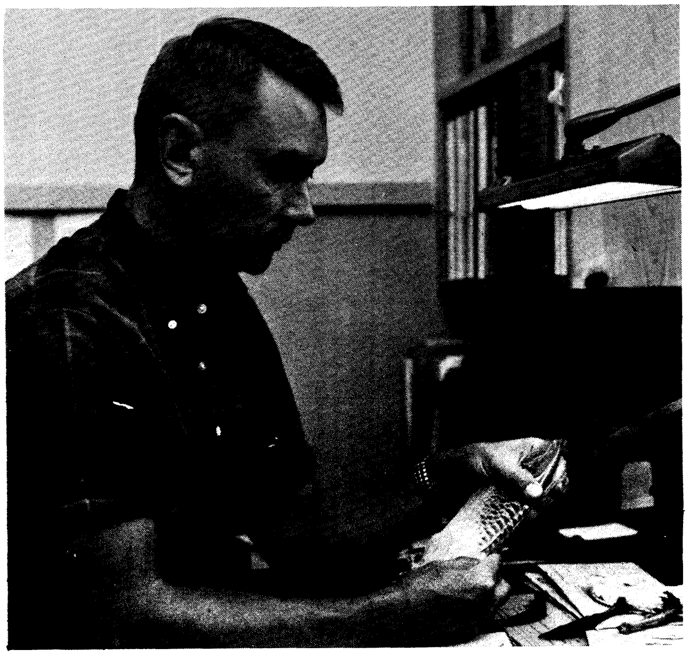
		Roadside Observations		Drive Counts	
County	Winter	No. Birds	Hens/ Cock	No. Birds	Hens/ Cock
Dodge	1952-53	364	7.7	87	7.7
Green	1952-53	445	7.4	130	15.3
Dane	1952-53	212	5.1	228	5.7
Dane	1953-54	179	6.5	170	7.5
Dodge*	1956-57	162	0.5	780	1.9
Unweighted mean			3.2**		5.3†

*Taken on the Horicon National Wildlife Refuge.

**Ratios and their equivalent percentages do not vary proportionately, the former increasing at a faster rate than the latter. An average of ratios is distorted accordingly. In this and all subsequent cases in this report where ratios are averaged they are converted to percentages first, averaged, and then changed back to ratio form.

†Different at the .01 probability level by chi-square test.

Winter sex ratio observations, spring crowing counts, summer brood observations, and fall age ratios in the harvest are used to estimate population parameters and calculate indices of population levels. These data, gathered annually by research and management personnel throughout the pheasant range, are used to set hunting seasons and fully utilize the pheasant resource.



MacMullan's (1960) data indicate that the relationship between snow depth and observability of hens, and consequently the effect on sex ratios, appears to be strongest in the range between no snow and 2-4 inches. Once the ground is covered with 4-6 inches, the relationship weakens, and added snow does not increase the observed sex ratios as much. Lemke (1953) reported a limited amount of data from Wisconsin which suggest that once snow reaches great enough depths at which visibility of hens is no longer a serious problem, weather may at times have an inverse effect on sex ratios. He noted a tendency for the observed proportion of cocks to increase as the weather became more severe in unshot Milwaukee County during the winter of 1951-52, and over the range at large during the winter of 1952-53 (Table 3). Data were collected under two subjective types of weather conditions — "mild to moderate" and "moderate to severe" — depending on the observer's judgment of snow depth and temperature. Chi-square tests show no difference between the Milwaukee County samples, but a highly significant difference between the statewide samples.

TABLE 2

Effect of Snow Cover on Observed Sex Ratios at University Bay, 1954

Snowless Conditions				Ground Covered with Snow			
Date	Cocks	Hens	Hens/ Cock	Date	Cocks	Hens	Hens/ Cock
Jan. 24	59	17		Jan. 30	39	38	
Feb. 21	13	2		Jan. 31	29	38	
Feb. 22	34	23					
Feb. 27	39	22					
Total	145	64	0.4		68	76	1.1**

**Different at the .01 probability level by chi-square test.

The explanation of this relationship, if it exists, may again lie in the differential behavior of the sexes. The intolerance of the cocks, and their tendency to segregate, may be damped when conditions become severe. They may be more prone to either join the larger aggregations in search of protective cover and food or to meet the hens at sites containing good food and cover.

Weather may thus operate on observed sex ratios in more than one direction. But as MacMullan (1960) pointed out, a great deal more information is needed before the degree of influence can be accurately assessed, and data corrected.

Effect of Observation Period

Several writers have observed a progressive increase in the proportion of cocks seen between February and May. Buss (1946:54) ascribed this to the possibility of a differential loss of hens. However, Linduska (1947) and Hickey (1955:349) have suggested that this is more likely a result of increasingly conspicuous behavior of cocks as they come into breeding condition. We agree with the latter interpretation. Cocks may be seen conspicuously along roadsides toward the end of winter, sometimes engaged in territorial battles and oblivious to passing traffic.

For this reason, and because of the difficulty in seeing hens when the ground is snowless, we feel as did Robertson (1958:40) that spring sex ratios do not accurately represent population values. We arbitrarily terminated all sex ratio observations on March 1 in order to avoid this bias as much as possible. Only those data gathered before this date are used in this report.

Our winter sex ratio data were taken similarly each year, by the same group of people, and in the same general areas. Year-to-year changes in these ratios have occurred with some uniformity in different parts of the state and they also vary regionally in a consistent pattern because of certain population and hunting pressure relationships shown later. Thus, we conclude that the variables involved in winter sex ratio observations do not invalidate their use as indices of yearly trends and for use in crowing count and productivity indices. The use of winter sex ratios in approximating the percentage of cocks taken during the fall hunting season is discussed in the next chapter.

TABLE 3

Effect of Severity of Weather on Observed Sex Ratios

		Mild to Moderate Weather		Moderate to Severe Weather	
Area	Winter	No. Birds	Hens/ Cock	No. Birds	Hens/ Cock
Milwaukee Co.	1951-52	1600	0.8	992	0.7
Range at Large	1952-53	2850	6.5	1031	4.2**

**Different at the .01 probability level by chi-square test.

Spring Crowing Count Census

Methods

Spring crowing counts run annually on prescribed transects were begun on a small scale in 1949 with three routes. In 1950 this was expanded to 23 routes, and since that year the total number of routes has gradually been increased to 35 (Fig. 13). The number run in any one year during this period has varied from 23-32.

The routes are run in a manner similar to that used elsewhere, and first described by Kimball (1949). The observer begins a route at ½ hour before sunrise, stops every mile, and counts the total number of calls heard at each stop for 2 minutes. Most routes are 15 miles in length, run only in good weather, and only once a year between April 28 and May 10.

The average number of calls per stop for each transect is multipled by the number of hens per cock observed the previous winter in that county or block of ecologically similar counties. The results give a spring hen index.

Use of Crowing Counts as Population Indices

When an index of breeding population level is needed, some index which takes the hens into account is essential. The crowing cock count alone is not sufficient (Dale, 1952) for two reasons. First, the number of young a given pheasant population is potentially capable of producing is entirely a matter of the number of hens present in spring, and bears no relationship to the number of crowing cocks, provided a small remnant is available to breed the hens.

Secondly, most of the cocks are shot each fall in Wisconsin, as we shall see shortly. Consequently they constitute a small fraction of the spring population and a smaller segment of subsequent fall numbers which are made up largely of young

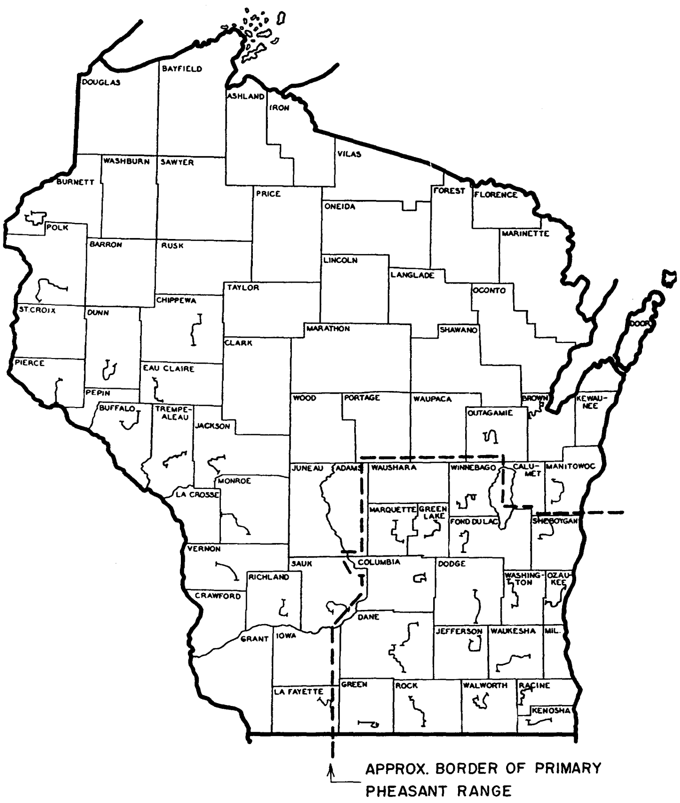


Figure 13. Spring crowing count routes run annually in Wisconsin.

of the year. Hence, fall numbers are largely a function of the spring hen populations and their reproductive success during the breeding season.

An example of this can be seen in our crowing count results (Fig. 14). Crowing cock and hen indices are given on a relative scale using the 1950 results as a starting point of 100. The trend between any 2 years is based only on transects run in both years. The results show that the spring cock populations declined during the middle 1950's, probably due to gradual increase in hunting season lengths. Meanwhile the hen indices increased, evidently reflecting the population increase that occurred over the state as shown by kill estimates and other indices. During the last two years of the series, the crowing cock index rose. This was probably due to sharp restrictions in hunting season length which were put into effect because of the population decline that occurred in 1959, and which is reflected in the relatively low hen indices of 1960 and 1961.

Since the routes are run only once in Wisconsin, we have no chance to evaluate within-route variation. Each year we incur the risk of running the routes on phenologically different dates, and not holding constant the phase of the seasonal crowing curve at which the counts are made. Hence, we feel that the technique, as used in Wisconsin, can not be used as a delicate index of the trend between any two years. It can, however, serve as a rough index of population level, and is used in this way in this report.

Cock Age Ratios in the Bag

Methods

Prior to the hunting seasons of 1953 through 1959, we sent out postage-free return envelopes to known pheasant hunters in connection with another study (Besadny, 1956). The hunters were asked to send in legs of pheasant roosters they shot during the season. The spurs were used as criteria for determining ages of wild-reared birds, and these provided the basis for cock age-ratio data in these years.

Problems in Age Criteria

The problem of using the spur as an age criterion has been widely discussed by other workers. In the first years after the technique was put into use, age was determined by the "age gauge" (Kimball, 1944). However, because the juvenile legs are still growing as the hunting season progresses, an increasing proportion of juveniles are shown as adults by the gauge (Trautman, 1955; Kimball, Kozicky, and Nelson, 1956:249). Variations in size of pheasants in different states pose another problem; and, as Kimball *et al.* (1956) caution, the gauge is probably not applicable in all areas.

Because of these problems, and because the age can be told with reasonable accuracy by the appearance of the spur (Trautman, 1955), workers in South Dakota (E. H. Smith, pers. comm.), Michigan (Eberhardt and Blouch, 1955), and other states have abandoned use of the gauge. We too have adopted the practice of visually separating juvenile from adult pheasants according to the characteristics of the spur described by Trautman.

This visual method is also subject to minor errors. But here again, where the age ratio is only needed as an index of year-to-year trend in breeding success, minor biases do not prevent its use as long as the bias is comparable between years. To prevent any yearly variation in errors of personal judgment, all pheasant legs were examined by C. D. Besadny during the period covered in our study.

Cock age ratios are subject to a number of serious sampling variables which must be taken into account. These problems are discussed in detail in Chapter VII.

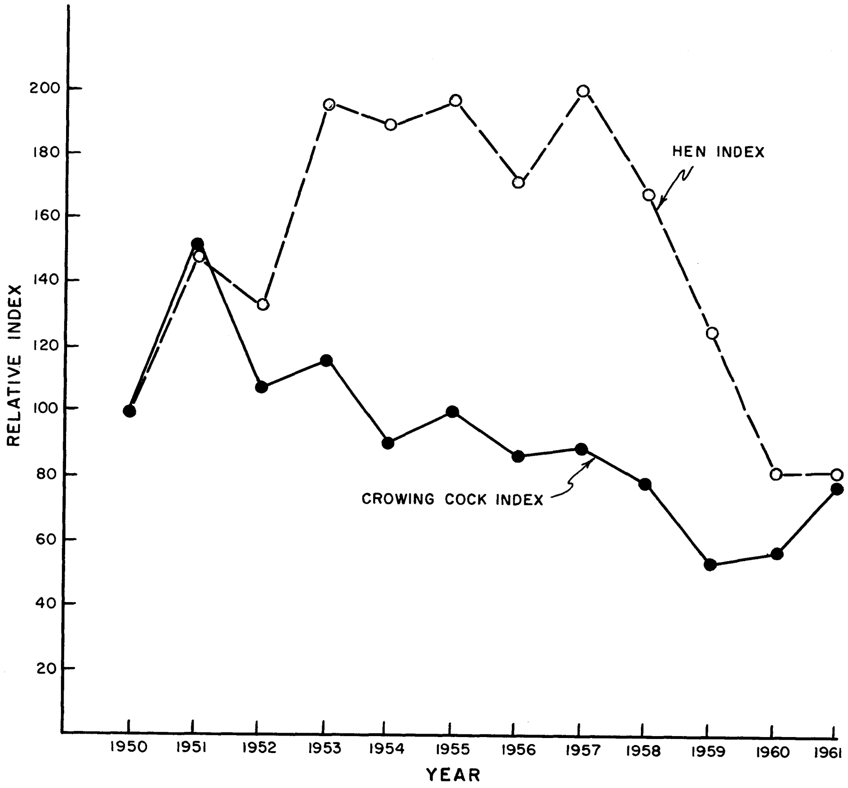


Figure 14. Comparison of density trends shown by the crowing cock count and the hen index derived from the product of the crowing count and winter sex ratios.

Summary

Early morning brood counts along roadsides were made by research personnel between 1946 and 1957 on four study areas—in University Bay and in the University Arboretum on the edge of Madison, in southern Green County, and in Milwaukee County—and by game management personnel over the entire state from 1946 to 1961. The data have been used for annual indices of reproductive success.

Winter sex-ratio observations have been made over the state both by research and management personnel. Because roadside observations—the principal source of the data—are more randomized, they appear to be superior to drive counts in blocks of cover. The latter also tend to be biased toward the hens. Weather seems to influence observed sex ratios in several ways, but as yet we do not have enough information to allow any corrections to be made on the data available. Observed percentage of cocks increases between February and May, probably because of their increasingly conspicious behavior. All Wisconsin observations have been terminated on March 1 to avoid this bias as much as possible.

In Wisconsin, 35 spring crowing-count transects, mostly 15 miles in length, have been used. They are run in good weather between April 28 and May 10, and each route is run only once in a given year. They are corrected with winter sex ratios which provide a hen index that gives a measure of the effective breeding population. Trends in crowing cock counts, uncorrected, may bear little or no relationship to the hen indices. As used in Wisconsin, this technique provides a rough index of the breeding population level.

Collections of pheasant legs between 1953 and 1959 from hunters have been used to provide cock age-ratio data. Age has been determined by visual inspection of the spur.

CHAPTER III. KILL ESTIMATES AS INDICES OF FALL POPULATION TRENDS

Between 1932 and 1960, a kill report card (Fig. 15) was attached to every Wisconsin hunting license. State law required that every hunter fill out and return his card after the hunting season whether or not he was successful. Technically, hunters who did not send in their cards could have been denied a license the following year. In practice this was not enforced, and the method resolved itself into essentially a voluntary system.

These cards served as the basis for a sampling system. Average kill of each species per hunter was calculated for the hunters reporting and total kill was then estimated by expanding these averages for the total number of hunters buying licenses.

One of the premises of this report is that the annual estimates of pheasant kill from this method can justifiably be used as indices of change in population level from one fall to the next. The validity of this assumption rests on two conditions: (1) the relationship between the estimated kill and the kill itself; and (2) the relationship between the kill and the population level. Basically, the first condition depends on the degree of sampling error. The second condition depends primarily on the proportion of the population that is shot annually, and on the factors affecting this proportion. These problems are discussed in the sections that follow.

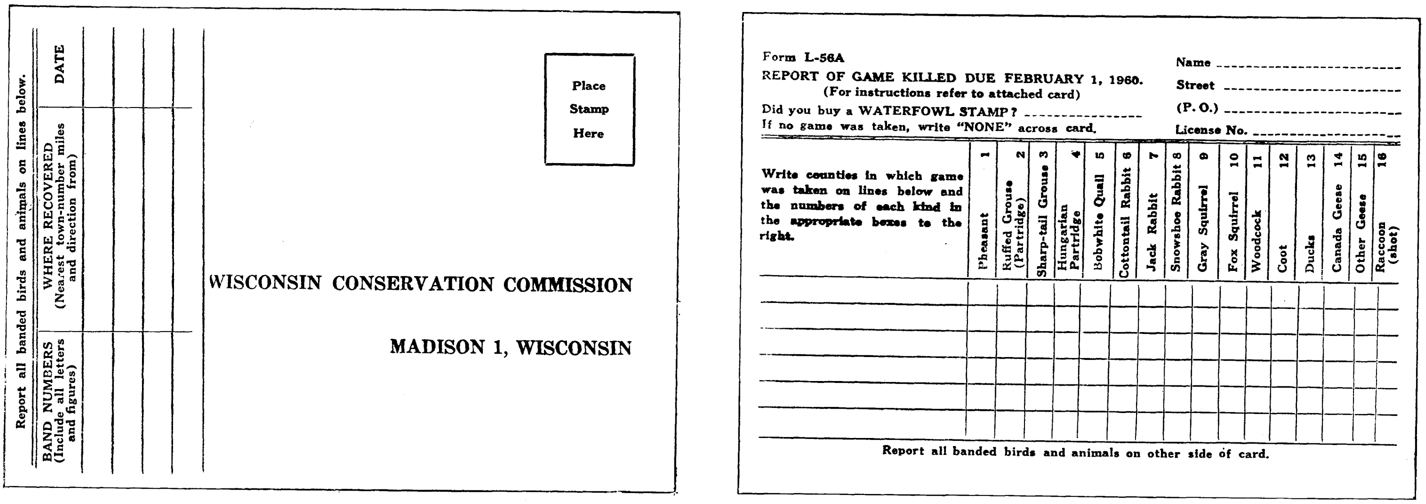
Relationship Between Kill Estimate and Actual Kill

One of the most frequent criticisms of kill estimates such as these is that the sample is not random, the more successful hunters being more prone to report than the less successful. Sondrini (1950) and Marquardt and Scott (1952) concluded that game kill estimates in Connecticut and Illinois, respectively, were inflated by this nonresponse bias. Hayne and Eberhardt (1954) found a similar inflation of Michigan deer-kill estimates. Blouch (1956) found slight evidence of bias in replies to a Michigan questionnaire on pheasant hunting success.

On the other hand, MacMullan (1950) found essentially no evidence of nonresponse bias in two tests of Michigan pheasant-kill estimates. Calhoun (1950) and Atwood (1956) found none in California fishing-take estimates and waterfowl kill estimates, respectively. Hence, nonresponse bias may not be invariably present in this type of estimate.

Thompson (1951, 1952, 1953) obtained estimates of the Wisconsin pheasant kill which were independent of the annual "compulsory" report method. Game kill questionnaires were mailed to a random sample of hunters. Those who did not reply were recontacted a second and third time until replies were received from roughly 90 percent of the original sample.

Comparison of Thompson's estimates with those based on the "compulsory" method (Table 4) suggests that the latter may be biased, the estimates averaging about 11 percent high. That the successful hunters were more prone to report was evidenced by the fact that Thompson (1951) found a higher



Report all banded birds and animals on lines below.

BAND NUMBERS (Include all letters and figures)	WHERE RECOVERED (Nearest town-number miles and direction from)	DATE

Place Stamp Here

WISCONSIN CONSERVATION COMMISSION

MADISON 1, WISCONSIN

Form L-56A

REPORT OF GAME KILLED DUE FEBRUARY 1, 1960.
(For instructions refer to attached card)

Did you buy a WATERFOWL STAMP? ________________

If no game was taken, write "NONE" across card.

Name ________________

Street ________________

(P. O.) ________________

License No. ________________

Write counties in which game was taken on lines below and the numbers of each kind in the appropriate boxes to the right.	Pheasant 1	Ruffed Grouse (Partridge) 2	Sharp-tail Grouse 3	Hungarian Partridge 4	Bobwhite Quail 5	Cottontail Rabbit 6	Jack Rabbit 7	Snowshoe Rabbit 8	Gray Squirrel 9	Fox Squirrel 10	Woodcock 11	Coot 12	Ducks 13	Canada Geese 14	Other Geese 15	Raccoon (shot) 16

Report all banded birds and animals on other side of card.

Figure 15. Between 1932 and 1960, a kill report card like the one shown was attached as a stub to every Wisconsin hunting license.

reported success on his first mailing than on the second and third. In another postseason questionnaire to pheasant hunters sent out for a different purpose (Wagner, 1955), we also found that the average success of hunters responding to a first mailing was higher than that of second-mailing respondents.

TABLE 4

Comparison of Annual Game Division Pheasant Kill Estimate With Special Survey Conducted by D. R. Thompson*

Year	Ann. Game Div. Estimate	Thompson's Kill Estimate	Difference	Percent Difference
1950	414,487	386,900	27,587	− 6.7
1951	466,357	348,600	117,757	−25.3
1952	486,589	481,000	5,589	− 1.1
Total	1,367,433	1,216,500	150,933	−11.0

*See Thompson 1951, 1952, 1953.

Lemke, Thompson and Bersing (1958) pointed out that the percentage of hunters returning cards in Wisconsin has declined steadily through the years—from 40-80 percent of license buyers in the first few years the system was used to about 8 percent in the latter 1950's. This decline gives rise to the possibility of a progressive increase in the extent of bias, and hence an increasing inflation of the kill throughout the period.

Lemke *et al.* (1958) also pointed out a complication of the nonresponse bias which may be unique to Wisconsin. In this state there are two types of resident, small-game hunting licenses: (1) a sportsman's license which includes fishing, small game and big game hunting, and trapping privileges; and (2) the regular small game license. Sportsman's license buyers shoot more pheasants, on the average, and return a higher percentage of report cards than small game license buyers. The difference between the return rates of the two types of licensees has varied between years. But the percentage reporting has generally declined faster among the small game licensees. These changes have produced an annually varying, but generally increasing, bias in the estimated kill.

Between 1949 (the earliest year that tabulations permit an estimate of this bias) and 1956, the inflation resulting from it has varied roughly between 3 and 6 percent (C. W. Lemke, unpubl.). Since it is not possible to make similar corrections for kill estimates prior to 1949, and since earlier values are needed in this report, we have not used the corrections for the years 1949-56 in order to keep them somewhat comparable with the earlier values. A 3-6 percent error seemed tolerable for this short period.

However, in 1957 the bias rose above 10 percent. We have therefore used kill estimates with Lemke's correction for the disparate return rates of the two groups of licensees in 1957-59.

In 1960, the "compulsory" license-stub system was abandoned in favor of a mailed questionnaire which had also been used in 1959 concurrent with the "compulsory" system. In order to calculate a value for 1960 comparable with the estimates of previous years, we determined the percentage change between 1959 and 1960 (−3.1 percent) in the new estimates derived from mailed questionnaires. We then used the regular 1959 estimate, with the sportsman's license correction, and deducted 3.1 percent.

Three other sources of bias are possible, and these would not be detected merely by comparing kill estimates calculated from two different questionnaire methods. Any post season questionnaire sampling method, regardless of how well randomized, could be subject to these. They are: (1) memory bias in which the hunter does not remember what he shot and records his kill incorrectly; (2) prestige bias in which a hunter consciously or unconsciously exaggerates his kill; and (3) party bias in which two hunters report shooting the same game, either because they both shot at and killed the same animals, or because one hunter helped another in filling his limit and both reported the same animals. The first two of these have been implicated in the inflation of kill estimates in California (Hjersman, 1951) and Illinois (Marquardt and Scott, 1952), and of waterfowl kill estimates (Atwood, 1956). Paul J. Moore (pers. comm.) concluded that the third (party bias) is an important source of error in pheasant kill estimates in Ohio and Illinois.

We have no information on the present extent of these additional biases in the Wisconsin kill estimates. However, one possible clue may be obtained by estimating the kill from data completely independent of hunter questionnaires. Approximately 50 percent of the 114,068 pen-reared cocks stocked in the state in 1954 were shot during the hunting season (Besadny, 1956). These cocks constituted 15.5 percent of the statewide pheasant kill that year. Expanding these data to obtain the unknown statewide kill, we obtain 367,936 cocks which is 27 percent below the regular Department kill estimate of 504,723 for 1954. The validity of this new estimate depends on the correctness of the 15.5 percent value and the 50 percent recovery rate.

In summary, two independent estimates of the pheasant kill suggest that it may be somewhere between 11 and 27 percent below our annual estimates. Nonresponse bias may be responsible for the lower of these values, and any additional error may be due to one or more of the three remaining biases listed above.

However, the presence of bias does not necessarily rule out the use of kill estimates as indices of year-to-year population trends. This is possible if the degree of bias does not vary seriously between any two consecutive years; or as Hayne and Eberhardt (1954) put it, if "... the computed estimate is some fairly constant, though unknown, multiple of the true value." They presented evidence that showed this multiple of the Michigan Upper Peninsula deer kill varied by more than 100 percent over a 15-year period. However, the difference between any two consecutive years was relatively small.

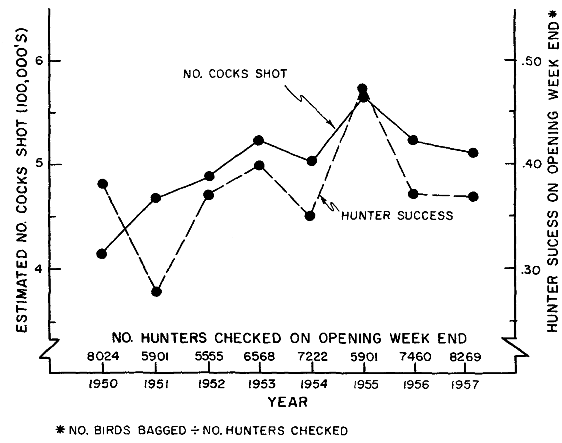


Figure 16. Comparison of trends shown by season-long kill estimates and hunter success checks made on opening week end of the pheasant hunting season. Checks are made by district game managers on Conservation Department public hunting grounds.

One suggestion that this may be the case in the Wisconsin kill estimates is provided by comparing them with information on opening weekend hunter success obtained by game managers on Department public hunting grounds (Fig. 16). During the 1950-57 period in which hunter-check data were compiled, the trends in the two indices differed sharply between only one pair of years. However, a correlation test of the two series gave a correlation coefficient of 0.487 that is not statistically significant.

Relationship Between Kill and Population Level

Proportion of Cocks Harvested Annually

If the kill is to serve as a reliable population index, it must bear some relatively constant relationship to the population. If the proportion of pheasants shot each year varied greatly, it would be possible for the kill to vary without any change in population level; and the population level could vary without any change in the kill.

At least in the more heavily hunted states, the pheasant is unique among game birds in annually sustaining a kill of the majority of legal birds available to the hunter. Hence, the kill is potentially a more reliable population index in this species than in any other game bird.

Two sources of data provide evidence of the proportion of cocks shot in Wisconsin. The first is winter sex ratios (Table 5). These have varied between 3.0 and 7.5 hens per cock, and have averaged 4.6.

The .05 confidence limits on these sex ratios range between 9 percent of the ratio with the smallest sample (1960-61) and 2 percent of the ratio with the largest sample (1940-41). We have not supplied these limits for each value in Table 5, however, because the biases involved undoubtedly exceed these limits to a considerable extent. One of the more obvious of these involves annual variations in the weight of samples from different levels of pheasant density. Sex ratios vary with pheasant density, and when sampling of different areas is not proportional between years (as between 1940-42 and the later years), they become less comparable. For these reasons, our sex ratios are obviously crude, and attempts at calculating percentage of cocks shot from them can only be considered as approximations.

Furthermore, the percentage of cocks shot cannot be calculated exactly from the sex ratios because of the lack of two needed statistics: prehunting-season sex ratios, and either the percentage of hens shot or the ratio of cocks shot to hens shot (Petrides, 1954; Selleck and Hart, 1957). However, the order of magnitude of these two values can be estimated from other information, and an attempt made by the method of Petrides at approximating the percentage of cocks shot.

Stokes (1954:87) showed that, with average reproductive success, prehunting-season sex ratios are about 1.36 hens per cock with an adult sex ratio of 5 hens per cock. Adult sex ratios as high as 10 or as low as 2 hens per cock only change this value to 1.43 and 1.20, respectively. We have arbitrarily used 5.1 as the adult sex ratio (because most years approximate this (Table 5), and no year has deviated by more than 2.5 hens), and consequently 1.36 as the preseason ratio.

Also, the percentage of hens shot in heavily hunted Ohio has approximated 22 percent (calculated from figures by Leedy and Hicks, 1945:82), while that in less heavily hunted South Dakota has ranged somewhere between 8 and 10 (S. Dak. Dept. Game, Fish and Parks, 1953). We have conservatively assumed a 10 percent hen loss for Wisconsin for the purposes of the present calculations.

Our method of estimating percentage harvest was to increase the number of hens per cock for each year in Table 5 by 10 percent to provide for hen loss. The resultant ratios and the assumed 1.36 preseason ratio were then used in the first method of Petrides' (1954) paper. They yielded the estimated percentages of cocks shot in the last column of Table 5.

The estimated percentages have varied between 59 and 84, and averaged 73. While they probably are conservative because of our assumptions, these percentages show the general order of magnitude and the range of variation between years.

The second source of evidence on the proportion of cocks shot is cock age ratios found in hunting season bag checks and collections of legs obtained through the mail from hunters (Table 6). These samples show an average cock age ratio of 11.2 young per adult.

Stokes (1954:76) showed that cock age ratios are importantly influenced by adult sex ratios. By interpolation from his Table 47 cock age ratios of 11.2 young per adult in the bag imply a breeding-adult sex ratio of about 6 hens per cock. These age ratios are somewhat higher than the population ratios because of differential vulnerability of juveniles to hunting (Chapter VI); and hence the implied sex ratio is inflated. The result seems to be an implied sex ratio at least approaching the order of magnitude of that shown by the actual sex ratio observations (Table 5).

It follows from these calculations that the majority of cocks in Wisconsin are shot each year. No pronounced change in the pheasant population level could occur without a parallel change in the kill in most years.

TABLE 5

Wisconsin Winter Sex Ratios and Estimated Percentages of Cocks Shot, 1940-61

Winter	Hens Per Cock	No. Birds Observed	Est. Percent of Cocks Shot
1940-41*	4.5	76,779	73
1941-42*	3.8	35,245	68
1950-51	3.5	19,052	65
1951-52	4.6	4,525	73
1952-53	6.1	6,836	80
1953-54	6.2	4,105	80
1954-55	5.4	5,310	77
1955-56	5.2	6,321	76
1956-57	4.8	3,859	74
1957-58	5.9	8,461	80
1958-59	7.5	13,142	84
1959-60	3.3	5,990	62
1960-61	3.0	3,541	59
Unweighted mean	4.6		73

*From Buss (1946:55-56).

TABLE 6

Cock Age Ratios Obtained from Bag Checks and Leg Collections, 1946-59

Period	Source of Data	Sample	Young Per Adult	Percent Young	95 Percent Confidence Limits
1946-54	Bag checks on 12 areas, largely Dept. public hunting grounds	2,222	8.2	89.1	87.6-90.3
1953	Leg collections, 4 counties	2,714	11.5	92.0	90.9-93.0
1954	Leg collections, 15 counties	6,620	12.8	92.8	92.1-93.5
1955	Leg collections, 18 counties	5,337	21.1	95.5	95.0-96.0
1956	Leg collections, 12 counties	1,669	16.8	94.4	93.2-95.5
1957	Leg collections, 12 counties	1,706	9.1	90.1	88.4-91.5
1958	Leg collections, 13 counties	1,750	7.5	88.2	86.5-89.8
1959	Leg collections, 2 counties	936	12.2	92.4	90.5-94.1
Unweighted mean		—	11.2	91.8	—

Factors Affecting the Proportion of Cocks Shot

Hunting Season Length

The length of pheasant hunting seasons has varied considerably since 1936 (Fig. 17), the earliest year for which we shall use kill estimates in this report. The effect of different hunting season lengths on the percentage of cocks shot (Table 5) is shown in Figure 18. We tested the relationship by transforming the season lengths to their equivalent logarithms and calculating a simple linear correlation coefficient between the logs and the harvest percentages. The resultant 0.815 is significant at the .01 level implying a strong correlation between the logarithm of season length and percentage of cocks shot.

Studies in other states have shown a heavy weighting of the kill in the first few days of the season (*cf.* Leedy and Hicks, 1945:68; Allen, 1947; Shick, 1952:84, Stokes, 1955). The implication from these studies is that additional days added to a minimum 2- or 3-week season contribute few additional birds to the bag. In Wisconsin, our kill is better distributed through the season (Wagner, 1955) and its length has an important influence on the percentage of cocks shot.

From the standpoint of using kill estimates as an index of change from one year to the next, changes in season length can only have an effect between pairs of years in which pronounced changes were made. Pairs of years since 1937 in which pronounced changes were made (1 week or more) were: 1938-39, 1941-42, 1943-44, 1950-51, 1955-56, 1956-57, 1957-58, and 1958-59. The curve in Figure 18 inflects at about 25 days, and changes in season length above 25 days have a minor effect. Hence, of the pairs of years listed above, the trends between all but the seventh pair were likely to have been materially influenced. This would be seven pairs of years affected out of 23.

From the standpoint of using the kill estimate as an index of actual population size, any variations in season length will reduce the refinement of comparisons. The gross configurations of population curves in Wisconsin pheasants should not be influenced, however, because the tendency has been to shorten seasons during population lows, and lengthen them during periods of high populations. This should not mask the general trends, although it probably has had a tendency to magnify the apparent amplitude of fluctuations.

Variations in Pheasant Density

An important sequence of concepts on pheasant population behavior originated with Allen (1942, 1946, 1947) who observed that a given area tends to have a point of diminishing returns below which cocks are difficult for hunters to find, and heavy hunting goes largely unrewarded. When an area has few cocks before hunting begins, only a few can be shot before the point of diminishing returns is reached. The percentage shot is thus relatively low. When there are large numbers of birds before the season, a large number (and a high percentage) can be shot before the point is reached.

Dale (1951) observed that the relatively low percentage harvest occurring at low densities would result in low (slightly distorted) postseason sex ratios. At high densities, percentage harvest and postseason sex ratios would be higher. Hence a relationship should exist between pheasant densities and postseason sex ratios. Dale demonstrated the operation of this principle geographically by showing that the Wisconsin winter sex ratios reported by Buss (1946) were more distorted in the better pheasant counties than in the poorer counties.

With pheasant populations in the state now mapped (Wagner and Besadny, 1958), Dale's principle can be shown more

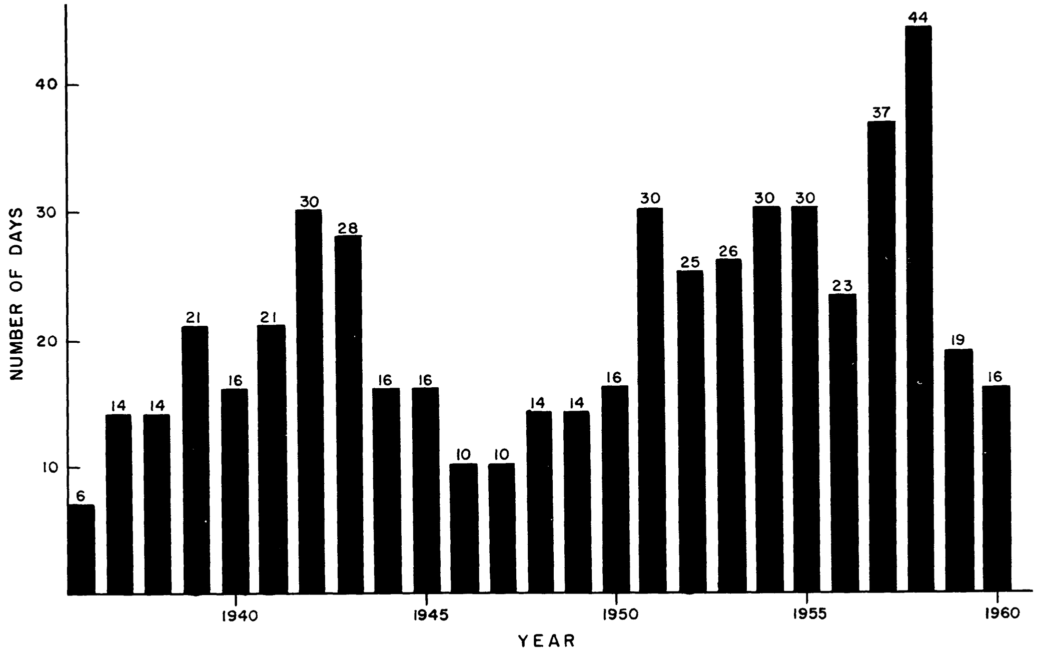


Figure 17. Pheasant hunting season lengths in the Wisconsin pheasant range, 1936-60.

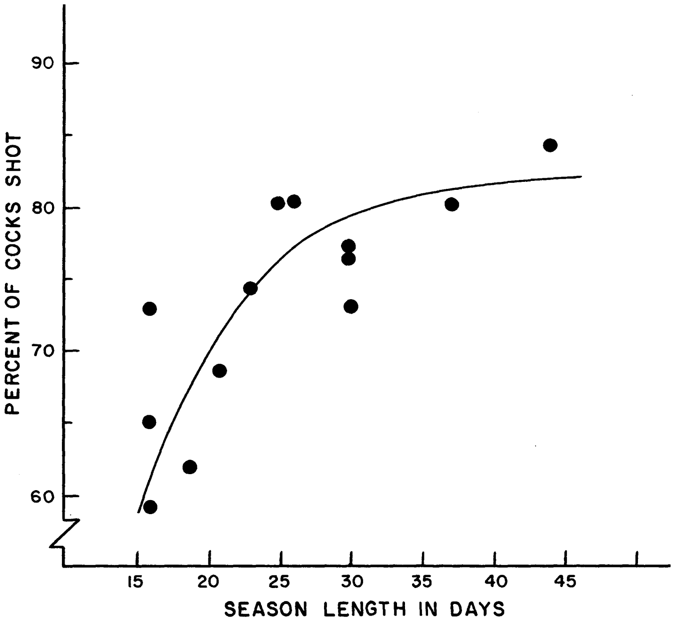


Figure 18. Correlation between hunting season length and percentage of cocks shot. The line was fitted visually.

precisely, both with the older sex ratio data and with those of recent years. These are shown in Table 7 with the data from each county placed in one of the three pheasant population categories shown, depending on its density. We used the ranking method on the 33 individual values in Table 7 and tested these with chi-square (Wilcoxon, 1949). Unless a 1 in 100 sampling mischance has occurred, sex ratios in the "Very Good" areas are higher than those in the "Good" areas, and the ratios in the "Good" areas are higher than those in the "Fair-Poor" areas.

Dale's principle should seemingly operate on a time scale as well as geographically. As a population builds up over a period of years, hunters should be able to take an increasing percentage of cocks, and winter sex ratios should become increasingly distorted. And as a population declines, the reverse should be true.

A thorough test of this hypothesis cannot be made with Wisconsin data because of the important variable of changes in hunting season lengths. One small test can be made by correlating the percentage harvest, as shown by sex ratios, with population level shown by kill (Fig. 19) for 5 years during which hunting season lengths fell in a limited range of 16-21 days. The correlation coefficient of 0.730 is suggestive but not statistically significant. A similar test of 6 years in which season length fell in the range of 25-37 days showed no suggestion of a trend. However the kill during these years only varied between 466,000 and 564,000 in contrast to the more-than-two-fold variation in the years covered in Figure 19.

Annual Variations in Hunting Pressure

The number of small game licenses sold in Wisconsin rose from about 242,000 in 1936 to 329,000 in 1941. Following a war-time drop to 287,000 at the lowest, the sales climbed gradually to a high of 476,000 in 1950, and then declined gradually to 344,000 in 1960 (Appendix B).

Where the kill is to be used as an index of actual population level, differences between years having very high and very low numbers of hunters could conceivably influence the percentage of cocks shot. The only evidence of any kind available is the sex ratios in Table 7.

Differences between the 1940-42 and 1948-57 ratios were tested by chi-square. Sampling in the two early years was weighted disproportionately in favor of the low density areas, and this would have overpowered the test in favor of the ratios in these samples. This heavy weighting of areas with low sex ratios accounted in part for the low statewide 1940-42 ratios in Table 5. In order to compensate for this, we combined all samples in the 1948-57 period, and determined the percentage contribution to this total of the samples from "Fair-Poor" areas. The samples for the 1940-42 "Fair-Poor" areas were then reduced so that they made up the same proportion when combined with the 1940-42 "Very Good" and "Good" samples.

The results indicate that, unless a 1 in 100 sampling mischance has occurred, the combined 1940-42 sex ratios were higher than those of 1948-57, the result being due entirely to the samples from the "Good" areas. If only the "Very Good" and the "Fair-Poor" areas are compared, the ratios for the later years were higher at the .05 level. The difference is not great, and part of this must be due to the 16- and 21-day seasons of the two earlier years compared with the predominantly 23-30-day seasons of the later years. At least on the basis of these data, it appears that the hunting

TABLE 7

Winter Sex Ratios by Pheasant Density Levels, 1940-57

	Hens/Cock in Winter According to Pheasant Density and No. Birds Observed*		
Winter	Very Good*	Good*	Fair-Poor*
1940-41**	10.7 (23,181)	7.3 (17,458)	2.6 (35,926)
1941-42**	4.9 (4,451)	6.4 (8,289)	3.1 (22,505)
Unweighted mean	6.9	6.9	2.8
1948-49	6.8 (1,011)	3.7 (165)	1.4 (55)
1949-50	7.2 (1,055)	3.8 (518)	3.5 (285)
1950-51	3.7 (9,247)	3.1 (6,161)	3.9 (3,644)
1951-52	6.3 (2,094)	3.9 (1,129)	3.6 (1,302)
1952-53	8.7 (1,348)	6.0 (2,353)	5.4 (3,135)
1953-54	11.4 (1,362)	5.2 (1,912)	4.5 (831)
1954-55	7.8 (1,788)	5.0 (2,416)	3.9 (1,106)
1955-56	8.0 (2,206)	4.5 (1,656)	4.0 (2,459)
1956-57	9.0 (841)	5.1 (1,145)	4.0 (1,873)
Unweighted mean	7.1	4.3	3.5

*See Wagner and Besadny (1958)
**From Buss (1946:55-56).

pressure of the early 1940's was sufficient to harvest the birds as thoroughly as they were harvested in the 1950's.

Where the kill is to be used as an index of population trend between pairs of years, pronounced differences in numbers of hunters over a period of 23 years will not be a serious source of error, as long as the change between any two years is not abrupt. The change in Wisconsin license sale between any two consecutive years has mostly been of the order of 10 percent or less. In three years it changed on the order of 20 percent, and in 1946 it increased about 30 percent.

Changes in Bag Limits

Daily bag limits of 2 cocks and a possession limit of 4 were in effect from 1932 through 1958. Beginning in 1959, a daily bag limit of 1 cock and possession limit of 2 for the first two or three days of the season has prevailed. This reduction in the daily bag limit could have influenced the yearly proportion of cocks shot in the past few years.

In 1946 and 1947, an experimental hen season was allowed in nine northwestern counties. However, these are marginal pheasant counties. Their contribution to the total kill is less than 10 percent, and this additional kill could not have greatly biased the total.

Changes in Numbers of Counties Open to Hunting

Our earliest pheasant kill estimates date back to 1932. By 1937, all of the counties in the state were open to pheasant hunting except for the northern forest counties which contribute practically nothing to the total kill. Thus, by 1937 all of the pheasant counties were hunted; kill statistics taken prior to 1937 were not used in this report.

Variations in Hunting Conditions

The timing of corn picking varies between years, and this probably is one of the most important year-to-year variables in hunting conditions. In years with warm summers, adequate rainfall and dry autumns, corn matures and dries early, and picking is advanced. One such year was 1952 when 90 percent of the corn was picked by early November. By contrast, the summer and fall of 1951 were cool and damp. Corn was late in maturing, and early frosts caught much of it not yet dented in the fields. By early November, about half of the corn was still unpicked.

In pheasant areas of such prairie states as Illinois and Iowa, 90 percent or more of the landscape may be under cultivation, and nearly half of the land in corn. Uncultivated areas are scarce, hunting must be largely done on croplands, and cornfields support much of it. In these situations, the status of corn picking may have an important influence on the pheasant harvest (Robertson, 1958:92-93; Richard Nomsen, pers. comm.).

In Wisconsin pheasant range, corn occupies a much lesser acreage (on the order of 20 percent), a larger fraction of the landscape is uncultivated (25-40 percent), and hunting is less dependent on cornfields. It seems likely that the status of corn-picking has less of a bearing on the harvest, although it may still have some influence.

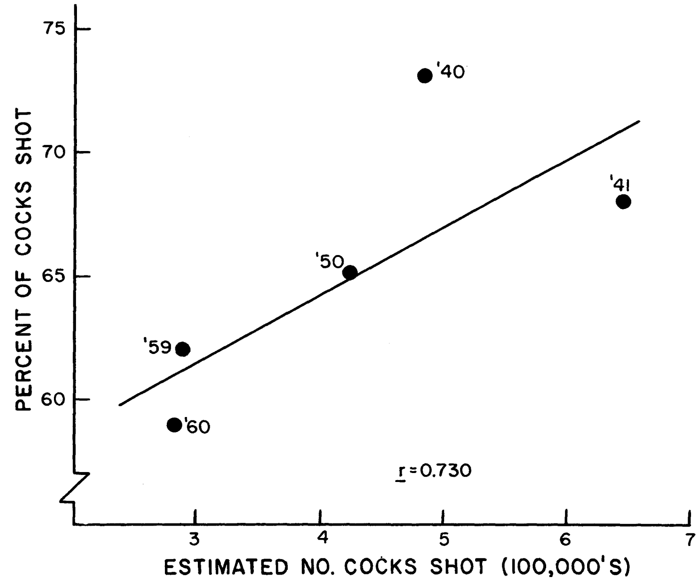


Figure 19. Correlation between pheasant population level and percentage of cocks shot in years when hunting seasons were between 16 and 21 days in length. The line was fitted by the method of least squares.

Other variations involve the weather and condition of natural vegetation. In some cases, the influence of these factors may operate in more than one direction, and be somewhat compensatory. For example, vegetation may be lush in a damp year, and marshes may be too wet and difficult to hunt—conditions which might tend to lower the kill. Yet, moist years are advantageous for the use of dogs, and flooded areas would preclude pheasant use resulting in concentrations in more vulnerable sites, a factor which would tend to increase the kill. Conversely, dry falls would allow hunters to hunt all favorable pheasant cover. These conditions would be unfavorable for dogs which could adversely affect the crippling loss and reduce the total reported kill.

On the whole, the role of hunting conditions here is difficult to assess, and one on which we have little information. MacMullan (1960:110-111) concluded: "Hunting conditions are popularly supposed to have considerable influence on the harvest of cocks . . . I was not able to detect any measurable effect these conditions have on total state kill for any season. Quite probably these conditions are less influential than the average hunter supposes, and quite probably conditions vary much less than he supposes." Short of extreme variations in corn-picking, these same views may apply to Wisconsin.

Comparison of Kill Estimates with Population Indices in Other States

A final basis for shedding light on the relationship between kill and population trend is a comparison of kill estimates with various independent population indices. Data from two states are available for comparison of a fairly lengthy series of years.

MacMullan (1950; 1960:20,103) compared trends in Michigan kill estimates taken in the same manner as the Wisconsin estimates with two independent indices. Fall flush-count data solicited over a 13-year period from a sample of 2,000 hunters by Jack VanCoevering, outdoors editor of the *Detroit Free Press,* showed a highly significant correlation coefficient of 0.876 with kill estimates. A similar test of correlation with July rural-mail-carrier brood counts yielded a coefficient of 0.978 for an 11-year period. These close relationships give one considerable confidence in the Michigan estimates.

Erickson, Vesall, Carlson, and Rollings (1951) presented annual kill estimates and August roadside counts for Minnesota in Table 5 of their paper (Fig. 20). We omitted the 1945 and 1946 roadside values because they were based on small numbers of miles driven. The 1945 value, based on the shortest distance driven, appears to be aberrant, but the 1946 value is quite in line with the trends. Test of the relationship produces a coefficient of 0.708, significant at the .05 level.

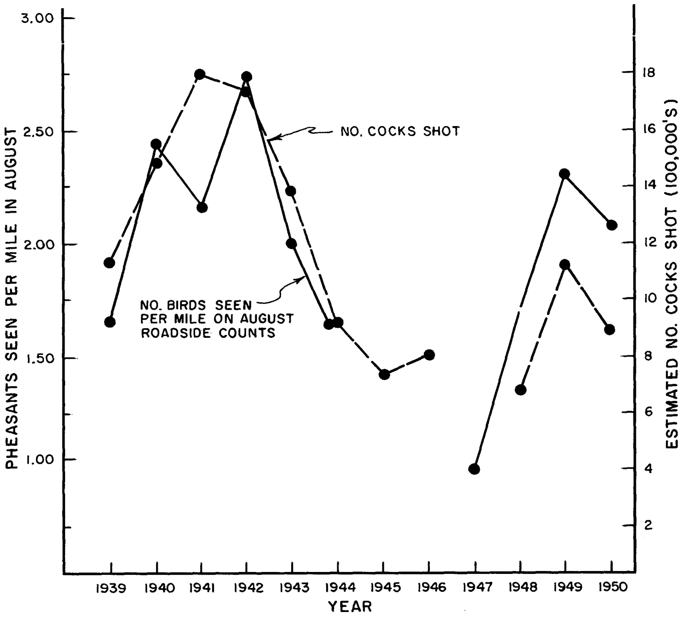


Figure 20. Comparison between trends shown by Minnesota pheasant kill estimates and August roadside counts. Data from Erickson, Vesall, Carlson, and Rollings (1951).

General Conclusions

The only fall index of population level available to us over a long enough period is the annual kill estimate. Reliability of this index depends on the error and biases in the kill estimation method, and on how closely the actual kill parallels population trends.

Evidently an average of at least 73 percent of the pheasant cocks are shot each year in Wisconsin, and in individual years it has varied between 59 and 84 percent. With this large majority of cocks shot, any major population change should affect the kill.

For this reason, and because kill estimates in Michigan and Minnesota follow other population indices quite well, the kill trends seem at least to grossly parallel the population curves. The apparent amplitude of variation may have been magnified somewhat above the true population change because hunting seasons have been lengthened during population highs permitting a higher percentage take, and shortened during lows which reduced percentage take. Variations in pheasant densities may have a similar effect.

Since the rate of reporting kill by hunters has been declining through the years in Wisconsin, there has probably been an increase in nonresponse bias. This would have a tendency to damp the real difference between population levels of the late 1930's and early 1940's on the one hand, and the late 1940's and 1950's on the other. The kill of the latter years would appear higher, relative to that of the earlier years, than actually is true of the populations.

Evaluation of kill estimates as indices of trend between pairs of successive years is more elusive. Comparison of trends in kill and in other population indices cannot be conclusive because the latter are subject to errors and biases of their own, and lack of agreement cannot all be ascribed to kill estimates. In Wisconsin, variations in hunting season lengths have probably been the most important variable besetting use of the kill, there having been marked changes in nearly one-third of the years in which we are interested. Statistical biases, which confound use of the kill for measurement of actual population level, probably are not so important in use of the kill as indices of annual trend because these biases may not vary greatly between pairs of successive years.

In conclusion, the precision with which population trends can be measured with our kill estimates is still somewhat of an open question. The errors and biases involved undoubtedly cost us some precision. On the other hand, these estimates may be no more variable than many other population indices. In the final analysis, we are left with a situation frequently facing the population ecologist: the availability only of rough indices such as fur records or kill estimates to provide needed measures of population behavior. One has no recourse but to use them, but it seems desirable to draw conclusions with care, and with full realization of the weaknesses inherent in the material. We have attempted to make known these weaknesses as much as possible in this chapter.

Summary

Kill estimation methods based on essentially voluntary return of kill report cards by samples of hunters often, but not invariably, can be shown to have nonresponse bias. A 3-year independent kill survey suggested that the true kill may be 11 percent below the annual estimate because of nonresponse bias. This bias has probably increased over the years. Prestige, memory, and party biases may play an additional part, the true kill possibly being 27 percent below the estimate because of all biases. Bias does not prevent use of the kill estimates as indices of trend, providing it is not markedly different between pairs of successive years. In one test, Wisconsin kill estimates paralleled hunter success on opening weekends of the hunting season, but not with statistical significance.

Wisconsin sex ratios and hunting season age ratios imply an average harvest of 73 percent of the cocks. Individual years have varied between 59 and 84 percent.

Hunting season lengths have varied in the state, and these suggest a correlation with the percentage of cocks shot. A higher percentage of cocks may be shot when pheasant populations are high than when they are low, when hunting season lengths are constant.

The number of hunters has varied over the years, but variations between pairs of consecutive years have seldom been large. Daily bag limits remained constant between 1932 and 1958. A reduction from 2 to 1 cock in the daily bag during the first two or three days of the hunting season took place beginning in 1959. No variation in the number of pheasant counties hunted occurred during the years covered in this report. Variations in the timing of corn picking may have a small influence on the kill, but the influence of changes in other conditions is unknown.

Trends in kill estimates in Michigan and Minnesota have generally followed trends in other population measures.

PART II—MECHANISMS AND CAUSES OF SHORT-TERM FLUCTUATION

Population phenomena frequently resolve into two major categories: (1) mechanisms and causes of year-to-year density changes within a given area; and (2) mechanisms and causes of differences in long-term mean density, or differences in the density range, between different areas. The two are related, but they can be studied independently to facilitate a better understanding of how each operates.

In Part II, we examine some of the mechanisms involved in annual pheasant population change. We extend our analysis to a consideration of the mechanisms of density determination in Part III.

We maintain an interstate perspective throughout this section to take advantage of having more data for analytical purposes. Also an analysis of the various factors affecting pheasant populations on a regional basis provides the opportunity to determine how the Wisconsin pheasant population functions within the broad framework of the midwestern range.

CHAPTER IV. NESTING PHENOLOGY

Sampling Problems

In studying the relationships between the hatch and the various environmental factors that affect it, it is desirable to observe variations from year to year in the phenology of the nesting season. Without actual nesting studies, observations on broods can be used with some reservation as indices of nesting phenology. Large numbers of broods can be observed in late summer, their ages determined, and these ages back-dated from the period of observation to their hatching date. The result is a large sample of dates on which nests hatched.

These dates can be averaged and the resultant average hatching dates used as indices of nesting phenology. Such use entails two risks which we must assume because of the lack of extensive nesting data: (1) Hatching dates of broods only provide indices of successful nests. They tell nothing about the timing of unsuccessful nests unless certain facts can be inferred from the shape of hatching curves. This fact alone makes them imperfect indices of nesting phenology. (2) Certain biases exist in brood observation techniques which further detract from their precision as indices of nesting phenology.

Smith (1950) and Podoll (1952) pointed out an important bias in field observations of hatching phenology which complicates the use of average hatching dates. They showed that for each successive week of observation, there is a tendency for the apparent hatching phenology to become progressively later.

This same trend is shown in our own data in Table 8, and the causes are evident. Observations made early in the year before all broods have hatched produce an earlier-than-normal hatching date because the later broods are not included in the average.

In addition, there tends to be a time-lag between the time the broods hatch and their appearance in the observations. Note in Table 8 that the tendency for the weeks of June 10 and 17 to stabilize as the peak hatching weeks does not occur until the observation week of July 29, some 6 weeks later. Hens with very young broods appear to be stealthier and more reluctant to show themselves than those with broods over 5 weeks of age.

By early or mid-August virtually all of the hatch is off; roughly 90 percent of the broods are 5 weeks old or older, are showing themselves, and can be observed. Accordingly, the advance in the observed average hatching date slows (Table 8) to the point where it proceeds more gradually than in the previous weeks.

The continued, slightly upward trend after early or mid-August is partly due to the seeming disappearance of broods hatched in April and early May as seen in Table 8. There is some indication that this may be due to a lack of reliability in the age criteria (Appendix A) for young over 12 weeks of age. In several instances we have assigned an age to relatively mature, road-killed chicks by our gross plumage criteria, and then checked the progress of the molt of the primary wing feathers. In each case the primary molt indicated that the bird was older than the gross plumage criteria indicated. We have evidence that our aging criteria, based on primary molt of penned birds (Woehler, 1953), over-age birds in much the same way reported by Stokes (1954:46). But even when allowances were made for this, the birds were older than the gross visual criteria indicated. Thus very old broods may be under-aged, and this would at least be partly responsible for the weekly advance in calculated hatching dates in Table 8.

In view of these biases, hatching dates from different areas and years cannot be reliably compared if the observations are made at greatly different times of the brood season. Since our observation periods have not been carefully controlled, it has seemed advisable to use observations only from an arbitrarily determined portion of the season. In some of the earlier years observations were not made until early September on some of the study areas. We have therefore chosen the latter part of the observation season, arbitrarily using August 1 as a starting date. This is about the last third of the observation period, and the time during which the advance in calculated hatching date slows down. All hatching dates and hatching curves in this report are based on observations made after July 31. Rejection of hatching date observations taken prior to August 1 does not involve much loss of data since about two-thirds of the observations are made after this date.

One other bias should be mentioned. On the basis of limited data, Woehler (1953) suspected that late-hatched birds molt their primaries faster than early-hatched birds. Our own cursory observation of known-age, late-hatched birds suggests the same tendency in the body feather molt. As a result, the later-hatched birds appear older than they are, and their apparent hatching date earlier than is the case.

The effect of this bias would be somewhat the reverse of the effect of the above-described flaws in our aging criteria. The net effect of both would be a tendency to damp the full magnitude of year-to-year variations in hatching dates. In a phenologically early year, when a relatively large fraction of the broods is in the older age classes, these birds would be under-aged because of the errors in the criteria. They would appear younger than they are, and the bias would be toward a later-than-true average hatching date. In a phenologically late year, the advanced rate of feather development of the late hatches would make them appear older than they are, and the bias would be toward an earlier-than-true average hatching date.

Demonstration of the full magnitude of variation in nesting phenology is further complicated by the fact that nesting phenology and hatching phenology are not synonymous. We shall present evidence shortly which suggests that years in which nesting begins comparatively early may also witness more renesting. Hatching dates from the latter effort, when averaged with first attempts, obviously result in a later average hatching date than if only the first attempts were compared. Consequently, the difference in average hatching dates between an early and late year is manifestly less than the full difference in phenology of the onset of nesting activity.

It is important to be aware of these tendencies which damp the full variation in nesting phenology. Average hatching dates, our indices of this phenology, suggest minor differences between years. Yet these small differences seem to be associated with significant population changes. Actual differences in nesting phenology are probably somewhat greater than our indices imply.

TABLE 8

Relationship of Frequency Distribution of Hatching Dates to Week of Observation, 1946-56*

	Number of Broods Hatching According to Each Week of Observation**																
Hatching Dates	5/20-6/2	6/3-9	6/10-16	6/17-23	6/24-30	7/1-7	7/8-14	7/15-21	7/22-28	7/29-8/4	8/5-11	8/12-18	8/19-25	8/26-9/1	9/2-8	9/9-15	9/16-22
4/8-14	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
4/15-21	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—
4/22-28	—	—	—	—	—	2	—	1	—	2	2	—	—	—	—	—	—
4/29-5/5	—	—	1	—	1	—	3	1	5	1	1	2	—	—	—	—	—
5/6-12	1	—	1	4	3	2	4	1	5	6	1	8	2	—	—	—	—
5/13-9	2	5	6	12	8	7	17	13	25	12	20	12	9	7	3	—	1
5/20-26	**6**	10	16	11	16	28	26	42	27	52	31	40	31	24	6	4	1
5/27-6/2	—	**10**	17	**34**	36	33	49	70	98	82	86	63	51	50	27	10	6
6/3-9	—	1	**22**	25	**45**	**42**	**56**	**79**	**117**	106	132	119	79	99	59	31	9
6/10-16	—	—	2	15	44	30	53	57	116	**123**	**230**	127	**154**	97	**67**	43	9
6/17-23	—	—	—	2	19	11	34	57	67	116	176	**188**	129	**111**	55	**57**	**13**
6/24-30	—	—	—	—	1	2	19	36	49	45	99	115	108	74	47	32	6
7/1-7	—	—	—	—	—	—	9	15	25	37	56	61	75	52	30	25	3
7/8-14	—	—	—	—	—	—	2	5	9	22	44	24	32	31	21	9	5
7/15-21	—	—	—	—	—	—	—	4	—	9	22	9	7	20	13	7	2
7/22-28	—	—	—	—	—	—	—	—	1	7	10	7	6	9	7	3	3
7/29-8/4	—	—	—	—	—	—	—	—	—	2	5	7	3	9	4	4	1
8/5-11	—	—	—	—	—	—	—	—	—	—	3	2	3	8	3	3	—
8/12-18	—	—	—	—	—	—	—	—	—	—	—	1	2	3	5	1	—
8/19-25	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	1	—
8/26-9/1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
Avg. Hatching Date	5/20	5/25	5/28	5/31	6/5	6/3	6/7	6/9	6/9	6/13	6/16	6/17	6/18	6/20	6/21	6/22	6/20
No. Broods Observed	9	26	66	103	173	157	272	381	546	622	918	785	692	596	348	232	59

*Based on data from all sources

**Boldface type—Mode for the Week of Observation

Average Hatching Dates

Variations Between Years

Average hatching dates for each year of observation for the three principal sources of data—statewide counts and research observations in Green and Milwaukee Counties—are shown in Table 9. The combined data indicate fairly consistently that 1947, 1950, 1954, and 1956 were the latest of the 10-year period. The years 1949, 1952, 1953, and 1955 were the earliest while 1948 was about average.

Some qualification must be made for 1951 and 1955. In 1951, two of the three averages were later than normal, while one was earlier than normal. The combined data suggest that it may have been about normal. In 1955, statewide and Green County averages were well ahead of normal. The Milwaukee County average was later than normal, but the sample was small and chance variation may have been involved. The combined data give a weighted average for 1955 that is the earliest year of the series.

In order to learn whether there is any uniformity in pheasant nesting phenology through large portions of the Midwest, we extracted information from the literature on this subject for several of the states (Table 10). The pheasant nesting phenology for each year is recorded as early, intermediate or normal, and late according to how it was described by the author, or according to the relationship of the years to each other in those cases where several years were described.

In addition to these, several reports on isolated years may also be noted. Bach and Stuart (1947), Mohler (1948), and Dustman (1950), reported that 1947 was a phenologically late year in North Dakota, Nebraska, and Ohio respectively. In addition to these published reports, pheasant workers from most states in 1955 and 1956 reported that these years were early and late, respectively.

Thus there seems to be a substantial element of uniformity in the year-to-year variations in pheasant nesting phenology. This apparently is true at least of the region from the Dakotas and Nebraska east to Michigan, Pelee Island, and Ohio.

Variations Between Wisconsin Areas

Milwaukee County hatching phenology appears to be slightly later than that farther west in the state. The average for Milwaukee County was later than the statewide average in 8 out of 10 years, the same in one year, and earlier in one year (Table 9). The 10-year averages for the two are June 18 for statewide, June 20 for Milwaukee. By *t*-test (Snedecor, 1948:65), this difference is barely short of significance at the .05 level.

Milwaukee County is adjacent to Lake Michigan which has a noticeable cooling effect on spring and summer climate and a pronounced retarding effect on phenology. Trees leaf out several days later than in Madison (75 miles due west), and hay mowing is several days later.

Mechanism of Annual Variations in Nesting Phenology

The manner in which nesting phenology varies from year-to-year involves the behavior of the hen, and has been discussed by Buss, Meyer and Kabat (1951), Buss, Swanson and Woodside (1952), Lauckhart and McKean (1956:63-64), and others.

We secured laying records from the Wisconsin State Game Farm based on the laying performance of the entire breeding flock of 10-12 thousand hens (Table 11). The hens are placed in breeding pens during the first part of March. The first egg is usually found during the last few days of March, and from this time on the number of eggs produced increases rapidly to a plateau period of maximum production. This plateau is first attained around April 25. The phenology of the onset of egg production at the game farm has been very nearly the same each year (Table 11).

From the various observations it appears that hens in northern states, whether in captivity or in the wild, usually begin laying during the latter part of April. The conclusion by Buss, Meyer and Kabat (1951) and by Lauckhart and McKean (1956:63) that this date is about the same each year for any given areas seems well supported by the game farm data.

Buss, Meyer and Kabat (1951) further observed that a group of 11 hens in pens dropped an average of 12.5 eggs at random after egg-laying began in 1944. These were laid at the rate of about one egg per 1.3 days. The hens then continued at the same laying rate, laid an average of two clutches apiece which they did not incubate, then each laid clutches which were incubated. The incubated clutches averaged 10 eggs, about the average clutch size for pheasant nests in the wild. Seubert (1952) reported similar behavior by hens in his study: random dropping of eggs immediately after onset of laying, then a period of laying in dump nests, and finally laying of subsequently incubated clutches.

The conclusion by Buss, Meyer and Kabat that this behavior is also typical of hens in the wild seems well supported by several sources of evidence: (1) The peak of hatching in Wisconsin is around the middle of June. If we back-date 37 days (14 for laying the clutch and 23 for incubation), we find that the peak of clutch initiation is around May 9. This is some 2 weeks or more after egg-laying begins as we have seen above. Buss, Swanson and Woodside (1952) noted that the peak of hatching in 1950 in southeast Washington was during the week of June 19 to 25. By back-dating, the

TABLE 9

Yearly Average Hatching Dates—Statewide and Green and Milwaukee Counties

	Statewide			Green Co.			Milwaukee Co.			Weighted Avg.	
Year	June Avg.	No. Broods	Std. Err. (Days)	June Avg.	No. Broods	Std. Err. (Days)	June Avg.	No. Broods	Std. Err. (Days)	June Avg.	No. Broods
1947	21	43	3.2	—	—	—	23	53	4.0	22	96
1948	18	60	2.4	17	56	1.6	18	78	1.6	18	194
1949	16	218	1.2	16	148	1.4	18	147	1.1	17	513
1950	21	166	1.1	24	147	1.3	24	148	1.2	23	461
1951	16	157	1.4	23	102	1.3	22	17	2.0	18	276
1952	15	238	1.0	13	112	1.3	17	60	1.8	15	410
1953	15	378	0.8	13	94	1.5	14	71	1.9	15	543
1954	20	306	0.9	21	77	1.8	21	48	1.1	20	431
1955	12	338	0.5	12	52	1.7	21	23	2.5	13	413
1956	21	261	1.0	18	29	3.1	26	8	6.2	21	298
Un-weighted mean	June 18			June 17			June 20			June 18	

average date of clutch initiation for these hatches must have been around May 20-25, or more than a month after egg-laying had begun as shown by the ovaries examined in that year.

(2) Buss, Meyer and Kabat (1951) observed that the ovaries of wild hens collected in June or later indicated that many more eggs were laid than the average clutch of 10 or 11. The number of eggs laid by hens killed on highways through the state during June 1946-49 ranged from 11 to 56, as shown by ovulated follicle counts.

(3) Randomly dropped eggs, laying in dump nests, and voluntary abandonment of clutches have been widely observed in nesting studies in Iowa (Hamerstrom, 1936; Klonglan, 1955), Michigan (Shick, 1952:30), Minnesota (Erickson, Vesall, Carlson and Rollings, 1951), Ohio (Dustman, 1950), Protection Island, Washington (Einarsen, 1945), on Pelee Island (Stokes, 1954:36), and elsewhere.

There is no question that nesting phenology varies from year to year, and it follows that this is determined by variations in the average date of initiation of clutches which ultimately are incubated. This variation is not necessarily due to variations in the onset of laying. The evidence instead suggests that the onset of laying is about the same each year. Buss, Meyer and Kabat concluded that "... apparently the stimulus which initiated egg-laying was not directly related to the phenomena which cause incubation."

This seems a good likelihood on physiological grounds. Egg-laying may be primarily governed by gonadotrophic secre-

TABLE 10

Comparative Pheasant Nesting Phenology in the Midwest, 1947-54

Year	So. Dakota[1]	Iowa[2]	Illinois[3]	Wisconsin[4]	Indiana[5]	Michigan[6]	Pelee Island[7]
1947	Late	—	Late	Late	—	Late	Late
1948	Early	—	Early	Intermediate	—	"Normal"	Early
1949	Early	—	Int. to early	Early	—	Early	Early
1950	Late	Late	Late	Late	Late	Late	Late
1951	Int. to late	—	Late	Int. to late	—	Intermediate	—
1952	Early	Early	—	Early	—	—	—
1953	Early	Late	—	Early	—	—	—
1954	Int. to late	Late	—	Late	—	—	—

[1] Smith, 1950; Podoll, 1952; Trautman, 1955a.
[2] Kozicky and Hendrickson, 1951; Klonglan, 1955a: Nomsen, 1956a.
[3] Robertson, 1958:63-79.
[4] This study.
[5] Ginn, 1950.
[6] MacMullan, 1948; Blouch and Eberhardt, 1953.
[7] Stokes, 1954:47.

tion from the anterior pituitary and female sex hormone from the ovary. Bissonnette and Csech (1936) showed that pheasant hens can be induced to lay in winter by artificial lighting and hence gonadotrophin secretion may be governed by day length. Since day length does not vary between years, one would therefore not expect annual variations in the onset of laying.

On the other hand, nesting behavior may be under the influence of the anterior-pituitary hormone prolactin (see review by Scharrer and Scharrer, 1936:76) which is also a primary regulator of incubation (cf. Lehrman, 1959:486; Höhn, 1961:36). Secretion of this hormone may be influenced by factors in the environment other than the photoperiod (Marshall, 1961:307-339). The possible factors involved will be considered in Chapter IX.

There is one final point to note. If egg-laying begins at about the same time each year, and if it is nest establishment that varies between years, it follows that the length of the period of egg-dropping and laying in dump nests varies between the years. As a result the total number of eggs laid would vary between years. In an early-nesting year the period between onset of laying and nest establishment would be relatively short, and few eggs would be dropped before nesting. In a late year when nesting did not begin until late, the egg-dropping period would be prolonged as appears to have been the case in 1950 in Washington (Buss, Swanson and Woodside, 1952), and the total number of eggs dropped or dumped would be great. Possibly in support of this, Klonglan (1955) commented on finding an unusually large number of dropped eggs and dump nests in Iowa in the late spring of 1954, as did Robertson (1958:70) in late years in Illinois. Buss, Meyer and Kabat (1951) noted considerable variation between years in the total number of eggs laid by wild hens.

TABLE 11

Phenology of the Onset of Egg Laying at the State Game Farm, Poynette, Wisconsin

Year	Percent of Peak Egg Production			Statewide Avg. Hatching Date of Wild Birds
	25% of Peak	50% of Peak	75% of Peak	
1953	April 7	April 11	April 15	June 15
1954	April 9	April 12	April 14	June 20
1955	April 8	April 12	April 15	June 12
1956	April 10	April 12	April 18	June 21
Mean	April 9	April 12	April 16	June 17

Between two-thirds and three-fourths of Wisconsin pheasant nests are begun during the month of May in an average year. The peak of nest initiation is usually between May 10-15. The peak hatch is about June 18.

Hatching Curves

When hatching dates for a given year are grouped by weeks, and the value for each week expressed as a percentage of the total number of broods for the year, the resultant curves depict the hatching season graphically. While conclusions can be drawn from the shape of such curves regarding the chronology of successfully hatched nests, deductions regarding the success of the hatch and the chronology of unsuccessful nests are more tentative.

We have amassed Wisconsin data from all observation sources for the period 1947-56 and constructed hatching curves for each year (Fig. 21). The weeks of peak hatch are shown below each curve and, except for 1947, parallel the phenological variations shown in Table 9. In 1947, the number of statewide and Milwaukee County observations was small, while the number of broods observed at University Bay and the University Arboretum was large, their hatching dates rather early, and they accordingly weight the 1947 curve in Figure 21.

Subjectively, it appears to us that the curves for the late years tend to be higher and more acute than those for the early years. In the late years, the week of peak hatch appears to be markedly dominant over the other weeks, while in the early years from one to three points seem to have almost as high rank as the peak hatching week. When each of the two groups of curves is combined into a single curve, one representing the late years and one representing the early years, the two curves suggest similar configurations. Peak value for the early years is 20.1 percent while peak for the late years is 22.6. Differences such as these would occur if the hatch were distributed over a longer period in the early years, while being concentrated in a shorter period in the late years. However, no test that we have applied indicates a difference between the shapes of the curves in the early and late years that is significant at the .05 level.

Seubert (1952) observed a terminal date—about the first week of July—after which most hens will not renest following destruction of their nests. Since the onset of the nesting period varies between years, and since the terminal portion of the nesting season tends to be more constant, as Seubert has shown, one would expect that the length of the nesting season would vary primarily with the time at which it began. If nesting started early, there would be more time between beginning and the terminal date. If it started late, the total time remaining before Seubert's terminal date would be shorter.

If the differences we have inferred from the curves in Figure 21 were real, they might bear out these expectations. Such variations in the curves between early and late years could result from the extent to which the season is squeezed between the varying onset of nesting and the less variable cessation period. The implication here is that there might be less renesting in the late (shorter) years than in the early years. When nesting begins early, there would be potentially more time for renesting before Seubert's terminal date, than in a year when nesting began late. Stokes (1954:44) has previously proposed the same hypothesis.

However, hatching curves from a number of other Midwest areas have not shown similar variations. Data from South Dakota (Smith 1950, 1951; Podoll, 1952; Seubert, 1954, 1955), Michigan (Blouch and Eberhardt, 1953), Pelee Island (Stokes, 1954:47), and Illinois (Robertson, 1958:62-79) showed no tendency for the steepness of the curve to be related to the lateness of the season.

Such variations in hatching curves have been shown to typify different areas within two midwestern states. Blouch and Eberhardt (1953) showed consistent differences between the hatching curves of southwest Michigan, a poor pheasant area, and the "Thumb" region, the area having that state's highest pheasant population. The southwest area tends to have steep, sharply single-moded curves with no skewing or peaks in the right-hand slope. The "Thumb" area has lower, wider curves with almost flattened tops. When the data are separated into small blocks of counties, the resultant curves display pronounced notching in their right-hand slopes, and the authors conclude "... that the distortion in the curves was due to a recurrence of once interrupted nesting effort—in other words, renesting ..." Smith (1950) and Podoll (1952) observed that the areas in South Dakota which experienced the highest reproductive success had hatching curves with subdominant peaks, whereas a medium to low rate of reproductive success was characterized by relatively symmetrical curves.

All of these authors, then, associate areas of high reproductive success or thriftier populations with lower hatching curves, often with subdominant peaks that may represent a degree of renesting. The areas of poorer hatch or less successful populations were characterized by single-moded, rather steep curves which may indicate relatively less renesting.

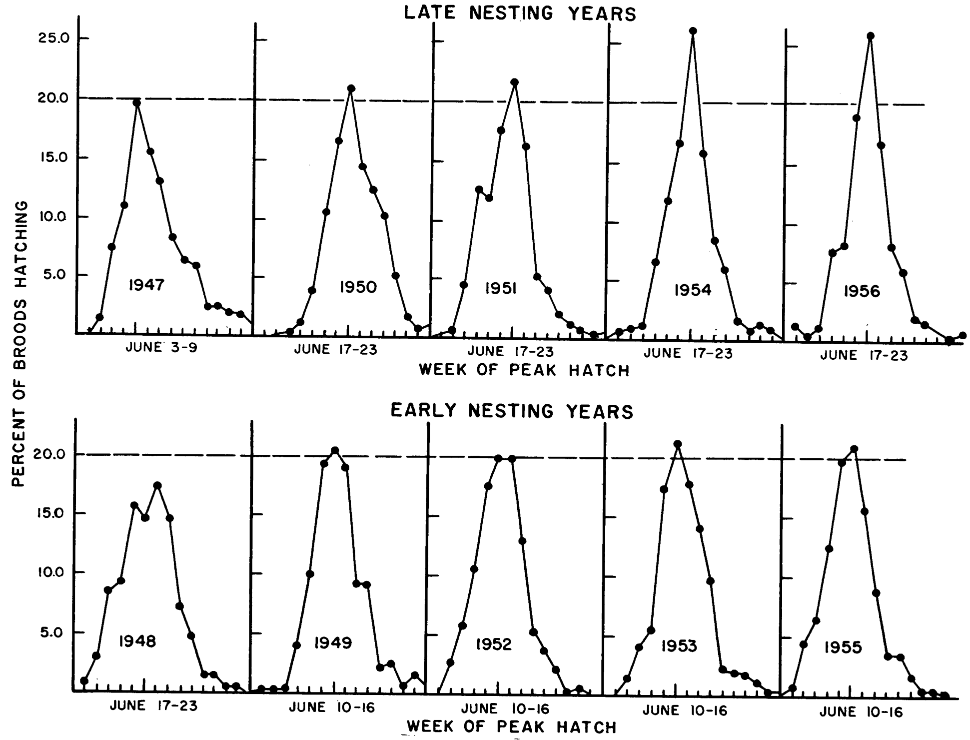


Figure 21. Annual variations in the shape of hatching curves for all sources of data. The number of broods represented by each curve from 1947 successively through 1956 are: 199, 273, 638, 502, 318, 418, 543, 431, 413 and 298. Classification of each year as early or late was based on Tables 9 and 10.

Summary

Average hatching dates are used as crude indices of nesting phenology. They are subject to the bias of a progressive change in observed average hatching date with successive weeks of observation because of the timing of the hatch, behavior of the birds, and probable errors in the aging criteria. In this study, we used observations made after July 31 in order to minimize the degree of bias. Actual differences in phenology between years may not be fully shown by average hatching dates.

The years 1947, 1950, 1954, and 1956 were phenologically late-nesting years in Wisconsin and through much of the Midwest; 1949, 1952, 1953, and 1955 were early; 1951 was average or late, and 1948 was early or average. Milwaukee County, adjacent to cooling Lake Michigan, appears to be phenologically later than areas farther west in Wisconsin.

Hens apparently begin laying eggs at about the same date each year. Variations in nesting phenology appear to result from variations in the time of onset of laying in incubated nests. A period of egg dropping, laying in dump nests, and clutch abandonment precedes laying in the incubated nest. This period seems to vary in length between years, depending on the date on which actual nesting begins. Hence there may be annual variations in the total number of eggs laid.

In Wisconsin, but not in South Dakota, Pelee Island, Illinois, or the Prairie Farm in Michigan, the late years may have been characterized by steep, single-moded hatching curves. Early years have been characterized by lower, truncate curves with from 1 to 3 weeks having almost as much weight as the peak hatching week, but these differences are not significant. High, acute curves could indicate less renesting than lower curves. Similar differences have typified the hatching curves of different pheasant areas in Michigan and South Dakota.

CHAPTER V. BROOD SIZES

In this and the next two chapters we discuss annual and regional variations in reproductive success as disclosed by three indices. We measured reproductive success in terms of the number of young reared to an age of self sufficiency—viz., 2-3 months—by a given number of hens starting the nesting season. This expression of reproductive success involves clutch size, nesting success of hens, and the related extrinsic and intrinsic mortality factors that affect the young in their early weeks of life.

This chapter is concerned with the average number of young reared by each successful hen, and with seasonal, annual, and regional variations in this number. As pointed out by a number of authors (e.g., Robertson, 1958), brood sizes only give part of the picture of juvenile mortality because they give no clue to the extent of mortality due to sudden and complete loss of entire broods. Other writers (e.g., Linduska, 1947; Smith, 1951; MacMullan, 1960:109; Linder, Lyon and Agee, 1960) have pointed out that variations between years in brood sizes are not sufficient to account for marked variation in reproductive rates, and that percentage of successful hens and/or loss of entire broods must be the more important influences.

We generally agree with these views, subject to the qualification that the full variation in brood sizes is sometimes damped by the observational method. Furthermore, brood sizes are discussed at some length in this chapter primarily because they serve as indices of certain basic phenomena apparently present in pheasant reproduction.

Sampling Problems

Importance of Only Using Completely Counted Broods

The majority of our brood observations have been made by the Area Game Management personnel of the Conservation Department. In our survey instructions we have stressed the importance of distinguishing between broods in which all chicks were believed counted, and broods in which the count was only partially complete. All discussion and data in this report on brood sizes from Wisconsin are based only on complete counts.

Lack of insistence on counting broods as completely as possible may well have prevented the demonstration of material year-to-year variations in brood sizes in other studies. When average brood sizes are not restricted to completely counted broods, the full variation between averages of different years tends to be reduced or masked, and it often is not possible to demonstrate statistical significance.

This can be shown with South Dakota data reported by Smith (1950 and 1951), Podoll (1952), and Seubert (1954). These authors reported brood sizes according to how completely the observer believed he had counted the chicks. Broods were rated "complete" if all chicks were believed to have been counted, and "good" if most chicks were believed to have been counted.

In each of 4 years, average brood sizes were calculated for both of these classes in addition to averages that included all broods observed whether "complete," "good," or otherwise (Fig. 22). Clearly, the extent of year-to-year variation is partly a function of the completeness of the counts. The average variation of the four points from the 4-year mean of each class is 3 percent for "all" broods, 5 percent for "good" broods, and 6 percent for "complete" broods.

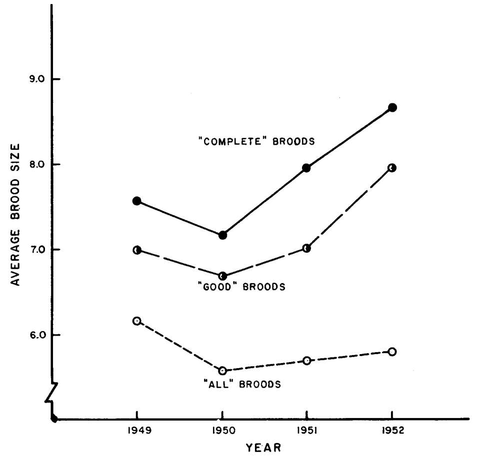


Figure 22. Relationship between intensity of observations and annual trends in brood size in South Dakota. Data from Smith (1950 and 1951), Podoll (1952), and Seubert (1954).

Failure to restrict average brood sizes to carefully counted, complete broods may also be responsible for some of the large variation in pheasant brood sizes reported in the literature. Reported sizes of broods over 2 weeks of age vary between 3.5 to 5.2 (Robbins and Hendrickson, 1951) and 8.5 to 9.1 (Randall, 1940). Some variation between areas undoubtedly exists, but if it is as great as that reported by these writers, it must imply profound differences in basic pheasant biology about which we need more study.

Effect of Population Density and Brood Mingling on Brood Size

Stokes (1954:52) found considerable difficulty in getting accurate brood observation data on Pelee Island due to the high densities. Brood mingling was common, and chicks often split away from broods and became independent at very early ages. We have observed some brood mingling in Wisconsin in the better pheasant range, although it is nowhere near the problem that Stokes found on Pelee. Isolated broods make up the bulk of our observations.

We adopted some arbitrary criteria for treating combined broods in analyzing our data. In a case where two age classes of chicks were present with two hens, the number of chicks of each age was recorded and this was treated as two broods. Where two hens were present with one age class of chicks, we arbitrarily treated it as one brood if there were 10 or less chicks, and the extra hen was recorded as a broodless hen. It is not uncommon to find one or two broodless hens associating with a hen and brood. Where two hens were seen with 11 or more chicks of the same age class, we arbitrarily treated this as two broods. Groups of chicks of a single age class but without hens were treated as one brood. Broods of two age classes with one hen were treated as two broods, the number of chicks of each age being recorded as the brood size of each age class. Broods of two age classes without any hen were similarily treated as two broods. Single chicks, with or without hen, if recorded as "complete" counts, were treated as broods.

Relationship of Brood Age to Brood Size

We segregated our brood data by weekly age classes, calculated brood sizes for each week of age, and constructed a curve from these means (Fig. 23). Data from all observational sources during the period 1946-56 were used. The 1-week class covers the period immediately after hatching to within 2 or 3 days of the 2-week class. The aging criteria are shown in Appendix A.

The curve shows a progressive decline in brood size from 1 to 6 weeks of age with the greatest decline coming in the first 2 or 3 weeks of age. It seems reasonable to assume that this slope is due to mortality.

From 6 to 12 weeks of age, broods apparently increase in size. This increase has been observed by other workers, and is generally attributed to mingling of broods (e.g., Baskett, 1947; Erickson, Vesall, Carlson and Rollings, 1951). After 12 weeks of age, brood sizes drop sharply, probably due to their disintegration.

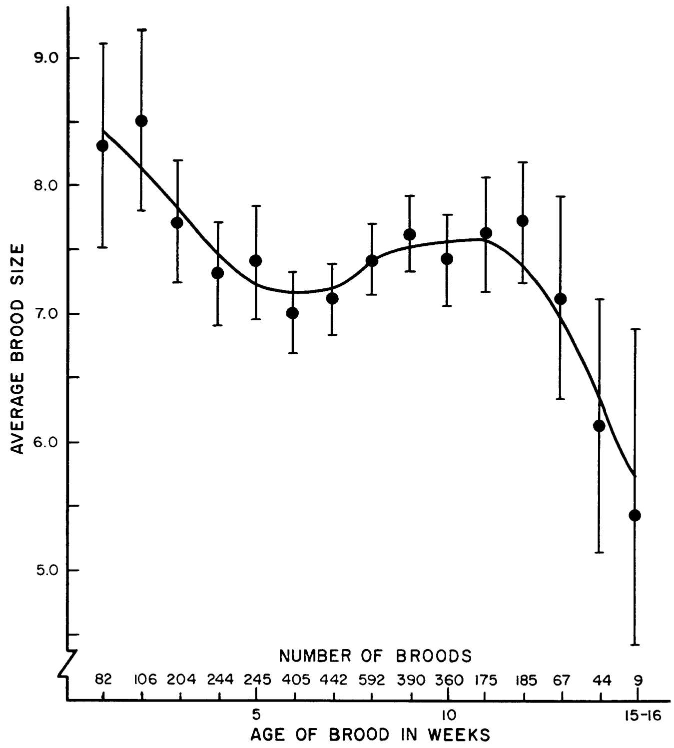


Figure 23. Relationship between brood age and brood size, 1946-56. The limits on each side of the mean represent twice the standard error of the mean. The line was drawn with three-point moving averages.

Brood sizes would be of maximum value as indices of juvenile mortality if we only compared the 1- through 6-week age classes between years. However, the data on these classes make up a minor part of the total brood observations (see sample sizes in Fig. 23). Our data are not sufficient to allow comparison only of these younger ages.

Average brood sizes composed of all age classes are an abstraction of the entire line shown in Figure 23, with the 6- through 10-week classes carrying the greatest weight because they are the most frequently observed ages. We will show later that the entire line depicted in Figure 23 shifts up or down between years. Thus the average brood size represents the height of this line on the graph. As such it is only an index of the entire brood picture for the year, and should not be assumed to represent the actual number of young in the average brood in late summer. Over the years, the average brood size has declined to slightly over 7 by 6 weeks of age (Fig. 23). Undoubtedly further shrinkage occurs by 15 or 16 weeks, yet the average of all ages is 7.4. We have no information on the mean number of chicks per brood at the time of break-up of broods; the average brood size, purely an index value, should not be assumed to constitute such a mean.

Relationship of Chronology of Observations to Brood Size

The most frequently observed age classes are 6 through 10 weeks (Fig. 23). This weighting of the data results primarily from the chronology of the observations. Most counts are made between the middle of July and the tenth of September, with the month of August supplying nearly two-thirds of all observations.

This chronology is influenced by a number of factors. The earlier limits are set by the time at which the broods can be seen. With much of the hatch coming off in June, and a 6-week lag between hatching and the appearance of most broods, they are not available for observation until the latter half of July and early August. Crop harvesting chronology is also involved. In Wisconsin, the first hay cutting is done largely in the latter part of June. Oats are usually harvested in late July. Thus it is not until the latter part of July that enough of the summer vegetative growth has been opened up to make it possible to see broods.

Late summer is also a season of heavy dewfall in this region. Broods may be appearing in openings in early mornings to avoid the dripping vegetation. Dry, dewless periods are notably poor for seeing broods (Klonglan, 1955).

The latter part of the observation period in mid-September is set by the time at which broods begin to break up and become difficult to count. And it is influenced by the fact that many broods are reaching the older ages, are difficult to distinguish from adult hens, and therefore complicate the problem of determining the proportion of hens with broods and accurately counting the number of young in a brood.

Variations in Brood Size Within the Year

Relationship Between Time of Hatch and Brood Size

In order to obtain a picture of the relationship of brood size to date of hatch, we have combined data for all years, grouped them by weeks of hatch, and calculated averages for each week (Fig. 24). To remove as much variation as possible, and to provide something approaching terminal brood sizes, we have only included broods 4 through 10 weeks of age. This eliminates the larger broods of the first few weeks of age, the larger combined broods of 11-14 weeks, and the small fragments of split broods 14 weeks and older(Fig. 23).

Broods hatched in mid-May are the largest of the season. From that time on brood sizes decline at an accelerating rate. Broods hatched in mid-May average nearly 8 chicks each at 4-10 weeks of age. By late July or August, the few broods that hatch this late average slightly over 4 chicks or less at 4-10 weeks. One explanation for this relationship between date of hatch and brood size doubtless lies in the seasonal decline in clutch size, a phenomenon well established by many studies (e.g. Errington and Hamerstrom, 1937; Randall, 1939; Leedy and Hicks, 1945:66; Stokes, 1954:26).

Whether or not variations in chick mortality rate are involved is less clear. To explore this question, we separated all brood-size data according to hatching dates, and divided them into three groups representing the first, second, and last thirds of the hatching season. Each of these three groups was then subdivided by successive weeks of age, and a line similar to that in Figure 23 drawn for each of the three groups. These lines show week-by-week change in brood size for broods hatched in the early, middle, and last thirds of the hatching season (Fig. 25).

The trends in each line again point to an increase in brood size in the older age classes as occurred in Figure 23. Hence any inferences about mortality must again be restricted to portions of the lines that represent the first 7 weeks of age. We tested the slopes of these descending portions of the lines (regression coefficients of -0.19 and -0.45 for the first and second thirds, respectively) and found the slopes for the first and second thirds of the hatching season statistically different (.01 level). Interpretation of the slope for the last third of the season is less certain and depends upon a subjective decision as to which values constitute the descending phase.

If the decline in brood size in the first 7 weeks of age can be used as an index of actual chick mortality rate, the difference in the slopes of the upper two lines (Fig. 25)

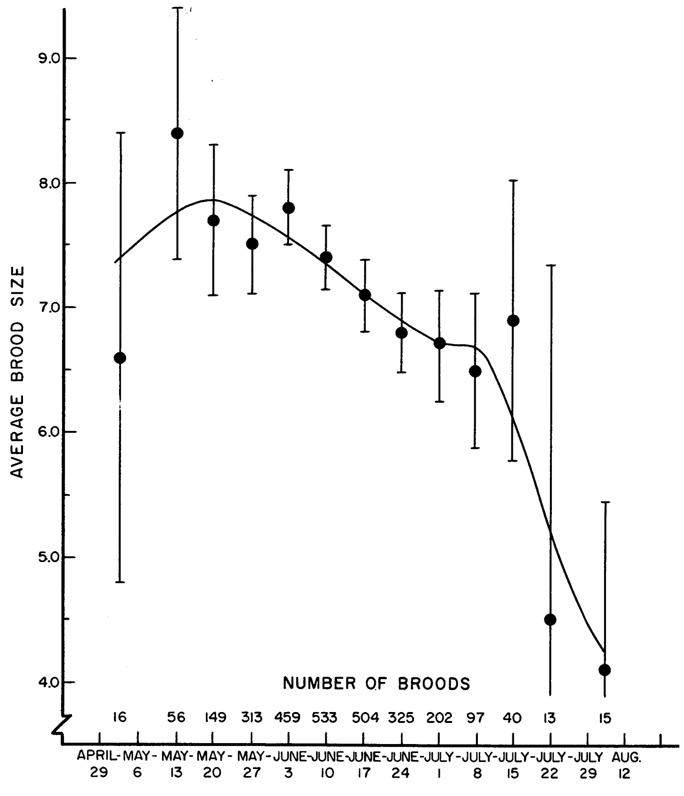


Figure 24. Relationship between time of hatch and size of broods 4-10 weeks of age, 1946-56. The limits on each side of the mean represent twice the standard error of the mean. The line was drawn with three-point moving averages.

suggests that broods hatched in the second third of the season shrink at a faster rate than broods in the first third of the season.

Stokes (1954:61) found the proportion of the early-hatched birds surviving to the hunting season higher than that of late-hatched birds even though the former had a longer period between trapping and hunting season through which mortality could operate. He also found that early-hatched birds grew faster than the late-hatched birds.

A similar phenomenon seems to take place in chicks reared at the State Game Farm. The percentage of birds in each hatch surviving to 40 days of age (Fig. 26) varies with the chronology of their hatch. Survival is highest in the earliest hatches, declines progressively through the hatching season, and is lowest in the last hatches that come off in early July.

Possible Cause of Seasonal Increase in Chick Mortality Rate

Stokes (1954:67) suggested that the seasonal decline in vigor of the chicks he observed may have been due to a shortage of food in the latter part of the season. The early hatches on Pelee Island were observed to feed heavily on large mayfly hatches, while mayflies were less abundant later in the season.

While food supply may have been involved on Pelee Island, it obviously is not the explanation for our game farm birds. And if the same phenomenon is occurring in our broods in the wild, it does not seem a likely possibility in this case either. If anything, the supply of insects and weed seeds in southern Wisconsin is greater in late June and July when the later broods hatch, than in May and early June when the early broods come off.

The effect may be due to more fundamental causes, and appears to be operative in a wide range of species. A seasonal decline in chick vigor is well established in the poultry literature: the mortality rate in young chickens increases, and the hatchability and growth rate decrease in successive hatches from early spring to late summer (Upp and Thompson, 1927). A seasonal decline in hatchability is characteristic of domestic turkeys (Marsden and Martin, 1944:188).

It appears to be present in a number of wild species other than pheasants. Leopold and Ball (1931) reported that late-hatched British red grouse are considered undesirable in a management program because of low vigor. Thompson and Kabat (unpubl. ms.) concluded that July-hatched young bobwhites of the same age groups weighed more in fall than those hatched in earlier or later months. Kluijver (1951) reported higher band recovery rates in early-hatched broods of the great tit than in the late broods. In this same species

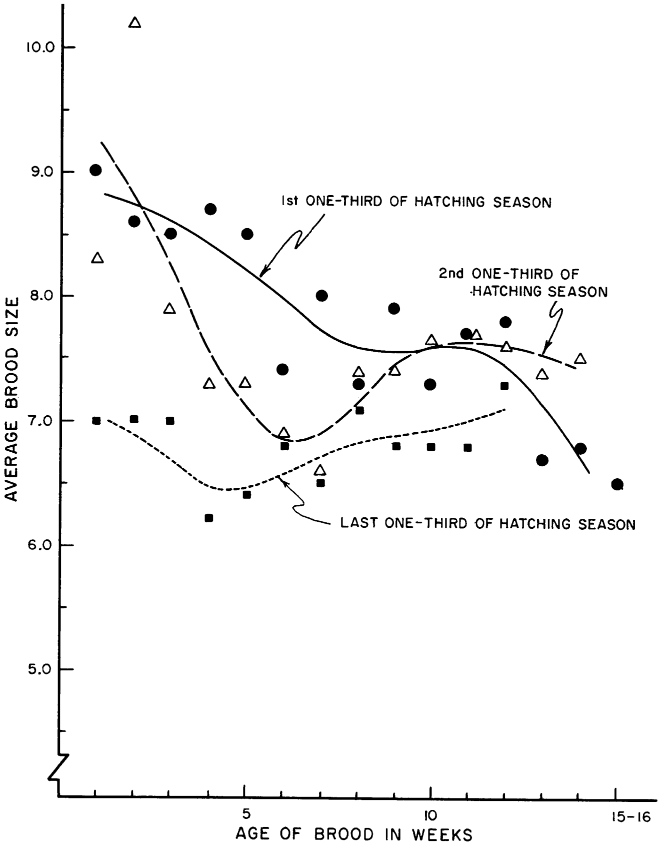


Figure 25. Week-by-week changes in sizes of broods hatched in the first, second, and last thirds of the hatching season. The graphs include data from all sources, 1946-56. The lines were fitted by the use of three-point moving averages.

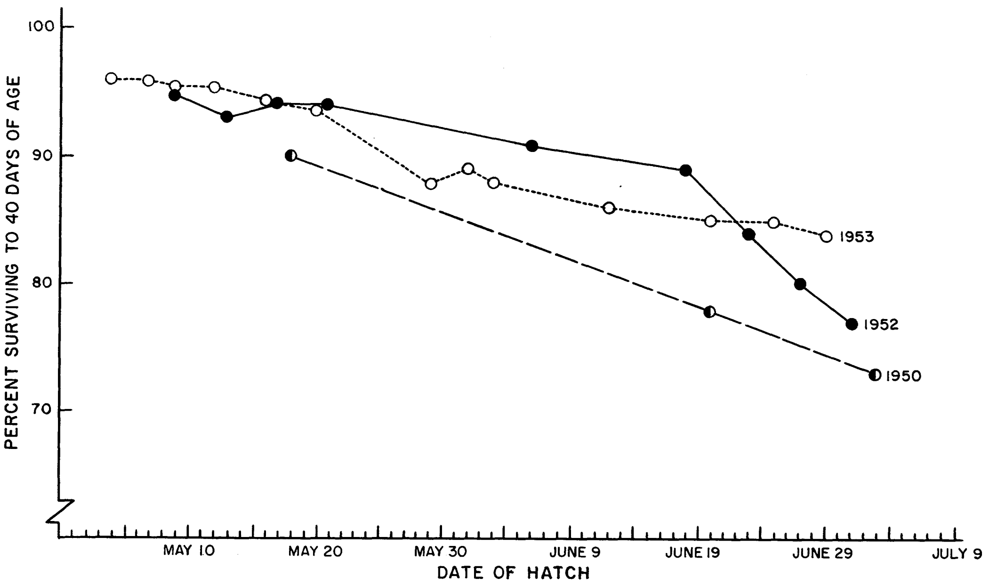


Figure 26. Relationship between time of hatch and chick survival at the Wisconsin state game farm. Each point represents the percentage survival to 40 days of entire hatches brought off on the dates shown on the abscissa. Each hatch numbered from several hundred to several thousand chicks.

Gibb (1950) found that nestlings in four second broods weighed less than those of first broods of the same age. Early-hatched mourning doves have been found to weigh more than late-hatched birds of the same age (F. H. Wagner, unpubl.).

Poultry workers generally attribute this seasonal decline in vigor to an increase in parasite infestation and disease in chickens as the seasonal temperatures increase. This does not seem to apply in our pen-reared pheasants where the difference in mortality is apparent immediately after hatching, certainly by the second or third day after hatching.

We suggest an alternative hypothesis. Kabat, Meyer, Flakas and Hine (1956) showed that the pheasant hen attains her peak physical condition for the year in April just prior to egg laying. From the onset of laying to late summer or early fall, her condition declines, apparently due to the successive physiological stresses of egg production, incubation, and molt. Much of this decline takes place during egg laying (Kabat, Thompson, and Kozlik, 1950). If the hen's physical reserves are declining during the laying period, the quality of the eggs and consequently the hardiness of the chicks could decline as well.

Such a seasonal decline in egg quality is amply documented in poultry. It is well known that the weight of the chicken egg declines from early spring to late summer (Atwood and Weakley, 1917; Bennion and Warren, 1933). The thickness of the shell declines (Wilhelm, 1940) as do both the weight of the yolk and albumin (Atwood and Weakley, 1917), and there is a seasonal decline in the vitamin A content (Sherwood and Fraps, 1932). In addition to these there are a number of changes in various physical properties of the egg (Wilhelm and Heiman, 1938; Sauter, Harns, Stadelman and McLaren, 1954). With changes such as these in the egg, it is not surprising to find the seasonal decline in hatchability and vigor of the chicks reported by Upp and Thompson (1927). We have no comparable data on pheasant egg weights or quality to determine whether or not they undergo similar seasonal changes.

Whatever its cause or causes, there appears to be a correlation between the chronology of hatch and the vigor of a number of species of birds. Evidence from Pelee Island and Wisconsin suggest that this relationship may exist in pheasants and be partially responsible for a seasonal decline in wild pheasant broods.

Variations in Brood Size Between Years

Yearly, average brood sizes were calculated for the three major sources of data, with the statewide observations making up the largest and most reliable samples (Table 12). The Green County trends followed these fairly well in the years when the samples were sizeable. The Milwaukee County trends, with smaller samples yet, show little agreement.

The combined data show that 1946, 1947, 1950, 1951, 1954 and 1956 had the smallest brood sizes. Average brood sizes for 1948, 1949, 1953, and 1955 were above the 10-year average.

Although brood observation methods vary between states, brood data from two other midwestern states tended to show somewhat the same year-to-year trends (Fig. 27). These include South Dakota trends in "good" broods for 1946-52, and Minnesota broods for 1946-55. Brood sizes were low in 1946 and 1947, increased during 1948 and 1949, dropped in 1950, then increased from 1951 through 1952. There is some further parallel tendency between 1952 and 1955 in Minnesota and Wisconsin. Correlation tests between the Wisconsin values and those of the other two states indicated a probability of about 0.1 that the similarities are due to chance.

Wisconsin brood sizes are inversely correlated with variations in hatching phenology (Fig. 28) shown in the last chapter. The correlation is significant at the .05 level.

Data are not available to determine whether these brood-size variations result from annual variations in clutch size. Variations between years in clutch size have been observed in a number of studies (e.g., Hamerstrom, 1936; Dustman, 1950; Shick, 1952) but seldom have these been related to hatching phenology. Salinger (1952) observed a mean clutch in his Idaho study area of 9.3 in 1949 and 10.3 in the cold spring of 1950. Stokes (1954:26-27) found almost identical mean clutch sizes on Pelee Island in phenologically early 1949 and late 1950.

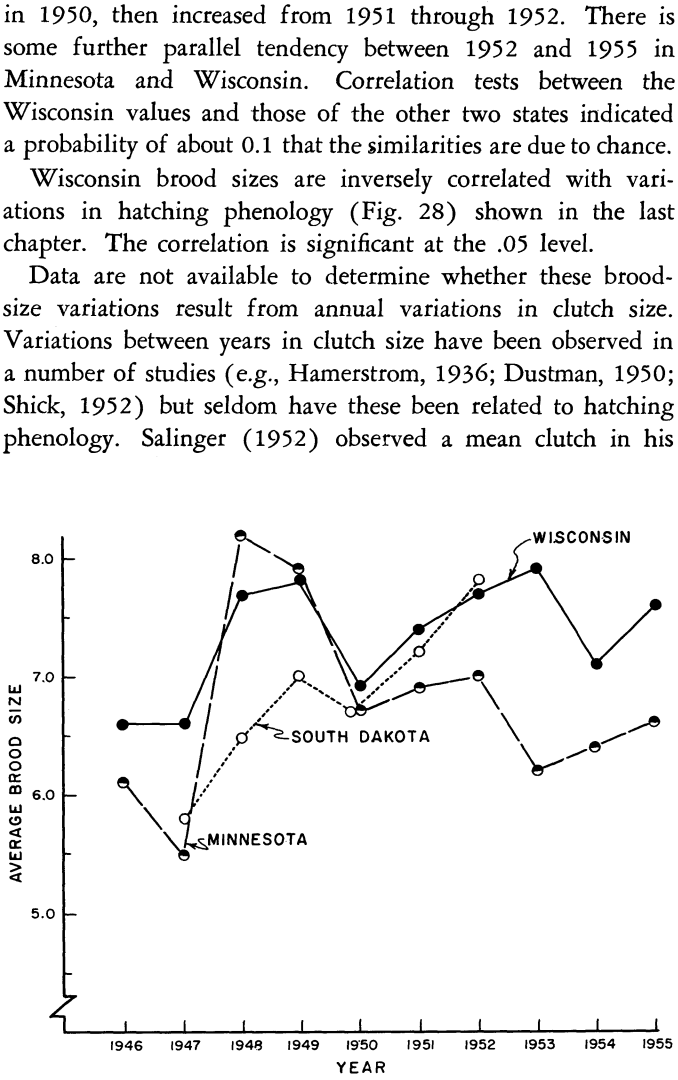


Figure 27. Annual trends in average brood size in Wisconsin, Minnesota, and South Dakota. Minnesota data from Erickson *et al.* (1951); South Dakota data from Janson (1949), Smith (1951), Podoll (1952), and Seubert (1954).

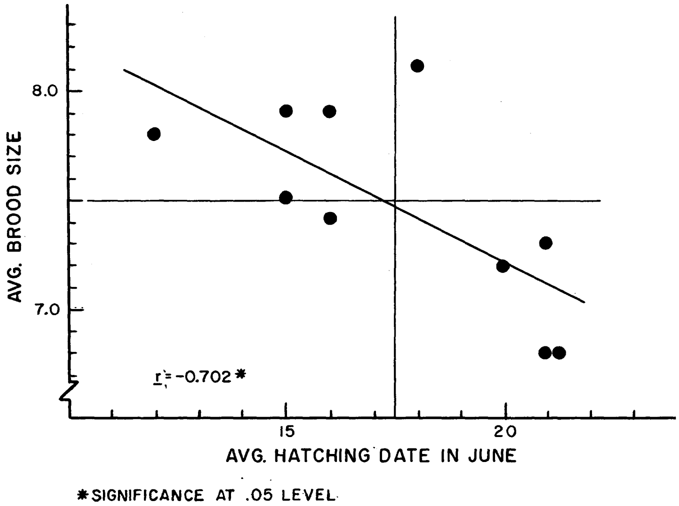


Figure 28. Correlation between average brood size and average hatching data, 1947-56. Each point is the mean for statewide data in Tables 9 and 12.

The evidence to show a relationship between hatching phenology and chick mortality rate is more clear cut than the clutch-size problem. Average brood sizes for successive weeks of age are shown in Figure 29 for the 5 early- and the 5 late-hatching years. Both groups of years show a week-by-week pattern similar to that previously shown in Figure 23 in which the combined data for all years were used. Brood sizes in the first 7 weeks of age decline more rapidly in the late years than in the early (Fig. 29). The trend is emphasized by the apparent tendency for 1-week-old broods to be larger in the late years (8.6) than in the early years (8.2). But the samples are small (42 and 36 respectively), and the means not significantly different.

We again calculated regression coefficients for the slopes represented by the points for the first 7 weeks of age. These coefficients (—0.18 for the early years, —0.35 for the late) are different at the .01 level. The mortality rate of young evidently is higher in late years than in early, and this contributes to the relationship between phenology and average size of all broods. This of course assumes that the descending phase of the line can be used as an index of chick mortality.

One possible cause of the increased chick mortality rate in late years may be found in the laying behavior of the hen and ultimate quality of the egg discussed earlier. Since hens may begin laying at about the same time each year, but show variation in the date on which the incubated nest is started, the possible result is variation in the number of eggs laid between onset of laying and onset of nesting. Thus, if a hen lays and incubates a clutch of 12 eggs, they might

TABLE 12

Yearly Variations in Average Brood Sizes in Wisconsin

	Statewide			Green Co.			Milwaukee Co.			All Data		
Year	Avg.	No. Broods	Std. Error	Avg.	No. Broods	Std. Error	Avg.	No. Broods	Std. Error	Avg.	No. Broods	Std. Error
1946	6.6	40	0.6	—	—	—	—	—	—	6.6	40	0.6
1947	6.8	59	0.3	—	—	—	6.5	31	0.5	6.7	90	0.3
1948	8.1	143	0.3	7.5	99	0.3	7.1	72	0.4	7.7	314	0.2
1949	7.9	265	0.2	8.1	101	0.3	7.2	64	0.4	7.8	430	0.1
1950	6.8	203	0.3	6.9	100	0.4	7.3	70	0.3	6.9	373	0.2
1951	7.4	170	0.3	7.3	69	0.3	7.7	13	0.7	7.4	252	0.2
1952	7.5	318	0.2	9.6	52	0.5	7.6	39	0.4	7.8	409	0.2
1953	7.9	371	0.2	8.2	62	0.3	6.8	27	0.3	7.9	460	0.1
1954	7.2	338	0.2	7.5	54	0.4	5.0	21	0.5	7.1	413	0.2
1955	7.8	329	0.2	7.0	46	0.4	5.6	16	0.4	7.6	391	0.2
1956	7.3	284	0.2	6.3	21	1.0	4.3	7	0.7	7.1	312	0.2
Unweighted mean	7.4		—	7.6		—	6.5		—	7.3		—

represent the sixth through seventeenth eggs she has produced; or they could be the twenty-first through thirty-second eggs.

If there is a progressive decline in the quality of each egg, a clutch early in the hen's sequence would be made up of better quality eggs than a late clutch. This could affect the vigor of the chicks, and explain the difference in chick mortality rates between early and late years quite analogous to mortality differences within the year in game farm and Pelee Island chicks.

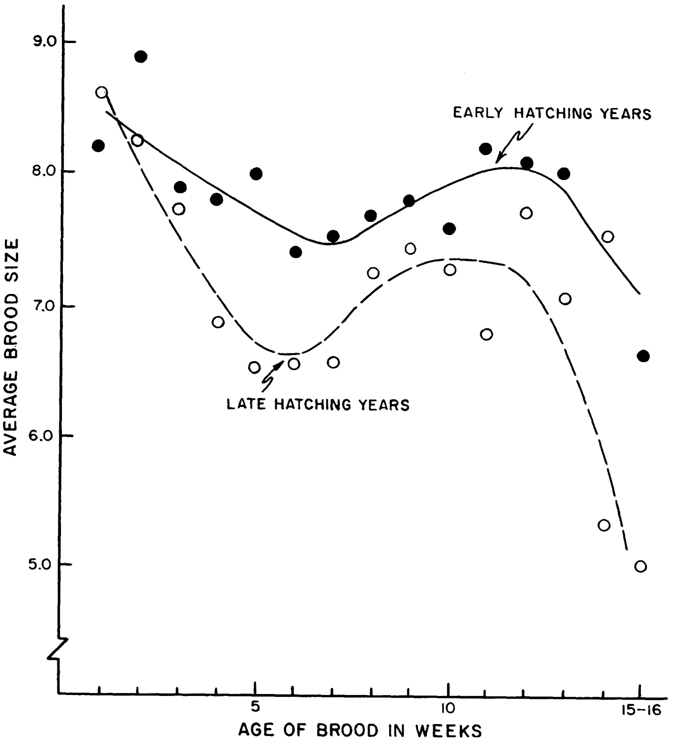


Figure 29. Week-by-week changes in brood size in late- and early-nesting years. The curves, fitted from three-point moving averages, include data from all sources for 5 late-nesting years (1947, 1950-51, 1954, 1956) and 5 early-nesting years (1948-49, 1952-53, 1955).

It may be pertinent that Stokes (1954:33-36) found a high degree of nest abandonment on Pelee Island which he attributed to the stress of high populations. Because of this, his hens had probably laid large numbers of eggs before they laid the clutch that was ultimately incubated. Perhaps as a result, Stokes (p. 65) found a juvenile mortality rate that seems high for what otherwise appears to be a highly favorable pheasant environment.

Whatever may be the cause or causes of the relationship between chick mortality rate and nesting phenology, it evidently exists. Hence the annual, average brood sizes serve not only as an index of the average number of young raised by successful hens, but as a clue to the vigor of the entire juvenile crop for the year.

This is the first of several indications that reproductive success, as described earlier, is importantly influenced by nesting phenology, a point that will be developed further in the two chapters that follow. It might be questioned whether the phenomena that we have been exploring should be considered as variations in reproductive success inasmuch as they clearly involve posthatching mortality of chicks. We choose to consider them as such because they appear to be intrinsic—determined before the young hatch much as variations in clutch size would be—and, as we shall see later, are not the result of the posthatching environment.

Variations in Brood Size Between Wisconsin Areas

Results from Study Areas

Average brood sizes for statewide, Green County, and Milwaukee County data were shown in Table 12. The Green County mean of 7.6 is not statistically larger than the statewide mean (7.5) for the same 9-year period. The difference between the Milwaukee County mean (6.5) and the statewide mean (7.5) for a similar period is highly significant, and is significantly smaller than the Green County mean at the .05 level.

Intensive observations on the University Bay and Arboretum areas were made from 1946 through 1949, and fragmentary data are available for 1950 and 1951. The average brood size and standard error of the mean for all data from University Bay are 6.3 ± 0.3 (150 broods). The mean and standard error for all Arobretum data are 5.0 ± 0.2 (109 broods). Both of these means are statistically smaller than the statewide mean.

Pheasant populations on the University Bay, Arboretum, and in Milwaukee County are declining coincident with human encroachment on all three areas, and passage of optimum plant successional stages in the case of the Arboretum. We are uncertain why brood sizes in these areas should be smaller than the statewide average, but they may be linked to the rapidly changing habitat conditions.

Statewide Results—Relationship of Brood Size to Population Density

We combined the statewide observations for all years, and split them into groups of counties representing "very good," "good," "fair," and "poor" pheasant density levels according to the distribution shown by Wagner and Besadny (1958). The average size and standard error of the mean for each of these levels are (1) "very good," 7.3 ± 0.1 (729 broods); (2) "good," 7.6 ± 0.1 (1,181 broods); (3) "fair," 7.9 ± 0.1 (517 broods); and (4) "poor," 7.5 ± 0.3 (87 broods).

If the data are similarly analyzed but grouped into the 5 early and 5 late years, exactly the same trends between county groups are shown although the average for each group is lower in the late years than the average for the same groups in the early years. This is, of course, what would be expected in view of the differences in brood sizes between phenologically early and late years. The same year-to-year changes in brood sizes occur throughout the state at all population levels.

These results suggest an inverse correlation between pheasant density and brood size, at least for the three highest density classes with substantial samples. The mean for the "good" areas is significantly higher (.05 level) than the mean for "very good" areas, and the mean for "fair" areas is significantly higher than the mean for "good" areas.

In order to explore this relationship in more detail, we subdivided the data for each of these three density groups into weekly age classes in the same manner as shown in Figures 23, 25, and 29. This allows us to determine the ages at which differences in brood size between the three areas are manifested (Fig. 30). The lines were fitted with 3-point moving averages.

The important point we have gleaned from this comparison involves variations in the chronology of changes in the curves. In the high density areas, the trough between the descending and ascending phases of the curves centers at about 7-8 weeks of age. The trough for the low density areas centers at about 5-6 weeks, the peak in the curve centering at about 10 weeks. The curve for the intermediate density areas is roughly intermediate between the other two in these characteristics.

These chronological variations accordingly influence the observed average brood size because of the chronological distribution of the sampling. The most frequently observed age classes are 6-10 weeks (Fig. 23). At these ages, we are concentrating our sampling on the trough of the curve in the high density areas. But in the low density areas, we are primarily sampling the ascending phase of the curve and the summit of the peak.

Consequently, variations in average brood size between different density levels may only be an artifact resulting from the interaction between (1) chronology of observations and (2) chronological variations in the inflection points of the curves. If we look only at the descending phases of the curves up to about 6 weeks of age, there are no differences in brood size indicated between the different density levels.

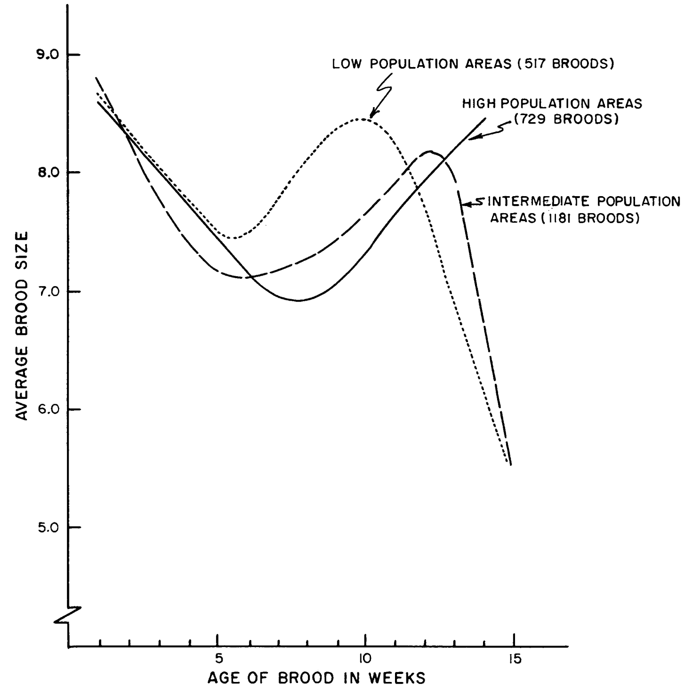


Figure 30. Week-by-week changes in brood size at different pheasant-density levels. The graph includes data from "statewide" observations only, 1946-56. The lines were drawn by using three-point moving averages.

While we have no definite explanation for these inflections in the brood size curves or their significance in the population dynamics of the species, they are quite evident in the data. They appear in the total mass of observations (Fig. 23), and in each partitioning of the data, whether by subdivision of the year (Fig. 25), subdivision between years (Fig. 29), or geographical subdivision (Fig. 30).

The possibility exists that brood mingling, combining of orphaned broods, and confusion of hens with young in the older age classes each may contribute to variations in average brood size between different density levels, although we have no direct evidence that these are the influential factors. The curves in Figures 23, 29, and 30 indicate that the increase in brood size in the later age classes amounts to only about one-half to one chick. Hence the increase involves the average addition of one bird per brood; or the addition of one brood to another, once in every 7-14 broods.

Summary

Failure to count all chicks in a brood masks full variation in brood sizes. All analyses in this report are restricted to completely counted broods. Certain criteria have been used in the analyses to minimize the effect of brood mingling.

Average sizes of broods decline from 1 through 6 weeks of age, then increase from 7 through 11 or 12 weeks, perhaps due to combining. From 12 through 16 weeks, averages decline as broods break up. Brood sizes between 1 and 6 weeks are probably of maximum value as mortality indices, but these age classes make up a minor fraction of the data. Hence, all data must be used, and an average brood size for all classes serves as an index.

Timing of Wisconsin brood observations—latter part of July through early September—is determined by the chronology of the hatch, of the crop harvest, and of dewfall. Broods 6 through 10 weeks of age make up a major fraction of the observations. Brood observations from other areas would not be entirely comparable with ours if not made at the same time.

Broods hatched early in the season are larger at 4-10 weeks of age than broods hatched late in the season. This decline is due partly to a seasonal decline in clutch size, and may possibly be due in part to higher juvenile mortality rates in the later broods than in the early ones. This seasonal increase in chick mortality rate, if present, might be the result of a seasonal decline in the quality of the egg which, in turn, may be due to a seasonal decline in the physical reserves of the hen.

Average brood sizes were above the 10-year mean in 1948, 1949, 1952, 1953, and 1955; below average in 1946, 1947, 1950, 1951, 1954, and 1956. These same trends appear to have characterized Minnesota and South Dakota broods between 1946 and 1952.

A statistically significant, negative correlation exists between Wisconsin average brood sizes and average hatching dates. Largest broods are produced in the earliest years. The role of clutch-size variations in this is not known, but variations in chick mortality rates probably are involved. These higher mortality rates in late years may stem from the possibility that the hen has dropped more eggs, her incubated clutch comes later in her egg sequence (and hence is of lower quality), and the vigor of the chicks may be lower accordingly.

Average observed brood sizes are inversely correlated with pheasant population density in Wisconsin. This apparently is not due to differences in clutch sizes or to differences in chick mortality rates. Rather, the correlation may result from regional variations in the chronology of change in the brood curve, and its relationship to the chronology of observation.

CHAPTER VI. PERCENTAGE OF HENS WITH YOUNG

Sampling Problems

If no hens died or broods disappeared during the summer, the percentage of hens with broods would begin at zero, increase slowly at first, then advance more rapidly during the main hatching period. It would then slow, and eventually level off at the percentage of hens alive at the beginning of the summer which successfully brought off a brood. Theoretically, the trend would follow an S-shaped curve.

It is problematical whether or not such a sigmoid curve could ever be clearly depicted by field observations. Hens die leaving orphaned broods, and broods undoubtedly disappear leaving broodless hens that will not try to renest. In addition, there are in the population at the time of brood observations hens trying to renest, incubating hens, and hens with broods of varying ages.

In spite of this complexity, the proportion of hens with young obviously increases during the summer, and eventually this increase should level off when all nesting has stopped for the year. We might reasonably expect that these trends could be determined from roadside observations, and that the final percentage after levelling off should bear some relationship to the actual percentage of hens that succeeded in rearing a brood. Seemingly, conclusions on the percentage of hens with young should be based on observations following this levelling-off point.

In order to test this hypothesis, we grouped the data from our roadside observations into weekly periods and calculated the observed percentage of hens with young for each week of the summer. Two such analyses were made: one for 11 years of study-area data, and one for statewide data gathered by game managers from 1953 through 1956. (Prior to 1953 our field forms and instructions were not designed to emphasize the importance of counting all hens seen.)

The results show an increasing percentage through the summer, and an inflection in the line somewhere around late July or early August (Fig. 31). The trend levels off at about 82-87 percent, and holds roughly constant until the end of the observation period in mid-September. If the data are divided into two groups representing early- and late-nesting years, the early August inflection point holds for both groups.

Presumably the percentage shown after the end of July in a given year could serve as an index of the proportion of hens successful in rearing broods in that year. This would not necessarily assume that the observed percentage would be the same as the actual percentage of hens starting the nesting season that succeeded. However, in serving as a year-to-year index of the actual percentage, it would assume that the variables are somewhere near constant between years.

For unknown reasons, trends shown by the voluminous South Dakota data on this subject (Janson, 1949; Smith, 1950 and 1951; Podoll 1952; and Seubert, 1954 and 1955) are markedly different (Fig. 32). The South Dakota percentages begin at about 10-30 percent in early July, increase more rapidly than in Wisconsin, and show no tendency to level off in early August. Instead the trend continues to increase, reaching 100 percent by late August in the early-hatching years.

In late years, the entire line in the South Dakota data shifts to the right by 1 or 2 weeks. The percentage of hens with broods on any given calendar date may vary between years, depending on the earliness or lateness of the season. However, the final percentage at the end of each season may be quite similar. For example, the percentage of hens with broods during the first week of August was 69 in 1949 (Smith, 1950), and 46 in 1950 (Smith, 1951). But by the end of the observation seasons, the 2 years compared closely with 89 and 87 percent, respectively. The latter value was attained two calendar weeks later than in 1949.

The important point, as the South Dakota workers (Smith, 1951; Podoll, 1952) have shown, is that in order to compare success between years, one must use the same phenological point. Comparing percentages for the same calendar period may show differences that are more due to variations in phenology than in hatching success.

A third variation in the seasonal trend is shown by Nebraska data (Kimball *et al.,* 1956:219). Here the percentage of hens with broods builds up to an early August inflection point, then declines through the remainder of the month. While the samples are large, they only represent one year. The trend found by Linduska (1947) in Michigan tended to be intermediate between the Wisconsin and Nebraska patterns, although an early August inflection point was again evident.

We have used the observed percentage of hens with young after July 31 as an index of Wisconsin reproductive success. While it may not be an entirely valid index, we have used it in this report with qualifications.

Variations Between Years

We suggested in Chapter IV that differences in the shape of hatching curves might imply a higher degree of renesting in early years, and possibly higher percentage of hens successful, than in late years. To examine this possibility further, we compared the observed percentage of hens with young after July 31 with average hatching dates for Green County and statewide (Fig. 33). Green County is the only study area for which we have data over a long enough period to allow comparison.

The trends in Figure 33 suggest that the percentage of hens with young may be higher in early years. But neither relationship is statistically significant.

We grouped the data from all 4 study areas in Table 13, dividing them between early- and late-hatching years. In three areas out of four (Milwaukee County does not agree) the percentage is higher in the early years than in the late; and the mean of the four values for the early years is higher (81 percent) than the mean for the late years (76 percent). When all data are pooled for the early and late years, the observed percentage of hens with broods in early years is 82, and is 80 in the late years. These trends are again suggestive of a relationship, but are not statistically different. Two tests were used: (1) the rank total test (Wilcoxon, 1949) on the individual values for each area; and (2) the chi-square test on the pooled data.

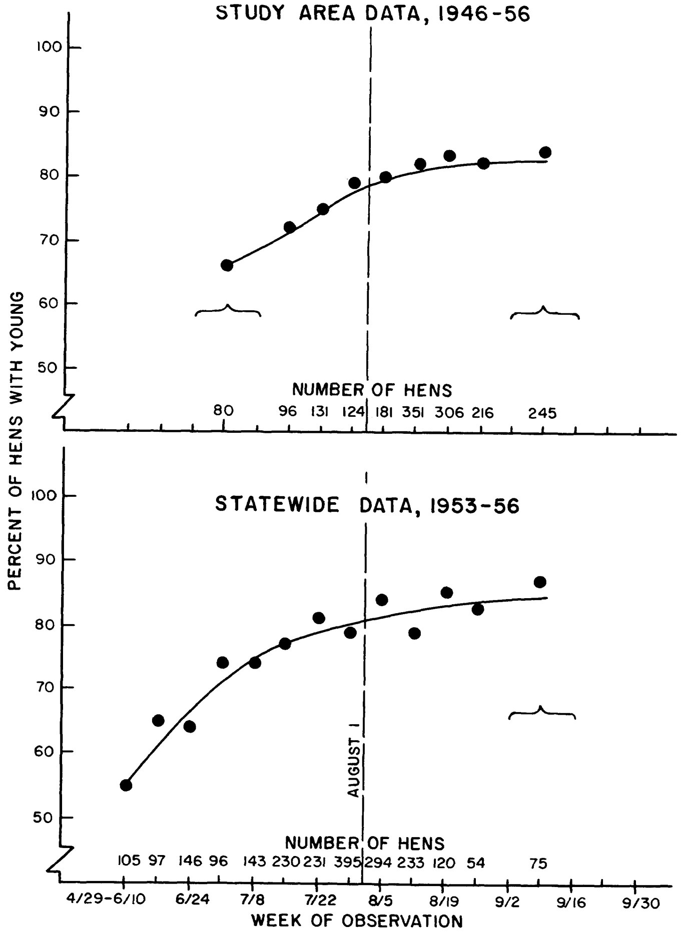


Figure 31. Seasonal trend in the percentage of hens with young seen along roadsides in Wisconsin. The lines were fitted visually.

A further indication of the relationship between percentage of successful hens and phenology may also be seen in Table 13. The mean percentage for Milwaukee County, where nesting is slightly later, is lower than that for Green County at the .01 probability level. The Milwaukee mean (78 percent) is also lower than the statewide mean (81 percent in Fig. 33), but the probability that this is a real difference is only about .80.

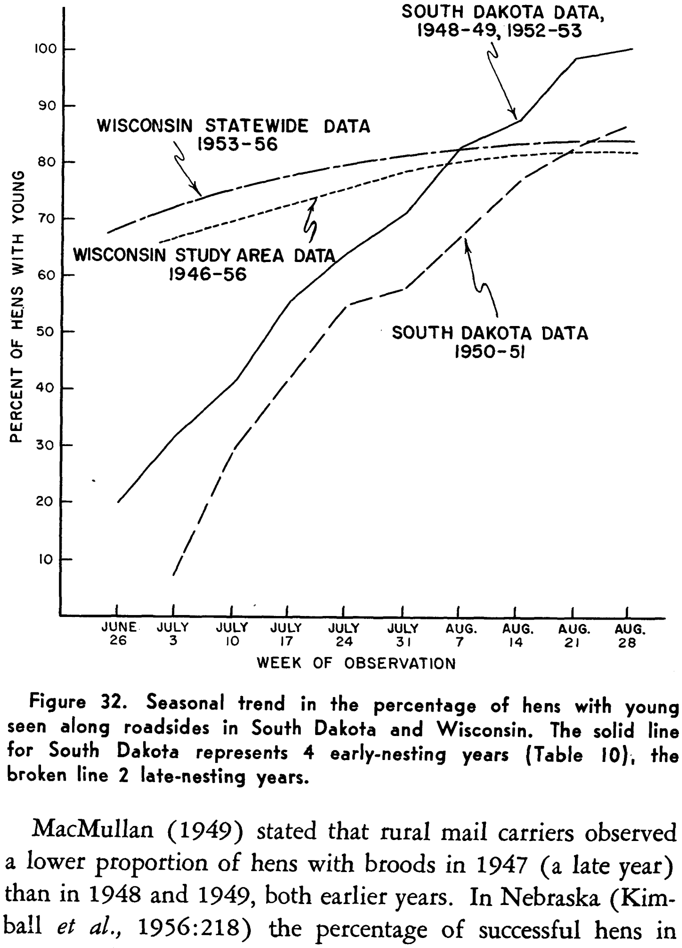


Figure 32. Seasonal trend in the percentage of hens with young seen along roadsides in South Dakota and Wisconsin. The solid line for South Dakota represents 4 early-nesting years (Table 10), the broken line 2 late-nesting years.

MacMullan (1949) stated that rural mail carriers observed a lower proportion of hens with broods in 1947 (a late year) than in 1948 and 1949, both earlier years. In Nebraska (Kimball *et al.,* 1956:218) the percentage of successful hens in 1950 (a late year) dropped below the values for 1948 and 1949. However, Iowa data (Kimball *et al.,* 1956:218) for the four years 1948-1951 did not follow the same pattern. We have seen that, for any given calendar period, the proportion of hens with broods in South Dakota is lower in late years.

All of these sources combined suggest a relationship between annual variations in nesting phenology and the success of hens in bringing off broods. Some authors (MacMullan, 1948; Stokes, 1952; Lauckhart and McKean, 1956:64) have even suggested that in very late years some hens may not attempt to nest. And the possibility also remains that the relationship, if real, may be due (1) to variations in the

TABLE 13

Percentage of Hens with Young After July 31 in Early- and Late-Nesting Years on the Four Study Areas

	Early Years*			Late Years**		
Area	Percent With Young	No. Hens	95 Percent Conf. Limits	Percent With Young	No. Hens	95 Percent Conf. Limits
Green County	90	317	86.0-93.1	85	272	80.2-89.1
Milwaukee County	76	302	70.8-80.7	82	210	76.0-87.0
University Bay	91	77	82.8-96.4	80	76	69.2-88.4
University Arboretum	65	82	53.9-75.0	56	73	44.1-67.5
Unweighted mean	81			76		
Weighted mean and total	82	788	79.2-84.6	80	631	76.6-83.1

*1948, 1949, 1952, 1953, 1955.
**1947, 1950, 1951, 1954, 1956.

calendar dates on which summer populations appear, and (2) failure to make proper phenological adjustments in the observing dates.

One of the difficulties in demonstrating a correlation between nesting phenology and percentage of successful hens may lie in the summer mortality of hens which appears to increase in late-nesting years (Wagner, 1957). This removal of hens may have a tendency to mask the true percentage of hens with and without broods available to the observer, and thereby complicate demonstration of any correlation.

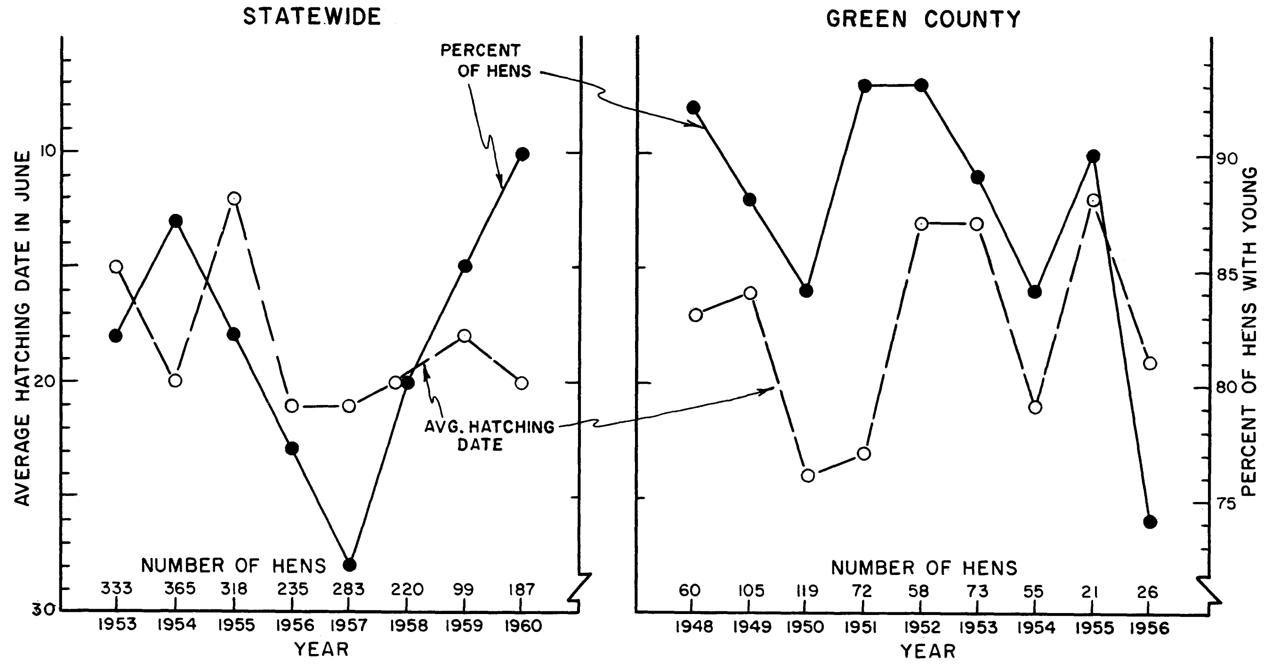


Figure 33. Comparison of the percentage of hens with young and nesting phenology, statewide and in Green County.

Variations Between Wisconsin Areas

Results from Study Areas

We have already pointed out that the percentage of hens in Table 13 for Green County is statistically higher than those for Milwaukee County. Phenology in the latter county is slightly later, apparently due to the cooling effect of Lake Michigan. The University Bay values are more comparable with those for Green County. The Arboretum apparently has the lowest proportion of hens with broods (significantly lower than statewide, Green County or Milwaukee County), as well as having the lowest brood sizes. This low productivity is probably related to the declining population on the area.

Results from Statewide Observations

The statewide data in Table 14 show some variations in percentage of hens with broods between areas. However, in view of the size of the sampling limits shown, and the lack of any coherent pattern in the variations, the probabilities are large that these are due to chance.

TABLE 14

Percentage of Hens with Broods at Different Wisconsin Pheasant Densities

	Percent Hens with Broods, No. Hens Observed, and 95 Percent Conf. Limits According to Pheasant Density Level											
Year	"Very Good"			"Good"			"Fair"			"Poor"		
1953-56	83	351	78.5-86.8	85	479	81.4-88.1	81	167	74.3-86.6	75	24	53.3-90.2
1957-60	79	306	74.0-83.5	79	351	74.3-83.3	71	84	60.2-81.3	93	44	81.7-98.6
Mean and total	81	657	77.7-84.0	83	830	80.2-85.5	78	251	72.4-83.0	87	68	73.4-92.9

Summary

In Wisconsin, percentage of hens with broods seen along roadsides builds up during the summer, and levels off in early August presumably coinciding with appearance of most of the hatch and with cessation of nesting attempts by hens. The percentage of hens with broods after July 31 seemingly could serve as a reproductive success index. Observed percentage of hens with broods in South Dakota increases during summer to around 90-100 percent by early September without an early August inflection. The line shifts from right to left between phenologically different years. At almost any given calendar date, percentage of hens with broods is lower in a late year than in an early one, although it eventually achieves the same final point.

Several sources of Wisconsin evidence suggest, but do not conclusively show, that the percentage of hens that successfully raises broods is lower in late years than in early years.

A low observed percentage of hens with broods seems to be characteristic of the declining University Arboretum and Milwaukee County populations. The percentage of hens with young is significantly lower in Milwaukee than in Green County, and suggestively lower than statewide. No regional correlations with pheasant density are evident.

CHAPTER VII. YOUNG-PER-HEN RATIOS FROM HUNTING SEASON DATA

Cock age ratios are a more common type of hunting season data than hen age ratios. When corrected with sex ratios of the previous winter or spring and multiplied by two, cock age ratios provide young-per-adult-hen ratios. We explore such ratios in this chapter.

Sampling Problems

Correcting With Sex Ratios

The necessity for correcting cock age ratios with adult sex ratios of preceding winter or spring has been well analyzed by other authors (Kimball, 1948; Dale, 1952; Stokes, 1954). The formula we use in this chapter for calculating young-per-hen ratios from cock age ratios is as follows:

$$\frac{\text{Number of young cocks per adult cock in fall}}{\text{Number of hens per cock in previous winter or spring}} \times 2$$

The fraction provides the number of young cocks per adult hen, and this is doubled to allow for both sexes of juveniles.

In correcting with winter sex ratios, we of course incur the risk of compounding the biases in the cock age ratios with those in the sex ratios. And we also make the assumption that the sex ratio does not change through differential loss of either sex class of adults between winter and the time the young are self-sufficient in summer.

Differential Vulnerability Between Adult and Juvenile Cocks

The important variable affecting the use of cock age ratios is the apparent greater vulnerability of young cocks than adults to hunting. As a result, the two age classes are not harvested in the same proportion as they are present in the population.

This bias manifests itself in a progressive decline in the proportion of young birds in the bag from the start to the end of the hunting season (Allen, 1941, 1942a, 1943; Mohler, 1943; Kimball, 1948; Eberhardt and Blouch, 1955). This decline is presumably due to the disproportionate kill of young birds early in the season, and the consequent increase in proportion of adults in the bag as the season progresses.

Effect of Variations in Hunting Pressure

Stokes (1954:77-78) and Hart (1954) suggested that expression of the vulnerability bias may be affected by intensity of hunting pressure. Declines in hunting season age ratios have not been observed on the heavily hunted California cooperative hunting areas (Ferrel, Harper, and Hiehle, 1949; Harper, Hart and Schaffer, 1951), and band recoveries there give no indication that juveniles are more vulnerable than adults (Hart, 1954). The vulnerability differential is evident on the more lightly shot, licensed game bird clubs in the state (Hart, 1954).

Hart concluded that there is an inverse relationship between hunting pressure and the degree of expression of the vulnerability differential. Both he and Stokes (1954) suggested that age ratios from heavily shot areas may represent the population ratios more accurately than samples from lightly hunted areas. The problem is apparently a behavioral one, the adults not being able to use their experience in evading hunters in crowded areas.

Effect of Variations in Proportion of Cocks Harvested

Eberhardt and Blouch (1955) and Nomsen (1956a) pointed out a mathematical variable. The proportion of young cocks in the bag is highest at the beginning of the hunting season. At this time, the difference between the age ratio in the sample and that in the preseason population is greatest. As more young are cropped, the ratios of successive samples decline as does that in the total sample accumulated to date. If every cock is shot, the ratio in the total kill will have declined to the ratio of the preseason population.

The implication here is that, the higher the proportion of cocks shot the closer the age ratio in the season sample will approximate the ratio in the preseason population. Nomsen (1956a) observed that his age ratios were lower in years when postseason sex ratios showed a higher proportion of cocks shot, than in years when the percentage shot was lower.

Areas like the Lake States, with heavy hunting pressure and a higher percentage harvest presumably yield bag-check age ratios that more reliably approximate population ratios than do areas like the Plains States with their lighter pressure. Where the percentage of cocks shot varies between years or between areas, comparison may become tenuous.

Comparison With Other Reproductive Indices

As Eberhardt and Blouch (1955) observed, satisfactory methods for correcting biases in using fall cock age ratios for determining young-per-hen ratios have not been developed for pheasants. In the absence of such corrections, some insight into the usability of these ratios may be gained by comparing them with other reproductive success indices.

We have compared yearly young-per-hen ratios with our statewide average brood size (Fig. 34) and percentage of hens with young. Our cock age ratios have been obtained incidentally to other studies and do not equally represent the same portions of the state each year. Southeastern counties in primary pheasant range were sampled in 1953 (2 counties), 1954 (7 counties), 1955 (6 counties), and 1959 (2 counties). Marginal counties (2 in 1953, 8 in 1954, 12 in 1955-57, 13 in 1958) were sampled over a longer, more continuous period. The latter were subjected to a correlation test with average brood size which provided a correlation coefficient of 0.718, significant at the .05 level. Correlation of the marginal area young-per-hen ratios and percentage of hens with broods provided a coefficient of 0.465 which was not significant.

Visually, the 3-year series from the primary range followed the trends in marginal range fairly well, but the point for 1959 was off for possible reasons that we shall explore shortly. Correlation of the four points with average brood size for the same years did not approach significance.

The correlation between brood size and young-per-hen ratios from marginal range suggests that, despite the probability of varying bias between years owing to variation in percentage of cocks shot (Table 5, Chapter III) and other sources, the young-per-hen index appears to reflect year-to-year differences in reproductive success fairly well. The percentage-of-successful-hens comparison does not suggest this, and we do not know, whether this invalidates the ratios, or whether the problem is one of greater variability in the percentage-of-hens index as previously discussed.

On heavily hunted Pelee Island, similarly derived young-per-hen ratios reported by Stokes (1952) did not parallel yearly changes in young-per-hen ratios derived from hen age ratios. Wagner (1957) attributed this discrepancy to hen mortality bias in the latter ratios. No other reproductive success indices are available from Pelee for comparison. But the young-per-hen ratios derived from the cock age ratios followed general Midwest pheasant population trends in the 4 years of Stokes' study (Wagner, 1957).

Nomsen (1956a) compared summer, roadside young-per-hen ratios with corrected cock age ratios for a 4-year period when the percentage of cocks shot varied from 46 to 66, and averaged 58. We have tested these two series and obtained a correlation coefficient of 0.667 which is suggestive, but not significant with a sample of four points and two degrees of freedom.

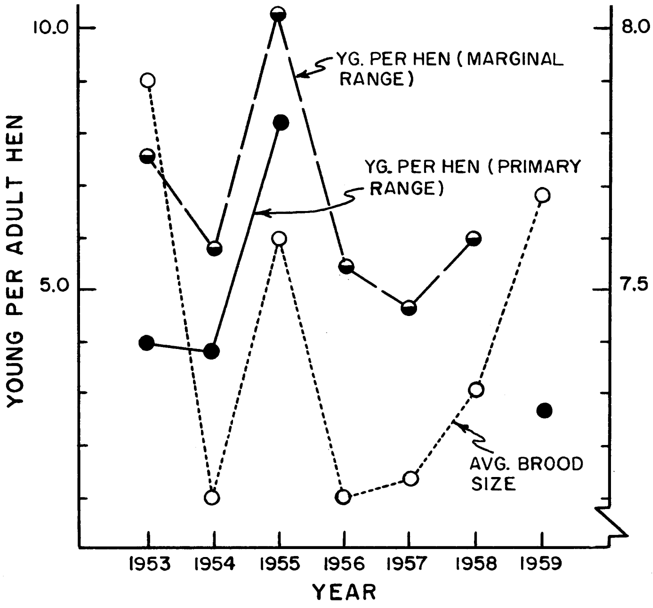


Figure 34. Comparison of young-per-hen ratios (derived from cock age ratios and adult sex ratios of the previous winter) and statewide average brood size.

Trautman (1955:5) reported ratios for young cocks per adult hen for South Dakota. We have doubled these to estimate the number of young of both sexes per hen, and compared them with young-per-hen ratios obtained from August mail-carrier surveys (Podoll, 1955). The two are not correlated (Fig. 35).

Dahlgren (1959) analyzed the various summer population indices for South Dakota during the period 1946-59, and reported good agreement in trend between the various indices, including the rural-mail-carrier counts, and fall population estimates. His findings suggest that these summer counts bear a substantial relationship to the population trends, and one might infer that it is the hunting season ratios in Figure 35 that deviate from the population parameters. South Dakota is more lightly hunted than the Lake States or Iowa, and young-per-hen ratios from hunting season data would be more affected by the bias discussed in the last section.

These combined tests seem to us to imply the increasing degree of bias, noted by the authors cited in the last section, with lowered hunting pressure. At some point between the hunting pressure levels of Iowa and South Dakota, the dependability of young-per-hen ratios may fade to the point where they do not reflect trends in reproductive success with any fidelity. The Wisconsin, Pelee, and Iowa indices appear to have some value as indices of this success.

The Wisconsin 1959 data merit special consideration for reasons mentioned above. Legs of 936 pheasants collected from Fond du Lac (J. M. Gates, unpubl.) and Dane Counties, both in good pheasant range, yielded a young-per-hen ratio of 2.6. This is the lowest ratio we have ever recorded (Fig. 34), and substantially below the previous 3-year mean of 5.3 for the better pheasant counties. The individual values for both counties were low (3.2 and 1.9, respectively) suggesting that a real drop rather than chance was involved.

The 1959 value fails to agree with the other reproductive indices which generally pointed to an average or good hatch. The statewide average hatching date was June 18, equivalent to the long-term mean, and perhaps indicative at least of an average hatch. The statewide average brood size was 7.7, the highest since 1953, and above the long-term mean of 7.4. The statewide percentage of hens with young was 85, higher than the long-term mean of 82. Thus, unless one of the two sets of data varied by chance, which does not seem likely, a discrepancy exists in the 1959 data.

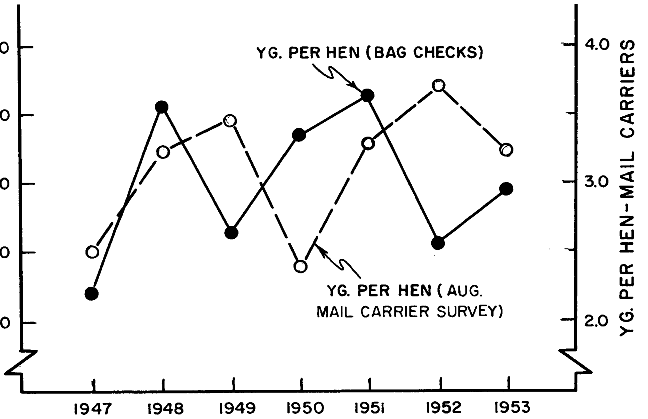


Figure 35. Comparison of South Dakota young-per-hen ratios obtained from hunting-season cock age ratios (adjusted with spring sex ratios) and from August roadside observations by rural mail carriers. Data from Trautman (1955) and Podoll (1955).

Two alternatives seem possible, and one or both may have been involved. The winter of 1958-59 was one of the severest on record in terms of amount and duration of snowfall, and severity of temperatures. The winter sex ratios—7.5 hens per cock, statewide—were the highest we have ever recorded. These followed a 44-day hunting season in 1958, also the longest we have ever held. One is inclined to attribute the high sex ratios to the long season, and doubtless this was involved. But conceivably, the severity of the winter magnified the number of hens per cock (as described by MacMullan, 1960, and by us in Chapter II) to some degree so that they were not comparable with previous years. An abnormally high sex ratio divided into a given cock age ratio will reduce the apparent young-per-hen ratio. This effect, possibly compounded with some of the other sex ratio variables discussed in Chapters II and III, could conceivably have made a faulty correction of the cock age ratios collected in 1959.

A second alternative involves a possible differential loss of hens. During the 1958-59 winter, we found our first substantial evidence of pheasant loss due to winter weather in Wisconsin. Heavy snow cover persisted until the last few days of March. Hens were observed with below normal weights (J. M. Gates, unpubl.) during March, and some hens undoubtedly entered the early stages of the breeding season in this condition.

Kabat, Meyer, Flakas and Hine (1956) suggested that subjection of hens with below normal physical reserves to the stresses of a breeding season could result in abnormal hen mortality. Wagner (1957) has discussed field evidence for the existence of hen loss due to reproductive stress.

If a large number of hens died between winter and summer without rearing broods, and a large fraction of the survivors successfully reared young, it could produce a disparity between summer indices and young-per-hen data from hunting seasons like the one in 1959. The low young-per-hen ratio would result from dividing the cock age ratio by the high sex ratio of the previous winter. The effective breeding sex ratio in summer would actually be lower, due to the hen loss perhaps in the early portions of the nesting season. The evidence however, is circumstantial. We only cite these as possible explanations of the 1959 discrepancy.

Variations Between Years

We compared Wisconsin young-per-hen ratios with the statewide average hatching dates (Fig. 36). The correlation coefficient between the marginal range series is −0.971, significant at the .01 probability level. The coefficient for the 4 years of primary range data is −0.821 which is short of significance.

Similar tests were conducted for shorter series of data from Pelee Island, Michigan, and Iowa. Wisconsin statewide average hatching dates were used as indices of nesting phenology on the assumption that phenological variations throughout much of the Midwest are comparable (Chapter IV); and that in the absence of average hatching dates from these areas, the Wisconsin dates could be used for crude tests.

The comparisons gave suggestive results, (Fig. 37), with high correlation coefficients for Pelee Island and Iowa (−0.903 and −0.868, respectively). The coefficient for the Michigan comparison was −0.500. None of these is significant at 2 or 3 degrees of freedom.

Similar comparison of Wisconsin average hatching dates with young-per-hen ratios from South Dakota (Fig. 35) showed no relationship.

These combined tests suggest a general correlation between nesting phenology and reproductive success as shown by young-per-hen ratios from hunting season data. South Dakota results do not support this conclusion, but perhaps the reflection of reproductive trends by these young-per-hen ratios is prevented by the biases discussed earlier in this chapter.

We have now examined a number of reproductive-success indices. All showed suggestive relationships with nesting phenology, but only a few were statistically significant. No one has yet unequivocally proved a relationship between phenology and total reproductive success as we have described it. But when the data are viewed in total, it seems probable to us that nesting phenology has an important influence on reproductive success in Wisconsin and probably over a large part of the Midwest. This has already been suggested by Kabat, Thompson, and Kozlik (1950).

We do not suggest that this is the only year-to-year variable involved. In some areas and in some years, its effects probably are masked by other overriding factors. But in many areas, particularly in the northern Lakes States and upper Mississippi Valley, it may be one of the most important influences.

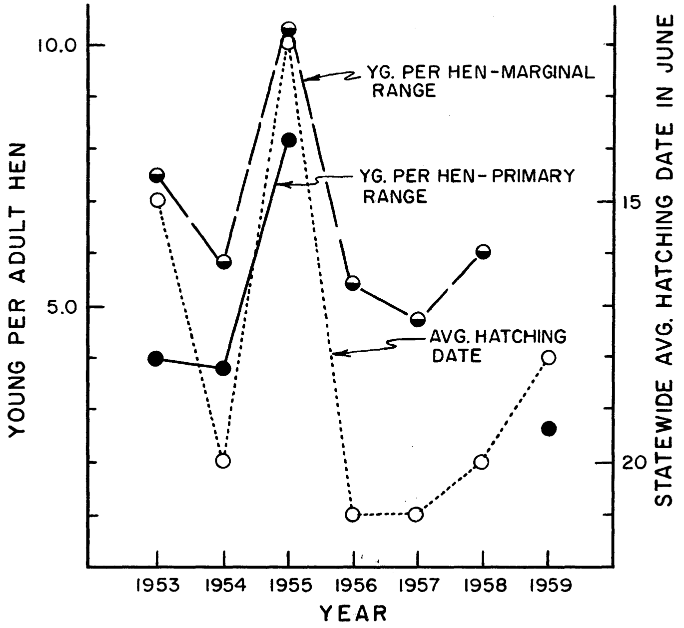


Figure 36. Comparison of Wisconsin young-per-hen ratios with statewide average hatching dates.

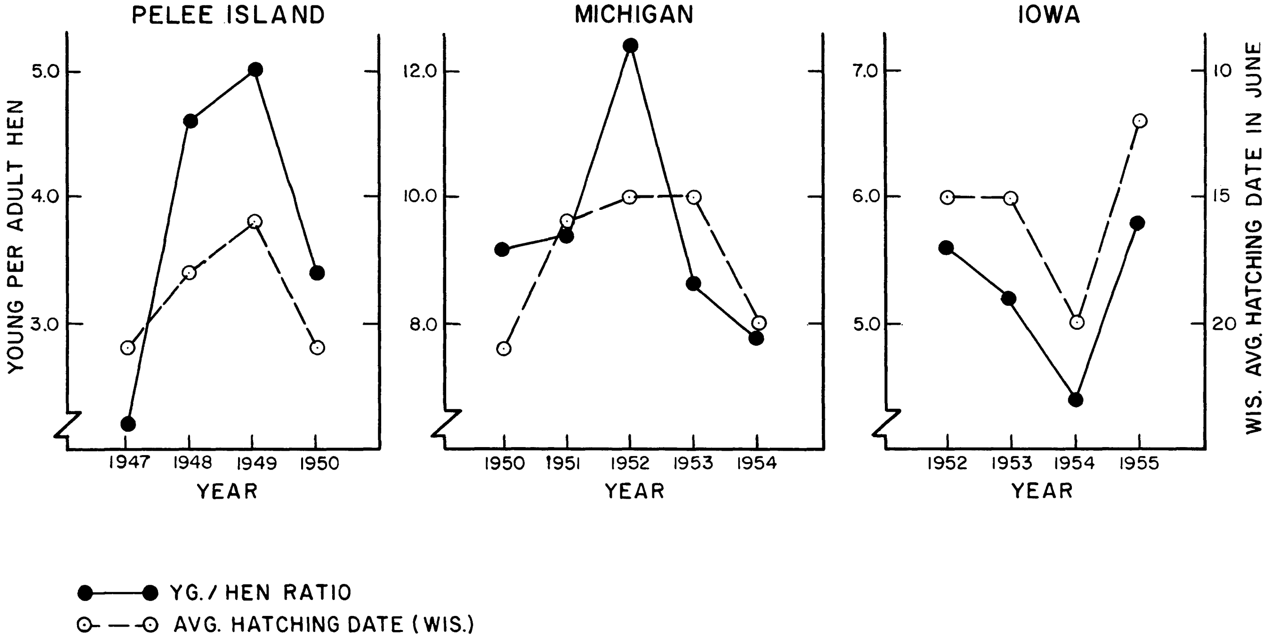


Figure 37. Comparison of young-per-hen ratios in Pelee Island, Michigan, and Iowa with Wisconsin statewide average hatching dates. Sources of young-per-hen ratios: Stokes (1952) for Pelee Island; Nomsen (1956a) for young cocks per hen for Iowa which we doubled to give young of both sexes per hen; and cock age ratios for Michigan by Eberhardt and Blouch, (1955) and Blouch (1955) corrected by us with sex ratios from Blouch (1952, 1953, 1954).

Variations Between Areas

For a 3-year period allowing comparison, young-per-hen ratios were higher in marginal Wisconsin pheasant range than in primary range (Fig. 34). Since the percentage harvest of cocks is higher in the primary range, as the sex ratios indicate, the marginal area ratios may be more inflated by the vulnerability bias. Hence it is not possible to compare these, or to learn whether productivity is higher in either of the regions.

Similarly, differences in young-per-hen ratios are evident between states (Fig. 36 and 37). But again the harvest rates vary, and the ratios cannot be corrected so that they can be reliably compared. In particular, the seemingly high Michigan ratios are probably not comparable because they are corrected with spring sex ratios reported by Blouch (1952, 1953, 1954). Spring sex ratios conservatively reflect the number of hens per cock (Chapter II).

Summary

Except under very heavy hunting pressure, cock age ratios are subject to bias by greater vulnerability of young cocks. The degree of this bias is inversely proportional to percentage of cocks shot. In areas such as Wisconsin, where a high proportion of cocks is shot annually, these cock age ratios appear to be representative of the true fall age ratio.

Wisconsin young-per-hen ratios derived from cock age ratios in marginal pheasant range are significantly correlated with average brood sizes. Relationships between a 4-year series from primary range and brood size, and with percentage of hens with young in summer, are not significant. Such ratios on Pelee Island (4 years) subjectively followed trends in other midwestern populations; in Iowa (4 years) were suggestively but not significantly related, and in South Dakota (7 years) were not related to summer reproductive indices.

Wisconsin young-per-hen ratios are significantly correlated in marginal range, but not significantly in primary range, with statewide average hatching dates. Similar tests for Pelee Island (4 years), Michigan (5 years), and Iowa (4 years) were suggestive but not significant, and showed no relationship in South Dakota. Reproductive data from all chapters collectively imply that nesting phenology influences reproductive success in Wisconsin and probably over a large part of the Midwest. Young-per-hen ratios from different areas cannot be compared because of variations in bias.

CHAPTER VIII.
POPULATION MECHANISMS IN SHORT-TERM POPULATION FLUCTUATION

Reproductive Success

A large number of references in the literature on ring-necked pheasants allude to a relationship between reproductive success and fall population levels or annual fluctuations. For review of various general phases of this problem, see Kimball (1948), Wandell (1949), and Allen (1950).

Several of the reports have shown correlations between annual fluctuations and changes in brood sizes, percentages of hens with broods, and/or changes in young-per-hen ratios. Thus, Leedy and Dustman (1948) and Studholme and Benson (1956:401) both reported that broods were smaller in Ohio and northeastern United States during the decline years of the middle 1940's than in the years of population increase preceding and following. Allen (1941, 1942a, 1943, and 1946a) and Patterson (1944, 1945) reported that brood sizes on the Rose Lake Experiment Station in Michigan averaged between 6.8 and 7.3 between 1940 and 1942. During the decline years of 1943 and 1944, broods averaged between 4.6 and 5.4.

Leedy and Dustman (1948) and Studholme and Benson (1956:401) also reported that the percentage of hens with broods was below average during the decline years. MacMullan (1948) reported that half of the hens had broods by the end of July in Michigan in 1947, the last of the decline years. In 1948, the first of the recovery years, two-thirds of the hens had broods. Mohler (1954) found over 80 percent of the hens had broods in 1948 and 1949 in Nebraska, years in which the population increased. In 1952 and 1953, this percentage dropped to 65 or lower, and the population declined in 1953.

Low young-per-hen ratios have also been found (Allen, 1950). Kimball (1948) observed low ratios in South Dakota in 1946 and 1947 during the decline. Mohler (1948) reported lower young-per-hen ratios for Nebraska in the period 1943-47 than was observed in 1942 and 1948. Nomsen (1956) observed a relationship between young-per-hen ratios and population trend in Iowa.

These findings are all useful. But in order to visualize more precisely the manner in which annual changes in reproductive success affect population change, and the relationships between density levels of different seasons of the year, data are needed over a prolonged series of years on reproductive success and on population levels of at least two seasons. A number of long-term studies, both intensive and extensive, have been underway since the middle 1940's that provide this type of information. We now examine several of these, beginning with our own data.

Wisconsin Findings

We tested correlations between fall population trends and six indices of reproductive success. The population trend index is the percentage change in the estimated kill from that of the previous fall. Reproductive success indices include statewide average brood size (13 years), percentage of hens with young statewide (7 years) and in Green County (9 years), young-per-hen ratios from cock age ratios in fall in marginal range (6 years) and primary range (4 years), and statewide average hatching dates (13 years).

Of these 6 tests, the 4 shown in Figure 38 suggest patterns with 3 significant at the .05 level. The 4-year sample of young-per-hen ratios from primary range, also suggestive, yielded a correlation coefficient of 0.633 but was not significant. Statewide percentage of hens with young did not suggest a relationship visually, and we did not test it.

In the tests involving average hatching date and average brood size, 1959 again appears as an aberrant year as we noted in the last chapter. Thus we omitted it from the other two tests shown in Figure 38, but included it in the 4-year sample of primary-range young-per-hen ratios. Hence, the brood size and average-hatching-date correlations apply to the period 1947-60 with 1959 excluded.

The results in Figure 38 show relatively strong relationships despite the fact that we are comparing two sets of

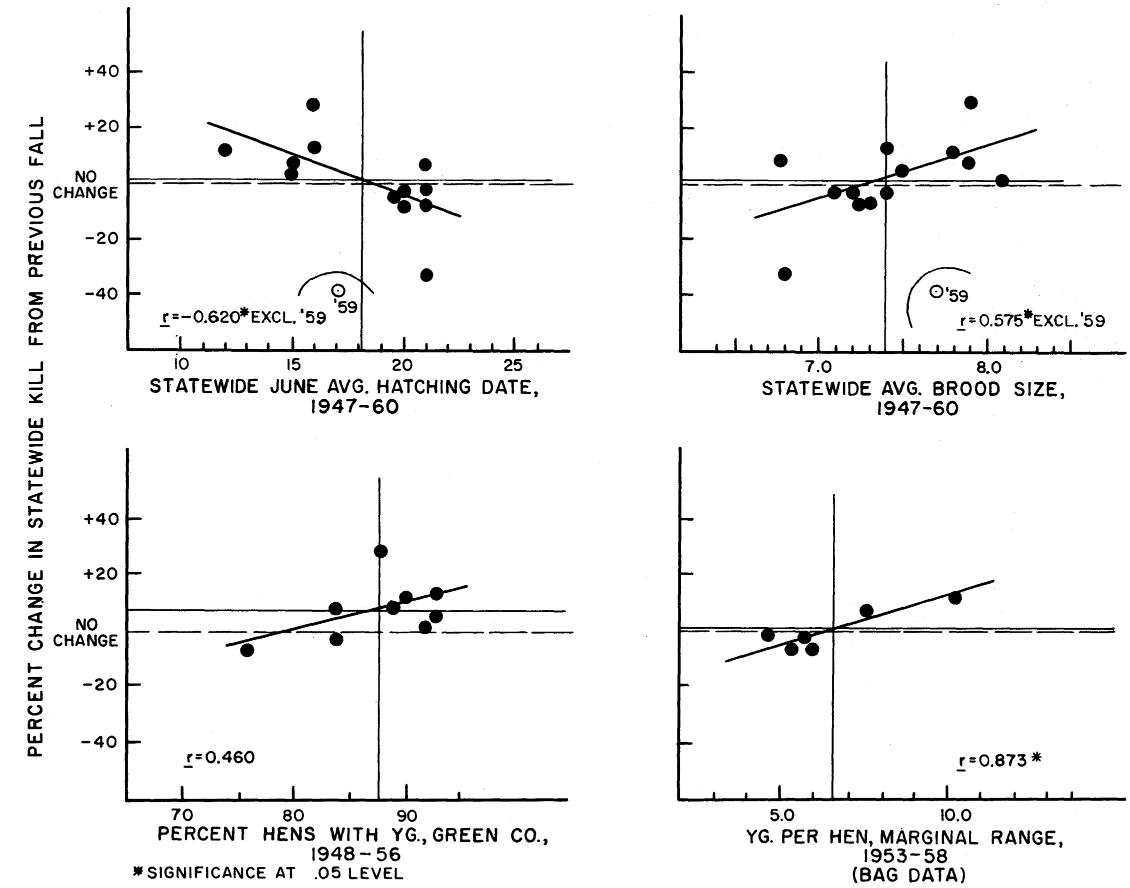


Figure 38. Correlation between reproductive success and short-term fluctuation in fall populations in Wisconsin.

variable indices that are subject to many biases. Thus, the true relationships may be even stronger than the correlation coefficients suggest.

The reproductive success of a given spring hen population is a function of (1) the percentage of those hens that succeed in rearing broods, and (2) the average size of their broods by an age of reasonable self-sufficiency. Some of the factors influencing these two components undoubtedly are different, and some of their variation is, in all likelihood, independent. However, some of their yearly variation is related through the common correlate, nesting phenology.

One of these components (brood sizes) and the index of total reproductive success (young-per-hen ratios), as well as the index of nesting phenology itself are all significantly correlated with population trend. This seems to us to heighten the probability of a strong interrelationship between nesting phenology and both components of reproductive success, and between reproductive success and population trend.

Before leaving the Wisconsin results, we would like to point out several implications of the correlations in Figure 38. First, if the series of observations shown is long enough to cover essentially the normal range of variation that occurs over a period of time, it is the departure from average reproductive success which results in population change. Years with average reproductive success are associated with no change in the population level.

This conclusion may seem simple and obvious, but it carries with it the implication that there is a tendency toward population balance.[1] If reproductive success is normally distributed around its mean, most yearly variations will cluster around the mean, and population changes will be minor. The small percentage of large deviations in one direction will be balanced by an equal number of similar deviations in the opposite direction. The net effect will be oscillations

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[1] The question of population balance is a complex one. Population students do not agree on its existence, or on whether or not there is a need for the concept (*cf.* Nicholson, 1933; Lack, 1954:7-20; Andrewartha and Birch, 1954: 20, 649). We explore the question more fully in later chapters. For the present, the concept as we use it implies a net population trend that is roughly level within the limits of short-term fluctuation, and without progressive increase or decrease. The number of animals born is approximately equal to the number of animals dying during that period. There may be fluctuations, but they tend to oscillate around the mean for the period.

Our point here is not whether balance exists or not, but that the population characteristics we are examining suggest a tendency toward balance.

around a long-term mean, provided the habitat is reasonably stable and the relationships in Figure 38 hold for a longer period of time than that covered by the observations we are reporting here.

A second implication of the correlations in Figure 38 is that variations in reproductive success are correlated with population change but not necessarily with population density itself. Thus, high reproductive success may result in an increase from the previous fall in population level. But if that previous level was low, the new level may still be low despite good reproduction and a substantial increase. Similarly, a year with poor reproduction could still be associated with good densities, despite some decline, as long as the density of the previous year was high.

A corollary of this last point is that variations in reproductive success are associated with variations in population level, but the two are not necessarily parallel in direction. For example, a very high reproductive rate may be associated with a substantial population increase in a given year. If, in the following year, the reproductive rate drops to a moderately high, but still above-average level, the population will increase again but to a lesser extent. Hence a decline from a previous year in reproductive rate can still be associated with a population increase as long as that rate remains above the mean. Only in years when the reproductive rate varies back and forth about its mean will these variations be parallel in direction with variations in population trend.

Findings From Other Midwestern Areas

We have attempted to correlate reproductive indices and population trends from Minnesota and South Dakota (Fig. 39). The Minnesota reproductive index is the average brood size while the population trend is based on late-summer roadside counts (from Erickson *et al.,* 1951; and Arnold B. Erickson, *in litt.*). The South Dakota data are young-per-hen and birds-per-mile statistics from rural mail carrier surveys in summer (Podoll, 1955; Dahlgren, 1956a).

Similar comparison for shorter series of years were made for Pelee Island and three midwestern states (Fig. 40). Pelee Island and Michigan young-per-hen ratios are those used in Figure 37. Population trend values for Pelee Island are based on change in number of hens alive from a point after the hunting season of one year to the number present before the hunting season of the next year (Stokes, 1952). This avoids the effect of variations in the proportion of hens taken during the hunting season in these 4 years. The Michigan population index is the annual kill estimate of the Game Division of the Michigan Department of Conservation (Blouch, 1954 and *in litt.*).

Iowa young-per-hen data were taken during late-summer roadside counts (Nomsen, 1956). The population index is based on roadside counts (Kozicky *et al.,* 1952; Richard C. Nomsen, *in litt.*). The North Dakota data are from roadside counts (Bach, 1944).

Except for the Michigan test, the results suggest a correlation between reproductive success and relative trend in late-summer or fall populations somewhat similar to that shown for Wisconsin (Fig. 38). However, none of the six is statistically significant. The Minnesota and South Dakota tests are each marred by a single, erratic point. Without these the Minnesota data attain the .01 level while the South Dakota data approach, but fall short of, the .05 level.

The span of years covered in each case is shorter than the total period covered by the Wisconsin data, and it is questionable whether they represent the full range of variation over a long enough period to reflect average reproductive success or average population trends. For example, the period covered by the North Dakota data coincided with a period

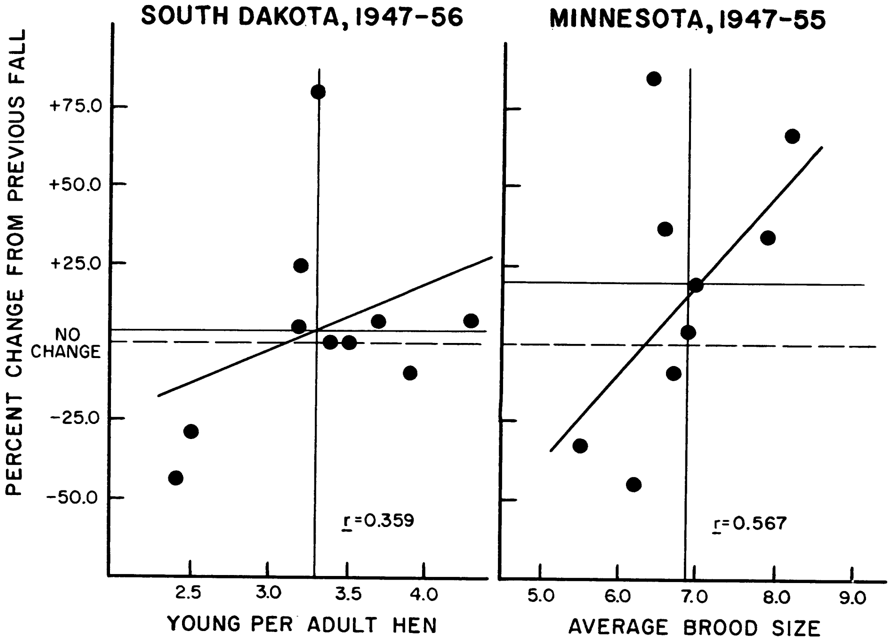


Figure 39. Correlation between reproductive success and short-term fluctuation in fall populations in South Dakota and Minnesota. See text for sources of data.

of population increase throughout the Midwest, and the large, average increase rate reflects this.

The large increase rates shown for Pelee Island are typical for that population as we will show in subsequent chapters. These rates are one of the unique features of the population mechanics on this island.

Hen Mortality

The correlation shown in Figure 38 would seem to imply one of two alternatives regarding annual mortality rates of hens in Wisconsin for the years studied: (1) Annual mortality rates must be fairly similar each year. If mortality varied markedly between years and were independent of reproductive success, the correlation in Figure 38 could not exist. (2) If hen mortality rates do vary markedly between years, these variations must be correlated with reproductive success. The reasoning is the same as for the first alternative.

What evidence we have on annual mortality rates in hens shows marked variations between years. McCabe's (1949) data for the University of Wisconsin Arboretum implied mortality rates varying between 46 and 84 percent per year. On Pelee Island, annual hen mortality rates varied between 36 and 58 percent in the 4 years of Stokes' (1952) study.

The mortality variations in these areas appear to have been correlated with nesting phenology and/or reproductive success (Wagner, 1957). Hence, the evidence seems to support the second of the two alternatives given above. And since reproductive success is correlated with population trend, it follows that hen mortality also tends to be correlated with population trend.

A number of observations from elsewhere in the Midwest bear out this deduction. Leedy and Dustman (1948) noted that the population decline of the 1940's in Ohio was characterized by a higher-than-normal proportion of cocks in September, suggesting increased hen loss. McCabe (1949: 142) concluded for the Wisconsin Arboretum that "Population decline on this area in the period 1943-44 to 1946-47 appears to have resulted not only from a declining production of young but from an apparently declining survival rate as well." On Pelee Island ". . . it appears that the large increase in pheasants between 1946 and 1949 was dependent upon high survival. The population failed to increase in 1950 because of lower annual survival . . ." (Stokes, 1952).

We conclude that the evidence now available suggests that annual hen mortality rates, at least in the northern Lake States, may be inversely correlated with reproductive success.

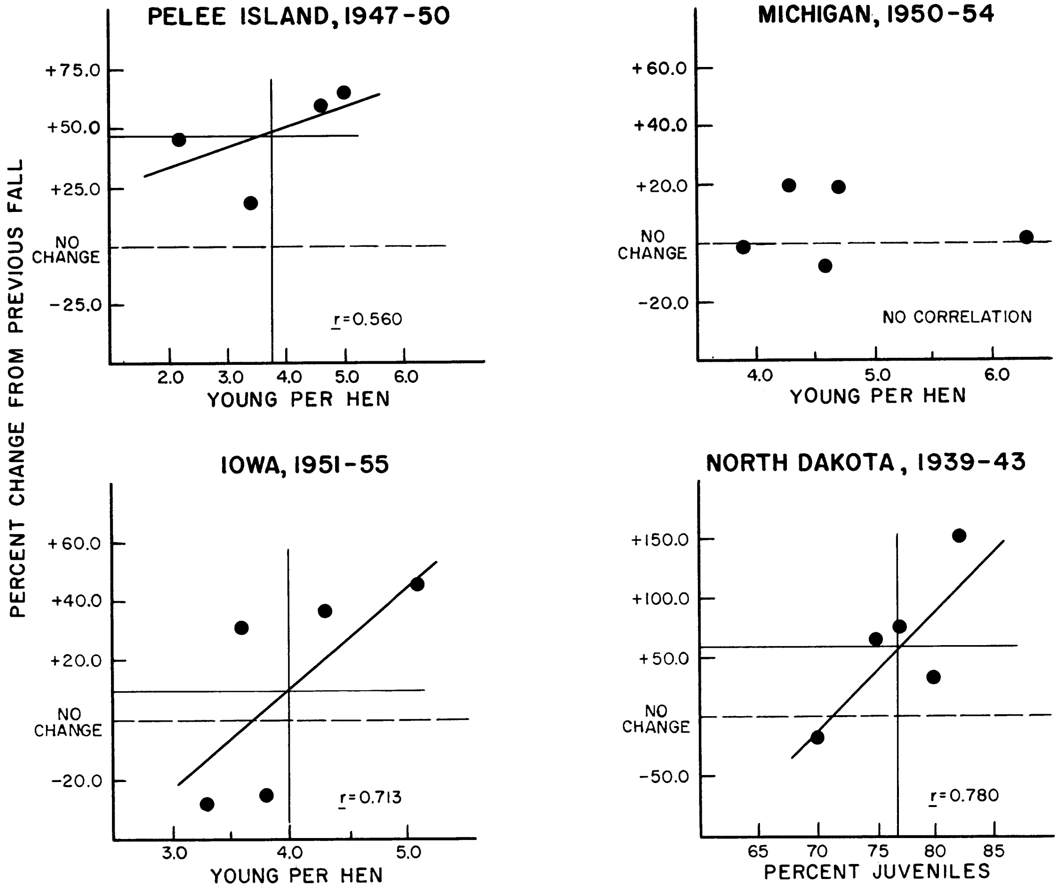


Figure 40. Relationship between reproductive success and short-term fluctuation in fall populations in four north-central areas. See text for sources of data.

Years of successful reproduction seem to be associated with low hen mortality. These factors together are correlated with population change. A thorough test of these conclusions must await findings from a number of long-term studies on annual mortality rates.

Some provisional deductions can be drawn regarding the seasonal pattern of hen loss. There already are indications from Wisconsin and Pelee Island of yearly variations in summer hen mortality, and these are correlated with total annual mortality rates and population change (Wagner, 1957).

What needs exploration is the pattern of variation in fall-to-spring loss. Kabat, Thompson, and Kozlik (1950) suggested that winter mortality in adult hens may be higher following a late nesting season in which hens have been subjected to above-average stress, and in which the molt and assumption of winter fat reserves are delayed. Furthermore, we suggested in Chapter V that the hardiness of the chick crop may be lower in a late-nesting year. Conceivably such a crop could be more vulnerable to winter loss than a healthier crop of young.

We have no direct measures of over-winter mortality, but some preliminary and tentative indications can be obtained deductively. Seemingly, average reproductive success could not restore fall densities to the levels of previous years when severe winter losses intervened to lower breeding densities. The correlations in Figure 38 imply that average reproductive success maintains fall populations at about the same levels.

To clarify this point, we set up a model using hypothetical values in an attempt to reconstruct the trends in two theoretical populations (Table 15). In one, fall-to-spring hen loss does not vary between years regardless of the phenology of the nesting season. In the second, fall-to-spring loss is inversely correlated with reproductive success, there being greater loss following a poor hatch.

We begin the first fall with 100 hens, and by the first spring we lose a hypothetical 50 percent or 50 hens. In both populations we start the first spring with 50 hens at step 3 of the table.

According to our findings an average hatch will bring this spring hen population back to the level of the previous fall. We assume further that there is no spring-fall hen loss in an average year and that average production for 50 hens is 50 young hens. (We know that some hen loss does occur between spring and fall of an average year, but for simplicity we will assume there is none in an average year, and some spring-fall loss in a poor year. The outcome in our model will be the same as if we allowed moderate summer hen loss in an average year, and heavy loss in a poor year as actually appears to be the case.) In this way, with a series of average years, population levels for successive falls will be the same as the situation in Figure 38 implies, and as is shown for steps 1-5 in Table 15.

We now assume that the average spring population of 50 hens at step 7 experiences a poor hatch in step 8. We add only 25 young hens, and subtract 10 adults for above-normal summer loss. We go into the third fall in both columns of the table with 65 hens, a reduction from the level of the second fall and again consistent with Figure 38.

TABLE 15

Hypothetical Construction of Hen Population Trends in Two Populations in Which Fall-Spring Mortality is Similar Between Years in One and Inversely Correlated with Reproductive Success in the Other*

	Fall-Spring Mortality Similar In All Years	Fall-Spring Mortality Higher Following a Late Hatch
1. **First fall hen population**	100 Hens	100 Hens
2. Deduct 50 percent fall-spring loss	−50	−50
3. First spring hen population	50	50
4. First breeding season: add avg. production of 50 young hens	+50	+50
5. **Second fall hen population**	100 Hens	100 Hens
6. Deduct 50 percent fall-spring loss	−50	−50
7. Second spring hen population	50	50
8. Second breeding season, late hatch: Add poor production of 25 young hens, deduct adult loss of 10	+25 −10	+25 −10
9. **Third fall hen population**	65 Hens	65 Hens
10. Deduct 50 and 62 percent fall-spring loss	−32.5	−40
11. Third spring hen population	32.5	25
12. Third breeding season: Add avg. 1:1 production	+32.5	+25
13. **Fourth fall hen population**	65 Hens	50 Hens

*The values in this model are hypothetical, and we do not imply that they represent actual population values. Their relationships to each other, and directions of change do represent what could be expected in a real population.

It is from this point on that an increase in fall-spring loss following a poor hatch will make a difference. In the first column, we deduct the standard 50 percent fall-spring loss, and follow with an average hatch at step 12. The population level of the fourth fall (step 13) returns to the same 65-hen level of the third fall as it should following an average hatch (Fig. 38).

In the second column, instead of the standard 50 percent fall-spring deduction from the 65 hens of the third fall, we deduct 40 hens or roughly 62 percent. This leaves a spring hen population of 25 which, with average 1:1 production at step 12 results in a population in the fourth fall of 50 hens. This is a 23 percent drop from the previous fall with an intervening average hatch which, according to Figure 38, should maintain fall stability.

It is possible to set up a similar model, comparing good and average reproductive success with less fall-spring mortality in the good year than in the average year. In such a situation one can get a fall population increase with an average hatch in a year following a good hatch. This again is contrary to the evidence in Figure 38.

If the assumptions of our model are realistic, these results and the correlation in Figure 38 give one preliminary suggestion that fall-to-spring mortality may not vary markedly between most years.

This conclusion must be reconciled with what we know about variations in winter loss. In Wisconsin, the one year during the period covered in this report that deviated markedly from the pattern we have described was 1959 and the events surrounding the fall population decline in that year.

The winter of 1958-59 was the most severe on record for the past 39 years in terms of low temperatures and snowfall. Mortality from a number of causes was higher than normal (Gates, 1959; Wagner and Woehler, 1960; Besadny, 1960). By spring 1959, the crowing-count hen index was 40 percent below that of the previous spring. The kill in 1958 had fallen 8 percent below the 1957 level. As we will see shortly, spring populations carry through in much the same trend as that of the previous fall. Hence some decline in spring 1959 was probably destined to occur as a result of the same decline in fall of 1958. But the 40 percent drop was considerably more than the 8 percent drop of the previous fall, and the additional drop in the spring breeding population very possibly was due to winter loss.

The kill of fall 1959 was 39 percent below that of fall 1958. Whether the hatch in 1959 was good or not, a 39-percent population decline is an unusually large one and was probably due, at least in part, to the heavy loss of birds in the 1958-59 winter.

The winters of 1942-43, 1947-48, 1951-52, and 1959-60 were considered severe in varying degrees; each was characterized by heavy snow cover and cold temperatures for prolonged periods. However, except for the extremely severe winter of 1958-59, we can find no direct evidence to indicate that winter loss in Wisconsin has been substantial in any year for which we have data. Allen (1950) has already suggested that, with the possible exception of the Plains States, winter loss in the Midwest may not be as important as sometimes thought.

The inverse correlation between reproductive success and spring-to-fall hen mortality carries with it certain implications regarding the degree of instability of midwestern pheasant populations. If the population mechanics were such that reproductive rates and mortality rates each year compensated for each other—if mortality rates increased when reproductive rate increased, and vice versa—the tendency would be to damp fluctuations. However, a successful breeding season apparently is accompanied, not by an increase in mortality, but by a decrease. The reverse is true regarding a poor hatch. Therefore, pheasant populations in much of the Midwest are predisposed to fluctuate to some degree.

Seasonal Changes in Density

Relation of Spring Density to Population of Previous Fall

If it is true that winter mortality is roughly constant between most years, it follows that spring population levels each year also must be a roughly constant fraction of the preceding fall levels. As fall populations fluctuate up and down through a series of years, the population levels of succeeding springs should follow parallel but lower trends. This could be tested by comparing trends in fall and spring indices over a period of years.

We have made such a comparison for Wisconsin using the kill estimates and the spring crowing-count hen indices (Fig. 41). They show parallel trends, and when subjected to a correlation test yielded a correlation coefficient of 0.879, significant at the .01 level.

Similar parallels between fall and spring populations can be seen in published data from other states. Bach (1944), Dahlgren (1959), Mohler (1948, 1951), and Linder, Lyon and Agee (1960) have shown this relationship for a short period of years in North Dakota, in South Dakota, and in Nebraska, respectively. It may also be observed in data from the Winnebago County study area in Iowa (statistics from Green, 1948; Baskett, 1947; Kozicky and Hendrickson, 1951). It may also be observed in Michigan data from the Rose Lake Experiment Station (Allen, 1942a, 1943, 1946, 1946a; Patterson, 1944, 1945) and from the Prairie Farm in Saginaw County, Michigan (Shick, 1952).

It does not necessarily follow from these findings that fall-to-spring loss is roughly constant. This may be the case, or the correlation could still hold if over-winter loss were relatively light but still variable (J. J. Hickey, pers. comm.). The correlation probably could not hold if winter loss were heavy (e.g. 50 percent or more) and variable.

The only conclusive test of the constancy of fall-to-spring loss would be comparison of fall and spring numbers based on actual counts over large areas, and it would be difficult to obtain such data. Comparisons can be made of study area censuses, but these rarely span a long series of years and take on the new variables of ingress and egress. Comparison of the summer chick populations and spring hen numbers reported by Linder *et al.* (1960) for a 4-year period show less than 10 percent variation between years in shrinkage from summer to the following spring. In 3 years on the Prairie Farm in Michigan (Shick, 1952) the percentage decline between the fall cock population (an index to the fall hen numbers) and the hen population of the following spring varied between 35 and 39—a maximum difference of about 10 percent. However, Einarsen's (1945) 5-year series for

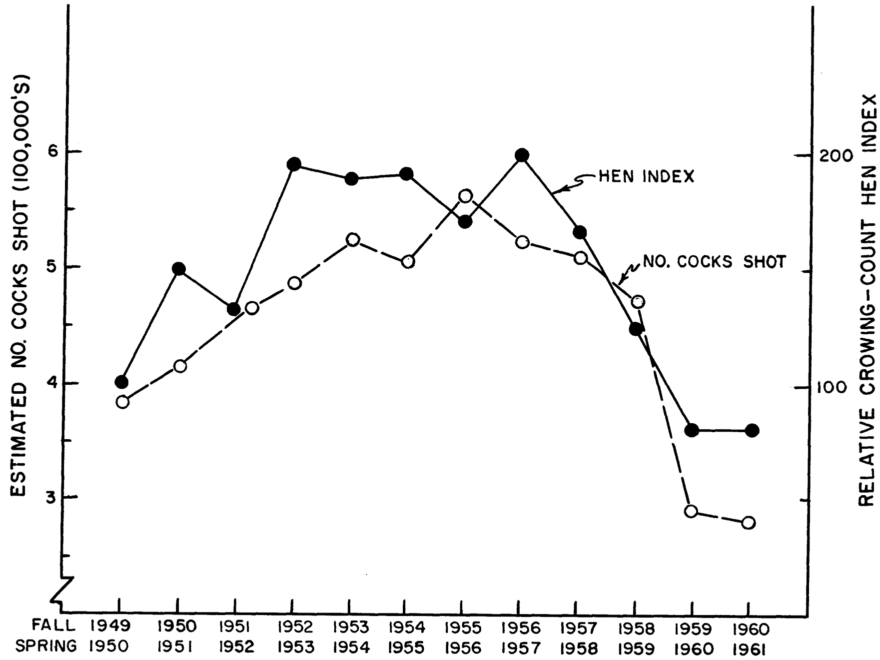


Figure 41. Comparison of spring population density with the population level of the preceding fall in Wisconsin. Spring density is represented by the relative crowing-count hen index (Figure 14) while fall density is reflected by the estimated kill.

Protection Island show over-winter losses that vary between 13 and 33 percent, and this is an environment that probably contained fewer mortality factors than most continental areas.

With present evidence, we conclude that fall-to-spring correlations imply that winter loss is roughly constant, or is relatively light and variable, between most years. These correlations indicate that trends in spring numbers are strongly influenced by the trends of the previous autumns. Fall trends, as we have seen, are mainly determined by the success of the breeding season and correlated hen mortality. Thus, the population trend from one fall to the next cannot be predicted by the trend of intervening spring level relative to the previous spring. These trends could be predicted by sufficiently accurate reproductive success indices without regard for spring population trends.

Relation of Fall Density to Population of Previous Spring

While relative spring-to-spring trends do not have a material influence on relative trends of fall populations following, actual fall densities are related to densities of the preceding springs. Note in Figure 41 that, if the kill estimate line were slid one point to the left in order to compare spring and fall indices of the same year, the two lines would still show a close relationship. Test of this new comparison produces a correlation coefficient of 0.831, again highly significant.

Similar tests can be made of the data in other states. Dahlgren's (1959) spring rural-mail-carrier's index and his prehunting season population estimates for the period 1947-58 in South Dakota give a correlation coefficient of 0.725, significant at the .01 level. Bach's (1944) North Dakota data for 1939-43 give a significant (.05 level) 0.898 for his spring and summer indices. In Nebraska (Linder, Lyon and Agee, 1960), spring hen populations between 1955 and 1959 suggest a correlation with the number of chicks produced in the following summer ($r = 0.613$) but the relationship is not significant. This relationship is also suggested by Mohler's (1948, 1951) seasonal indices.

The published data for the Winnebago County area in Iowa are not continuous, but suggest a correlation between spring and fall densities. Spring hen populations varied between 17 and 40 per section in 1936-38 (Green, 1938) and 1949-59 (Kozicky and Hendrickson, 1951), and were followed by fall densities on the order of 100-125. In 1940 and 1941, spring densities numbered 54 and 83 per section, and fall densities rose to 210 and 370, respectively. The series of spring and fall densities for the Rose Lake Station in Michigan (cited above) for 1940-45 did not suggest a correlation.

These findings suggest that fall levels are a function of spring densities. And they seem to imply that reproductive success varies between limits that are narrow enough to allow the expression of this correlation, which in some cases is quite strong. In the case of Wisconsin, the correlation coefficient implies that about 69 percent ($0.831^2 = 0.691$) of the variation in fall density during the period 1949-61 was associated with the variation in the spring hen population, leaving limited space for the influence of reproductive success.

This may at first glance seem to be a reversal of the position we have emphasized earlier in this chapter largely deduced from Figures 38-40: that population change is importantly a function of reproductive success and its possible correlate, spring-to-fall hen mortality. Some elaboration is needed in the interests of clarity.

The correlation between reproductive success and population change (Figs. 38-40) seems to be a strong one, the correlation coefficients averaging 0.612. This is not at variance with the 0.831 correlation between spring and fall numbers. The latter implies that somewhere near 69 percent of the variation in *fall density* per se during the period 1949-61 was associated with variation in spring density. The space remaining for variation in fall density due to other causes, particularly variation in reproductive success, is limited (31 percent at most). This is borne out by the range of population change shown in Figure 38. Increases in Wisconsin of more than 30 percent have been rare.

But within this degree of annual change that has occurred, variation in reproductive success and its possible correlate spring-to-fall hen loss, varying with weather, has assumed an important role. We will also find later that variations in density, operating through the reproductive rate, have also been associated with a major part of the annual change that occurs, limited though that change may be.

It follows that populations often change gradually, their previous densities acting as drags to prevent sudden change, i.e. they display marked serial correlation. The Wisconsin declines of the 1940's and late 1950's required 5 and 4 years, respectively. The buildup to the 1955 high required 8 years following the 1947 low.

Alternative Hypotheses

The concepts we have proposed need to be reconciled with two other, somewhat differing, interpretations of pheasant population behavior. The first of these may be termed, for convenience, the "winter-bottleneck" hypothesis. Lauckhart (1955) and Lauckhart and McKean (1956) have been among its principal advocates.

These authors concluded that reproductive success, and hence fall densities, vary between years. But winter environments can carry only a limited number of birds. Fall populations are reduced to the level of the winter carrying capacity or "squeezed" through the "winter bottleneck." Spring levels tend to be fairly constant, and ". . . on a given piece of range . . . represent its winter carrying capacity . . ." (Lauckhart and McKean, 1956:62).

This concept would seem to carry with it several implications: If fall levels vary and spring densities are roughly constant, fall-to-spring mortality must vary markedly and be density dependent. High fall densities must experience heavy winter loss in order to be reduced to the winter or spring asymptote. Low fall densities would sustain lighter losses in being cut to the carrying capacity level. And finally, fall densities would bear little or no relationship to the levels of the following springs.

These implications are at variance with the data we have examined. Some variation is possible in winter loss within the limits of the fall-to-spring correlation, but this relationship appears to be stronger than the spring-to-fall correlation. In Wisconsin, the higher *r* value implies that 77 percent of the variation in spring density is associated with variations in densities of the previous falls, while the reverse relationship was 69 percent. The strength of the fall-to-spring relationship has led a number of biologists to call attention to it (cf. Dahlgren, 1959; Linder *et al.,* 1960), although the spring-to-fall correlation is infrequently noted.

The evidence we have does not seem to support the pronounced winter-bottleneck phenomenon. This concept also implies little, if any, serial correlation in pheasant populations which is quite evident in the data we have examined, and a frequent characteristic of animal populations (Cole, 1954).

The second hypothesis may be termed for convenience the "inversity" hypothesis. Its main proponents have been Allen (1953; 1956:436-437, 459-461) and Linder, Lyon and Agee (1960). The essential feature of it is that an area can support only a given number of birds in summer or fall. Spring densities may vary, and the rate of spring-fall gain will vary accordingly. When spring populations are low, the number of hens successfully hatching nests (Linder *et al.,* 1960) or perhaps the survival of young (Allen, 1956) may increase in order to reach the summer or fall carrying capacity. At most times, the hens on an area are capable of producing more young than the environment can carry, and so there tends to be an excess of hens.

How fixed and narrow the limits of carrying capacity are, according to these views, apparently varies between the authors and is not easy to infer exactly. Allen has spoken of it being "well-defined" and "limited" (1953) and has pointed to the similarity in fall population level in 3 years on the Winnebago County, Iowa, study area (1956:437). But elsewhere (1950) he has pointed to variation in fall numbers, apparently due to the effects of weather on reproductive success.

Linder *et al.* (1960) imply that carrying capacity in any one year is fairly exact in terms of the number of successful nests or broods a given area will support. But this level will vary between years, depending on the quality of the cover, and hence variation is possible in fall densities.

However, these authors emphasize that areas frequently have surplus hens. Thus fall density is primarily a function of the characteristics of an area, and hence bears little relationship to the number of hens present above a certain minimum.

It is difficult to discuss the similarities and differences between these concepts and our own without more precise description because it is probable that any difference is more quantitative than qualitative. We agree that different areas support different mean pheasant densities. But it does not appear to us that these are well-defined or narrowly limited. Midwest areas have typically fluctuated over the past 25 years through spring and fall densities that have varied by a factor of 2 to 4. It is also clear to us, as we shall note in a later chapter, that a degree of inversity is evident in pheasant population behavior—i.e. that reproductive output per hen is inversely correlated with spring density. However, this is only a single factor in a multifactorial complex operating on reproductive success which is frequently overridden by the other influences.

Consequently, we do not feel there is the compensatory flexibility that we infer from the writings of the above authors. Reproductive success seems to vary between restricted limits. The small influence inversity has on the pheasant cannot entirely pull reproductive success out of the heavy confinement of these limits, and produce a large fall population with a small or even average breeding density. Hence, the number of hens available in spring is important, and we do not infer from our findings that surplus hens are generally present.

Regional differences may prevent any precise generalizations for the entire Midwest. Dustman and Wagner (1960) observed that renesting flexibility in hen populations may be greater in the more southerly portions of the pheasant range such as Nebraska, Illinois, and Ohio. Nesting seasons there may be longer, the potential for renesting accordingly greater, and perhaps compensatory flexibility more pronounced.

Summary

Of 6 comparisons between reproductive success indices and fall population trends for Wisconsin, 5 showed suggestive correlations (3 were significant), and a sixth did not suggest a relationship. Departures from average reproductive success apparently are associated with population change, and the population approaches balance around its long-term mean. Variations in reproductive success are correlated with population change but not necessarily with population density itself. Similar comparisons for shorter series of years are suggestive in 5 of 6 other states.

Adult hen mortality rates may vary inversely with reproductive success. Variations in annual mortality rates seem to result primarily from variations in spring-to-fall loss. Fall-to-spring mortality is roughly constant or relatively light and variable in most years, except perhaps in the Plains States. Hence trends in spring densities are importantly determined by trends in the preceding fall populations. Fall trends can possibly be predicted from reproductive indices without regard for spring trends.

While spring trends do not have a strong influence on fall trends, actual fall densities are related to densities of the preceding springs. Hence, the range of variation in reproductive success must be somewhat limited.

The concept of a relatively limited winter carrying capacity, rough constancy in spring densities, and varying, density-dependent winter loss does not seem to be borne out by the midwestern data. Spring population levels vary as widely as fall levels.

Our views do not differ as much with the concept of a relatively limited summer or fall carrying capacity, inversely varying rates of spring-fall gain, and surplus hens being the rule. While there does appear to be a limiting density range in any area, and while there is an inverse correlation between spring population and reproductive rate, we hold that fall levels vary markedly and that any carrying capacity effect is a loose one. Inversity is a limited influence operating in a complex of factors that often override it, and fall numbers are a function of spring numbers.

CHAPTER IX. WEATHER IN SHORT-TERM POPULATION FLUCTUATION

A detailed analysis of the many ways in which weather and its many patterns of influence might operate on pheasant populations is beyond the scope of this report. In this chapter we examine the factors affecting nesting phenology in some detail because of the evident influence of phenology on reproductive success and hen mortality, and consequently on population trend. We consider a number of implications of these relationships to population fluctuation, but only cursory consideration is given to the various other weather influences that may affect Wisconsin pheasants.

Prenesting Temperatures

Relationship Between Spring Temperatures and Nesting Phenology

The question of what factors govern the breeding season in birds has been studied in a variety of species. It is now generally recognized that the two proximate factors of major importance in temperate and boreal latitudes are photoperiod and temperature (Baker, 1938).

Day-length may be the primary factor determining the rough limits of the breeding season for many species (Burger, 1949 and 1953; Wolfson, 1952; Engels and Jenner, 1956). Bissonnette (1938) and Bissonnette and Csech (1937, 1941) demonstrated the importance of this factor in the reproduction of the pheasant.

However, day-length does not vary between years and cannot influence the annual variations in nesting phenology with which we are concerned. The factor that has been found to cause such variations in a variety of temperate latitude species is prenesting temperatures (cf. Kendeigh and Baldwin, 1937; Marshall, 1949; Thomson, 1950; Kluijver, 1951; Farner and Mewaldt, 1952). That spring temperatures may influence pheasant nesting phenology has been suggested by a number of authors (cf. Leedy and Hicks, 1945:84; Allen, 1946; Buss, 1964a; Carlson, 1946; MacMullan, 1948; Stokes, 1954:47; Kozicky and Hendrickson, 1956).

Comparison of pheasant nesting phenology in California with that of comparable latitudes in the Midwest gives one clue to the influence of spring temperatures. Between 1946 and 1950, the peak of the pheasant hatch on study areas in the Sacramento Valley occurred around the second or third weeks of May (Twining, 1946 and 1947; Ferrel, 1949; Harper, 1949 and 1951). At similar latitudes east of the Rockies, hatching peaks varied between May 25 and June 8 on two study areas in southern Nebraska (Hamilton and Linder, 1955 and 1956), and between June 1 and the second week in June for the state as a whole (Heyl, 1955; Johnson, 1956 and 1957). Pheasant nesting in Nebraska is some 2-3 weeks later than in California.

Similarly, Linsdale (1933) noted that the breeding seasons of a number of birds were considerably later in Kansas than at the same latitude in California. He attributed this to difference in spring temperature. Comparison of California and Nebraska mean temperatures (Table 16) shows an evident difference.

Analytical Problems

In order to analyze the relationship between temperatures and pheasant nesting phenology in more detail, we have attempted a number of different correlations between average hatching dates and spring temperatures. One problem that arises in such analyses involves the question of temperature

TABLE 16

Monthly Normal Mean Temperatures in Sacramento, California and Lincoln, Nebraska*

Month	Mean Temperatures (°F) Sacramento, Calif.	Lincoln, Neb.
January	44.3	25.4
February	49.7	29.7
March	53.9	39.4
April	58.2	52.9
May	64.0	63.3

*Data from U.S.D.A. (1941).

uniformity over the area represented by the average hatching dates.

We tested the degree of correlation between mean temperatures for the first week in May at three weather stations well separated in the Wisconsin primary pheasant range, and for the period 1938-57. The coefficient between temperatures at Brodhead (Green County) and Oshkosh (Winnebago County), roughly 100 air miles apart, was 0.945. Between Williams Bay (Walworth County) and Oshkosh, about 100 miles apart, it was 0.986.

There is evidently a great deal of uniformity between temperatures at widely spaced points in Wisconsin, apparently because these are determined by the large air masses that cover major portions of the continent. As we shall see later, there is even considerable uniformity between stations in different states. It therefore seems justifiable to use temperatures from a single Wisconsin station to compare with statewide average hatching dates. We have used Madison temperatures because this station is in the primary pheasant range, and it is one of the few primary weather stations in the state. Its record is a long and dependable one.

Correlation Between Temperatures and Average Hatching Dates

If we allow 23 days for incubation, 1.3 days per egg laid (Buss, Meyer and Kabat, 1951), and an average clutch size of 12 eggs, a period of 39 days normally elapses between laying of first egg in the incubated clutch and hatching. The long-term average hatching date in Wisconsin is June 18; thus nests are started around May 11. We would therefore expect temperatures for some period before May 11 to influence the time at which nesting begins.

We calculated mean temperatures for short periods between January and mid-June, and for each year of the period 1947-57. The number and lengths of these periods were: 18 one-week periods, 13 ten-day periods, 9 two-week periods, 9 three-week periods, and 8 four-week or one-month periods. We then correlated the 11 years of average hatching dates with the 11 yearly mean temperatures for each of these 57 periods (Fig. 42).

The values for the 1-week and 10-day periods show a great deal of variation. Several values approach or attain the .05 probability level, some perhaps by chance and some representing real correlations. Temperatures show considerable day-to-day and week-to-week variations, and variations in the correlation coefficients for these short periods reflect this.

The trends begin to smooth out in the 2- and 3-week and 4-week to 1-month values, with the 3-week values showing the clearest trend. The influence of temperatures on average hatching dates appears to begin in March, and increases in effect as spring progresses. Maximum influence is apparently exerted in the last 10-15 days of April and the first 10-15 days of May immediately prior to onset of nesting. After about the middle of May, the relationship drops off.

Swanson (as cited by Lauckhart and McKean, 1956:63) reported that pheasants in Washington will not begin nesting until the cover has attained a certain height. Since vegetative growth in spring is not only influenced by moisture but by temperature, it seems possible that Swanson's correlation between vegetative development and nesting phenology may be indirect and not necessarily involve cause and effect. The correlation between the two might be due to the fact that both are causally related to the same factor, temperature. Robertson (1958:61, 70) observed that, in exceptionally retarded springs like 1947 and 1950, pheasants in Illinois will eventually attempt to nest in poorly developed cover and even in plowed fields. This implies that, like the song sparrow (Nice, 1937:102), pheasants will begin nesting at progressively lower temperatures as spring advances.

Physiological Mechanism of Temperature-Phenology Relationship

Determination of the actual physiological mechanism involved in this relationship must await laboratory study, but one possible hypothesis involves a stress response pattern like that discussed by Selye (1946, 1949). According to Selye, when an animal is under stress its adaptive responses are controlled by ACTH secretion. Production of this hormone appears to take precedence over production of the other hormones, and when an animal is under stress, the need of ACTH may be such as to slow or stop secretion of the others. The demands made on the hen's physiology for maintenance of body temperature during subnormal spring temperatures may conceivably be sufficient to retard or delay the physiological processes involved in nesting and broodiness. If this is the case, the stress is apparently not great enough to influence the physiological processes involved in egg laying since hens appear to begin laying at about the same time each year.

The promiscuous dropping of eggs, laying in dump nests and abandonment of clutches prior to nesting would seem to be an uneconomical situation, biologically. While occasional dropped eggs have been reported in some species, and the phenomenon of dump nests is encountered in some ducks, it is not developed in other species to the degree that it seems

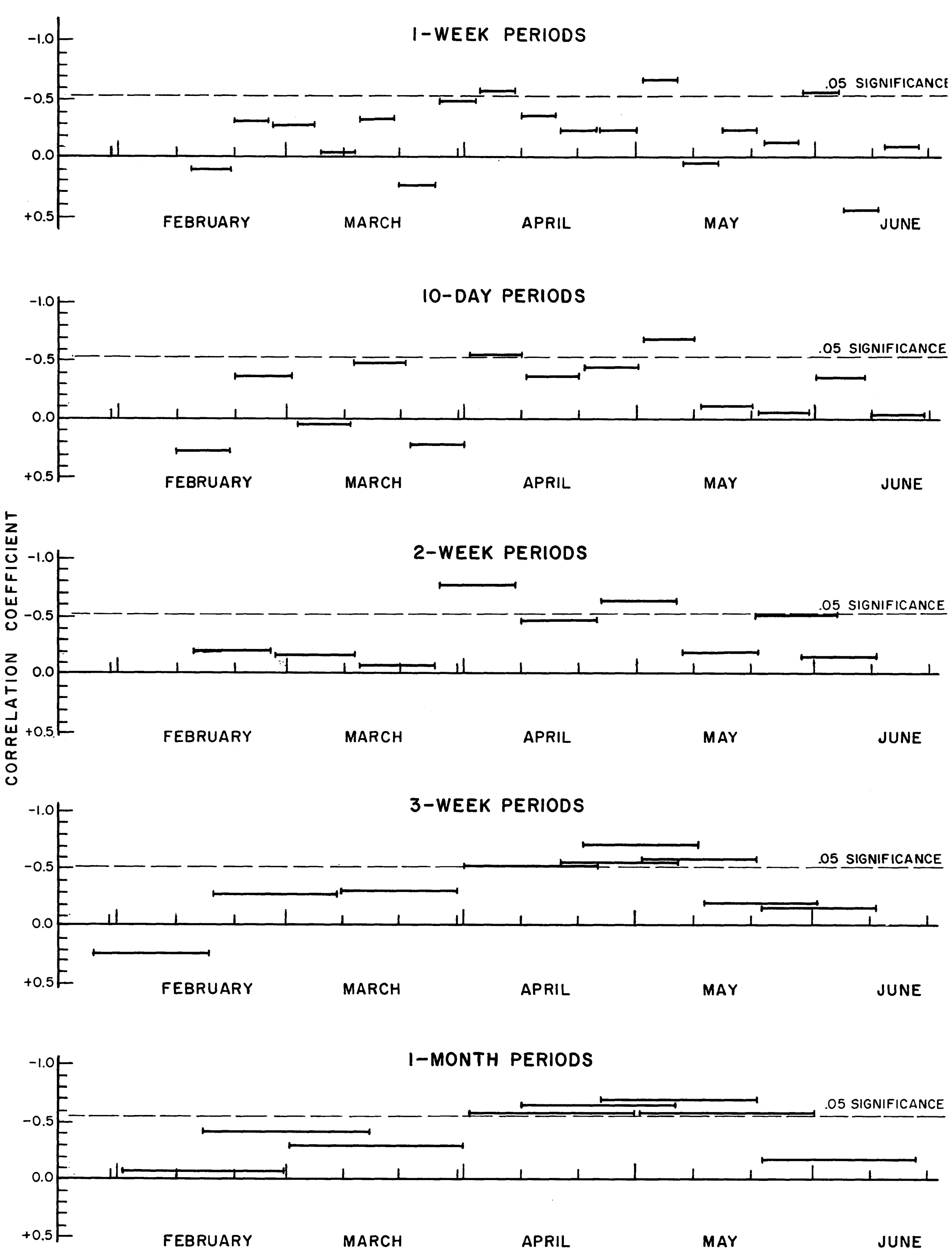


Figure 42. Correlation coefficients for Madison mean temperatures of varying spring periods and Wisconsin average hatching dates, 1947-57. The position of each line, relative to the 0.0 base line, indicates the magnitude of the correlation coefficient. The horizontal length of each line represents the calendar period for which the mean temperature was calculated.

to occur in North American pheasants. Most birds are ready to nest when they are ready to lay, or more often nest building precedes egg laying by several days.

This egg loss situation might be a symptom indicating that central North American pheasants may not be adjusted to the temperature-photoperiod combination of this region. Mean monthly temperatures for several parts of the world pheasant range (Table 17) show that winter and spring temperatures in north central U.S.A. are colder than those of China to which the bird presumably is adapted. In fact, the temperature pattern in the native range is approximately the same as that of Dallas, Texas. Winter and early spring temperatures in northwestern Europe also appear to be generally milder than those of the Midwest, although by April the temperatures from the Midwest have caught up with the more slowly advancing maritime temperatures of west Europe. In general, however (Berlin and Des Moines are exceptions), prenesting temperatures in Europe and China appear to be milder than those of north central U.S.A.

Whether or not a period of egg dropping and communal laying precedes general nesting in southeast China has not, to our knowledge, been recorded. It is true that pheasants nest much earlier in that region than in north central U.S.A. Beebe (1926:46-47) reported that the main hatching months are April, May and June; and he saw one nest with three eggs on February 17. Hence nesting may begin from 1-2 months earlier in southeast China. This cannot all be due to temperatures as the latitude is some 10° lower, and hence the longer spring photoperiod probably has some effect.

A better insight into the temperature-egg-dropping relationship can be had by noting pheasant nesting phenology in New Zealand at 35-40° South. These are latitudes approximately comparable with those of Kansas (the Kansas-Nebraska border coincides with 40° North), and hence with similar day lengths. Westerskov (1955) showed that New Zealand pheasants begin nesting as early as August and September (months comparable with February and March in the northern hemisphere). This is some 2 months earlier than the nesting phenology in southern Nebraska cited above. He informed us (pers. comm.) that he found no evidence of egg dropping in New Zealand. On the other hand, Twining (1947) reported dropped eggs and dump nests in California's Sacramento Valley where temperatures are comparable with those in New Zealand.

Witherby, Jourdain, Ticehurst, and Tucker (1949: v. 5, p. 236) reported that the first pheasant eggs are generally laid in the British Isles in early April, but the majority are not laid until 2 weeks later. If this represents laying in nests, it suggests that British pheasants nest somewhat earlier than ours in spite of the 10° higher latitude. Whether or not a period of egg dropping precedes nesting is not reported, but some communal laying apparently does occur (Morris, 1891:12; Witherby *et al.*, 1949).

The evidence is not adequate at present to state whether the egg-dropping and communal-laying habit are abnormal for the pheasant — at least to the degree found in central North America — and a function of spring-temperature and day-length combinations that differ from its native environment. The problem is apparently confounded by density influences (Stokes, 1954).

TABLE 17

Monthly Normal Mean Temperatures for Different Areas of the World Pheasant Range*

Area	Mean Temperatures (°F)		
	January	April	July
Southeast China, 30-45° N. Lat.			
Shanghai	39.8	57.8	82.2
Hankow	40.1	61.9	85.4
Chungking	48.4	67.4	84.0
Mean	42.8	62.4	83.9
Northwest Europe, 50-55° N. Lat.			
London	38.5	47.6	58.8
Amsterdam	37.5	47.1	63.3
Berlin	30.2	45.8	64.4
Mean	35.4	46.8	62.1
North-Central U.S.A. 40-50° N. Lat.			
Lansing, Michigan	22.9	42.8	71.1
Madison, Wisconsin	16.7	45.7	72.2
Des Moines, Iowa	22.2	50.4	76.3
Huron, South Dakota	13.8	46.4	73.3
Mean	18.9	46.3	73.2
New Zealand, 36-40° S. Lat.	(July)	(Oct.)	(Jan.)
Wellington	47.7	73.0	77.7

*Data from U.S.D.A. (1941) and from U.S. Dept. of Commerce—Climatological Data.

Relationship Between Spring Temperatures and Population Trend

That pheasant population fluctuations have been associated with weather—possibly some combination of subnormal temperatures and/or above-normal precipitation—at some time during the breeding season has been widely suggested in the past (cf. Kimball, 1948; Wandell, 1949; and Allen, 1950, for summaries). That fluctuations have been associated specifically with spring temperatures has been suggested by Buss (1946a) for Wisconsin; and has been demonstrated by Kozicky, Hendrickson, Homeyer and Nomsen (1955) and Nomsen (1956) for Iowa. Kozicky and Hendrickson (1956) further concluded that the relationship operates through a nesting phenology link.

Hence a relationship between spring temperatures, nesting phenology, and population trend has already been demonstrated statistically, at least for Iowa. Our efforts here are to examine the relationship in some detail for Wisconsin, to ascertain whether or not it can be demonstrated with data from other states, and to consider what other environmental factors may influence population trends.

Evidence for Wisconsin

As in the analysis of temperatures and average hatching dates, we calculated mean temperatures for successive 1-week, 10-day, 2-week, 3-week, and 4-week to 1-month periods in March, April, May, and early June; and for each year during the period 1938-56. We then correlated the percentage change in kill for each of these years with these temperature means (Fig. 43).

The results are similar to those in Figure 42. The coefficients for the shorter intervals are quite variable, and it is difficult to infer any coherent trend. But in the 2- to 4-week intervals, the trends smooth out, with the coefficients gradually rising from low values in March, to significance in the latter part of April and early weeks of May. They then drop off in the latter part of May and June. Apparently population trends are most strongly influenced by temperatures of about the last 10 days of April and the first 10 days of May. The correlation coefficient for this period is 0.530.

Evidence for Other States

Time has not permitted analysis of the data from other states in the same detail with which we studied Wisconsin. We simplified the problem by correlating population trend information with individual temperature means for late April and early May—the period found to be most clearly associated with Wisconsin population trends.

Kill estimates were used as population indices for Michigan (Janson, 1957), Indiana (Wm. E. Ginn, in litt.), and Minnesota (Erickson *et al.,* 1951; S. W. Harris, in litt.). Several years in the Indiana and Minnesota series were omitted (Fig. 44) because they were years in which hen seasons were held, and in Minnesota there was no open season in 1947. We consulted the "Monthly Climatological Data", published by the Department of Commerce for temperatures at Lansing, Michigan; Fort Wayne, Indiana; and Worthington, Minnesota.

The test for Pelee Island was based on the percentage change between number of hens alive after one hunting season to the number present at the start of the next. Hen data were from Stokes (1952), and C. O. Barlett and H. G. Lumsden (in litt.). Temperature data were for Sandusky, Ohio.

The correlations for Michigan and Minnesota (Fig. 44) are significant at the .01 level, that for Indiana at the .05 level. The Pelee Island correlation, while suggestive, falls short of significance. All four correlation coefficients exceed the 0.530 for Wisconsin, suggesting that prenesting temperatures account for as much, or more, variation in fall population levels than they do in Wisconsin. Furthermore, if spring temperatures have an influence over a longer calendar period than the 3 weeks tested, as appears to be the case in Wisconsin, then the correlation coefficients for the limited periods shown only reflect part of the total association between spring temperatures and population change.

Among states west of the Mississippi, population indices span shorter time intervals, and/or rely on various types of summer or fall roadside counts which we suspect are more variable than kill estimates. Nevertheless, we obtained a coefficient of 0.469, significant at the .05 level, for annual changes in Iowa roadside counts (Kozicky *et al.,* 1952; R. C. Nomsen, in litt.) and Des Moines mean temperature for the period April 17-May 7. We were not able to get a correlation of any strength between South Dakota rural-mail-carrier counts reported by Dahlgren (1956a) and Huron temperatures. Road-count data for North Dakota (Bach, 1944; Bach and Stuart, 1947) for the period 1938-47 yielded a significant (.05) coefficient of 0.741 with April 24-May 14 mean temperatures for Bismarck. We were not able to find a significant correlation in conservation-officer and mail-carrier counts from Nebraska (C. Phillip Agee, in litt.).

The Pheasant Decline of the Middle 1940's

The pheasant decline of the 1940's warrants some consideration here in light of the evidence we have been examining on prenesting temperatures.

Correlations of April 17-May 7 temperatures between midwestern states (Table 18) show a high degree of uniformity in temperature patterns. The relationships are strongest between adjacent states; they weaken with increasing distances between stations. Since the decline was a region-wide phenomenon with considerable synchrony, (Table 19), we would expect the responsible influence or influences to operate with some uniformity over the region.

The data in Table 19 show that population increase was general in 1940. Trends in 1941 and 1942 were variable, although over half of the states listed were still on the increase. Apparently no general decline had set in.

In 1943, 6 of the 7 states shown reported a decline. In 1944, the trends were again variable, but declines once again were general in 1945, 1946, and 1947. Every state listed reported population increases in 1948. Hence, general decline occurred in 4 of the 5 years between 1943 and 1947; and in general, the decline period appears to have been 1943-47.

In order to compare these trends with prenesting temperatures, we calculated spring temperature means for each year of the period 1942-48, and for 7 midwestern weather stations (Table 20). We noted earlier that population trends in North Dakota, Minnesota, and Michigan showed correlation with temperatures of the period April 24-May 14; while in Wisconsin, April 21-May 11 seems to be the most influential period. In the next tier of states to the south, Indiana and Iowa trends correlated with temperatures of a slightly earlier period, April 17-May 7. This probably relates to the earlier pheasant nesting phenology in these states. Temperatures for the same period were used for the Nebraska comparison in Table 20.

Temperatures were below normal at 6 of 7 stations in 1943, and population declines were general. Temperature means were below normal at 5 stations in 1944, and population trends were variable. In 1945, temperatures were uni·

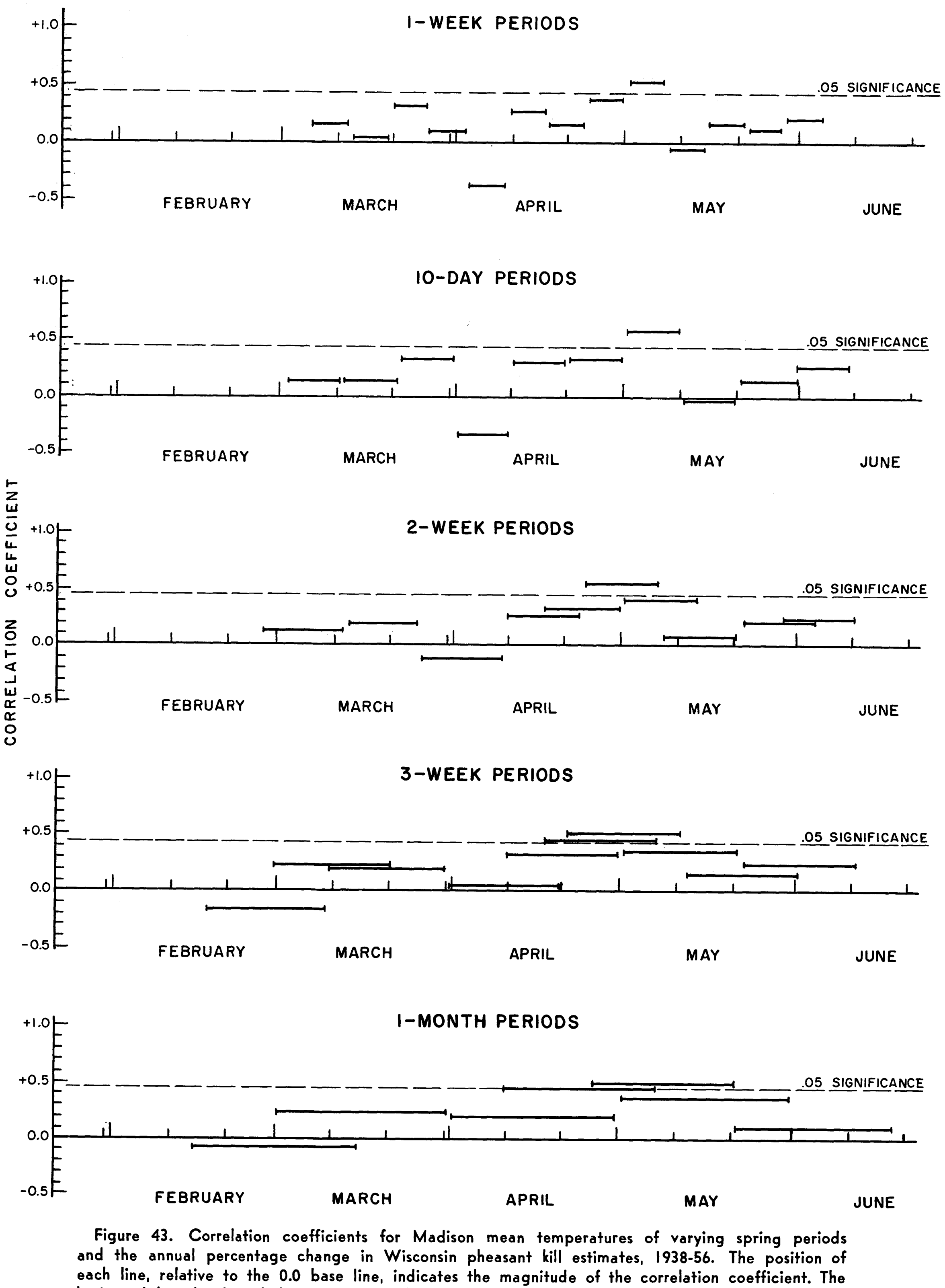


Figure 43. Correlation coefficients for Madison mean temperatures of varying spring periods and the annual percentage change in Wisconsin pheasant kill estimates, 1938-56. The position of each line, relative to the 0.0 base line, indicates the magnitude of the correlation coefficient. The horizontal length of each line represents the calendar period for which the mean temperature was calculated.

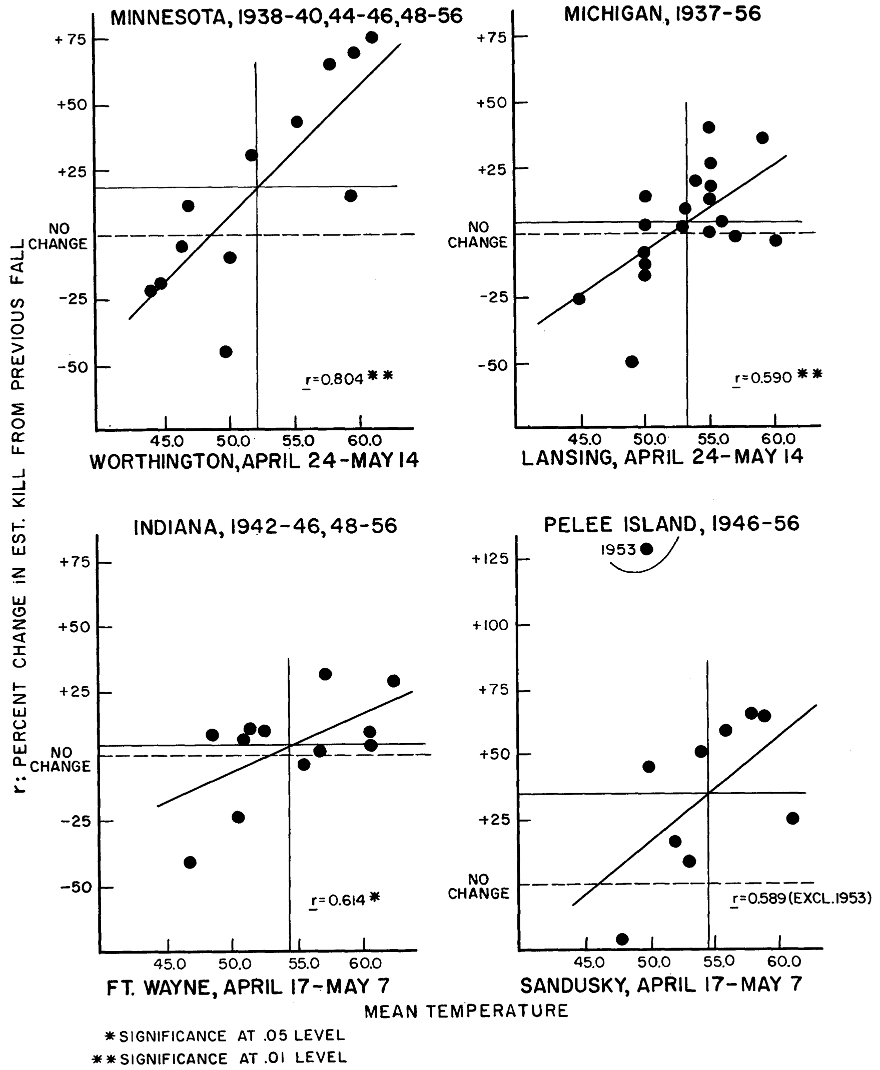


Figure 44. Correlations between mean temperatures and annual percentage change in estimated kill in Minnesota, Michigan, and Indiana; and in percentage change in between-season hen population on Pelee Island. Mean temperatures for the periods shown gave the highest correlation coefficients of any 3-week spring period.

formly low and decline general. In 1946, as many stations showed above-normal temperatures as below, but populations declined in 5 of the 8 states listed. Finally, in 1947 below-normal temperatures and population declines prevailed. A correlation test of the percentage of stations reporting below-normal temperatures (Table 20) and percentage of states reporting population declines (Table 19) for the period 1942-48 produced a correlation coefficient of 0.813 (significant at the .05 level).

The population slump therefore appears to have occurred during a 5-year period with predominantly below-normal prenesting temperatures throughout the Midwest region. These findings only bear out the concensus of opinion of earlier authors (cf. Kimball, 1948; Wandell, 1949; Allen, 1950 for summaries) that weather was a dominant factor in the decline of the 1940's. Our contribution has been to pinpoint prenesting temperatures.

Other Weather Factors

The evidence we have examined indicates that prenesting temperatures are one factor responsible for short-term fluctuations in Wisconsin pheasants. Findings elsewhere in the Midwest suggest that this factor has also been associated with population change in a number of states in the region.

The evidence for other weather influences is more superficial and less conclusive. We conducted several preliminary tests on nesting- and brood-season weather. A test of the correlation between the average June rainfall of 21 southeastern Wisconsin weather stations (Fig. 45) and population trend between 1938-56 yielded a coefficient of −0.100 indicating no relationship.

Findings from other states on summer precipitation are also inconclusive. Ginn's (1948) paper, one of the more frequently cited, reported a correlation between pheasant trends in Indiana and April-July rainfall in the 7-year period 1940-46. Since 4 of these were years of the regional population decline, it is not certain whether spring temperatures,

TABLE 18

Correlations of Midwest Temperatures of the Period April 17-May 7 for the Years 1938-56*

Stations	Corr. Coef.	Calc. (*F*)
Correlations between adjacent states		
Lansing, Mich.-Columbus, Ohio	0.914	87.09**
Lansing, Mich.-Madison, Wis.	0.929	107.41**
Madison, Wis.-Springfield, Ill.	0.935	118.43**
Des Moines, Iowa-Omaha, Nebr.	0.934	114.13**
Bismarck, N.Dak.-Huron, S.Dak.	0.838	40.29**
Correlation between alternate states		
Columbus-Springfield	0.895	67.78**
Lansing-St. Cloud, Minn.	0.799	29.87**
Madison-Huron	0.783	26.87**
Bismarck-Omaha	0.751	21.91**
Correlation between states having two or more intervening states		
Lansing-Omaha	0.757	23.02**
Lansing-Huron	0.652	12.57**
Columbus-Des Moines	0.692	15.68**
Columbus-Bismarck	0.463	4.65†

*Data from U.S. Dept. of Commerce—Climatological Data.
**Significant at .01 probability level.
†Significant at .05 probability level.

or summer rainfall, or both were involved. Flooding of nests has been reported for limited areas and individual years (e.g. Leedy and Hicks, 1945; Carlson, 1946, Dustman, 1950; Erickson *et al.*, 1951; MacMullan, 1952; Iowa State Conservation Comm., 1954). That rainfall (not flooding) during clutch laying has caused hens to abandon their efforts has been reported to us for Illinois and Ohio (Ronald Labisky and W. R. Edwards, pers. comm.).

On the other hand several authors have failed to detect a serious effect on pheasant numbers from rain during the reproductive season (e.g. Dale, 1942; Wandell, 1949; Janson, 1949; Buss and Swanson, 1950; Kozicky *et al.*, 1955). Some writers have pointed out that rainfall around hatching time may be beneficial to pheasants by delaying the average date of hay mowing and allowing more nests to hatch before cutting begins.

It is difficult to find any evidence that indicates a strong association between rainfall during the reproductive season and statewide pheasant trends, although the evidence for local areas is more suggestive. But rainfall is quite variable geographically. (We made 6 year-by-year comparisons of 1938-56 June rainfall totals between five weather stations in southeastern Wisconsin. Correlation tests only yielded significance in 2 of these.) Consequently, its effect on statewide populations is probably spotty, and the correlation between statewide rainfall and population trends is probably weak, if present.

Correlation tests of 1938-56 population trend and Madison mean temperatures of the latter half of May (Fig. 43) and June also failed to approach significance. However, Kozicky *et al.* (1955) concluded that May and June temperatures influence population trends in Iowa. Studies by English (1941) and MacMullan and Eberhardt (1953) have shown considerable resistance of eggs to cold. These latter findings make it seem unlikely that widespread egg loss will occur during the May laying period when daily mean temperatures in Wisconsin are into the 50's, and minima seldom fall below 32° F.

Winter weather is another complex problem meriting special attention. In very preliminary tests involving correlations between 1938-56 population trends and (1) yearly mean Madison temperatures for the period December-February, and (2) yearly mean December-February snowfall averaged for 21 southeastern Wisconsin stations (Fig. 45), we obtained

TABLE 19

Midwest Pheasant Population Trends in the 1940's

	Fall Population Trend from Previous Year									
State	1940	1941	1942	1943	1944	1945	1946	1947	1948	Reference
N. Dakota	Up	Up	Up	Down	Up	Down	Down	Down	Up	Bach, 1944, 1947; Stuart, 1951
S. Dakota	*	*	*	*	*	*	*	Down	Up	Dahlgren, 1952
Minnesota	Up	**	**	**	**	Down	Up	Down	Up	Erickson *et al.*, 1951
Wisconsin	Up	Up	Up	Down	Down	Up	Down	Down	Up	This study
Michigan	Up	Up	Down	Up	Up	Down	Down	Down	Up	Janson, 1957
Nebraska	*	*	Up	Down	Down	Down	Down	Down	Up	Mohler, 1948; C. Phillip Agee, in litt.
Iowa	Up	Down	Up	Down	Up	Down	Down	Down	Up	Kozicky *et al.*, 1952
Indiana	**	**	**	Down	Up	Down	Up	*	*	Ginn, 1955
Ohio	*	Down	Down	Down	Down	Down	Up	Down	*	Kimball, 1948
Percent showing decline	0	40	33	83	43	88	63	100	0	

*No index available for this and/or preceding year.
**Hens were legal game in this or preceding year. Minnesota populations declined after 1941 or 1942, and Indiana populations declined after 1940, but it is impossible to separate out the effects of the hen shooting.

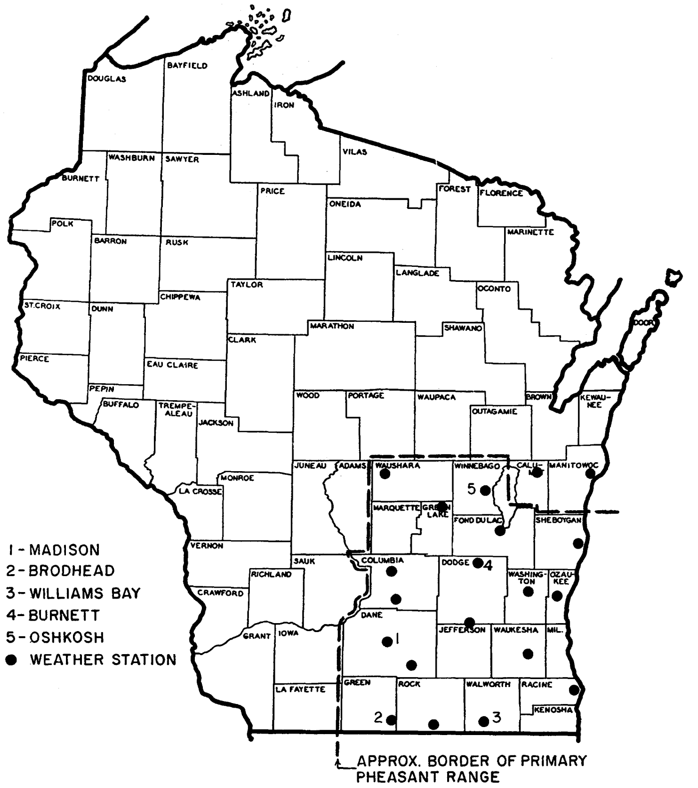


Figure 45. Weather stations used for estimating mean southeastern Wisconsin rainfall and snowfall.

coefficients of −0.016 and 0.091, respectively. These suggest no relationship. Subjectively, the severe winters of the period have been 1939-40, 1942-43, 1944-45, 1947-48, and 1950-51 (Leopold and Jones, 1947; Kabat *et al.,* 1956). The kill estimates decreased following only 1 of these 5 winters (1942-43, and this was followed by a cold spring), and they increased after the other 4. However, as we previously noted, there was a pronounced effect on pheasant trends following the severe winter of 1958-59.

In other states east of the Mississippi, Allen (1941a, 1946) and Dalke (1943) concluded that winter loss is of little consequence in Michigan, as did Leedy and Hicks (1945:84) for Ohio. West of the Mississippi, winter losses have been reported for almost every pheasant state. Reports for Iowa (Green and Beed, 1936), Nebraska (Mohler, 1952), and Colorado (Swope, 1953) seem to implicate only occasional winters. In Minnesota (Erickson *et al.,* 1951) and South Dakota (Nelson and Janson, 1949; Kirsch, 1951; Trautman, 1953) losses apparently are more frequent. But even in the latter state, Dahlgren (1959) concluded that statewide losses were fairly constant from 1947 to 1959. North Dakota appears to be the only state where severity of winter has been markedly associated with general population changes over a series of years (Stuart, 1951; Sjordal, 1953; Fischer, 1956).

TABLE 20

Departures from Normal of Midwest Spring Temperatures in the 1940's

		Departure of Mean Temp. from Normal (°F)						
Station	Weather Period	1942	1943	1944	1945	1946	1947	1948
Bismarck, North Dakota	April 24-May 14	−3	−4	0	−7	−2	+2	−1
Worthington, Minnesota	April 24-May 14	+2	−1	−4	−7	−1	0	+8
Madison, Wisconsin	April 21-May 11	+5	−1	−2	−6	0	−3	0
Lansing, Michigan	April 24-May 14	+7	−3	0	−8	−3	−4	+2
Omaha, Nebraska	April 17-May 7	+2	0	−9	−3	+4	−2	+4
Des Moines, Iowa	April 17-May 7	+1	−1	−5	−4	+4	−2	+4
Fort Wayne, Indiana	April 17-May 7	+4	−3	−1	−7	+6	−5	+2
Percent of stations with temperatures below normal		14	86	71	100	43	71	14

Discussion

Based on the evidence available to date, our general concept of the relationship between weather and pheasant population trends in the Midwest is one of a mass of annually varying influences and combinations of influences. Most of these are probably minor, and many of their yearly variations may cancel each other out. In most areas, it appears that a small number of factors—in many cases only 1 or 2—operate with sufficient consistency and strength to account for a major share of the variation in pheasant numbers. In Wisconsin, prenesting temperatures appear to be the most influential. We have not been able to detect a relationship with other weather factors with available indices and analytical procedures.

Elsewhere in the Midwest, prenesting temperatures seem to be among the more important factors in a number of states, and may be the prime weather influence in the upper Mississippi and northern Lake States. But as we move away from this region, other factors shade into importance in some states. For example, severity of winter loss may exist as a gradient from southeast to northwest, rising as a dominant influence on population trends in the latter portion of the region. Similarly, reports by Mohler (1959:20) and Linder *et al.* (1960) for Nebraska, Yeager and Sandfort (1958) for Colorado, and R. B. Dahlgren and J. L. Seubert (pers. comm.) for South Dakota regarding the influence of drought on pheasants suggest the possibility that a similar gradient may exist from east to west involving this factor.

Weather may operate directly, as in the case of prenesting temperatures, or through some other factor that interacts with it. For example, cover may be filled with snow in a severe winter, and birds may become vulnerable to heavy predation loss (R. A. McCabe, pers. comm.). Other variable interactions have been reported between weather and cover (Yeager and Sandfort, 1958; Linder *et al.*, 1960) and between weather and land use (Robertson, 1958), with consequent effects on populations. In these examples, predation or land use has been the factor directly responsible for population change, but only because of the basic independent variable, weather. Interactions like these would be included in a correlation between population change and weather. Failure to demonstrate such a correlation would imply that the net effect of the interacting, dependent variable on population change was not great.

The correlations between temperatures and annual population trends (Fig. 44) imply population balance at local weather norms. The mean population trends in the Indiana and Michigan examples—+4 percent in each case—suggest that the net population trend has been very close to "no change" over the years included in the tests. The corresponding mean Wisconsin trend for the period 1938-56 has been +9 percent, also close to the no-change line. The 18 percent Minnesota mean is somewhat higher, perhaps because we had to delete several years in the 1940's, and a number of these were decline years that would have reduced the mean. The mean population trend on Pelee Island is quite high, as discussed in the last chapter, suggesting an increasing population under the densities tolerable on the island.

Summary

Experimental manipulation of day-length has shown this factor to be a major determinant of pheasant breeding phenology. Variations in nesting phenology between California and Nebraska, and statistically significant correlations between Wisconsin average hatching dates and prenesting temperatures indicate that variations in the latter are responsible for variations in nesting phenology within the limits set by day-length. The influence may begin in March, build up to maximum influence in late April and early May just prior to nesting, and then fade out in effect. The causal link may involve a stress reaction wherein the pituitary-adrenal complex responds to the energy needs for body temperature maintenance at low environmental temperatures, and at the expense of reproductive physiology. The prenesting habits of egg dropping, laying in dump nests, and abandonment of clutches seem uneconomical biologically, and may suggest that the bird has not yet become adjusted to the temperature-photoperiod combination of central North America.

Temperatures of the latter part of April and early May, which exert maximum influence on Wisconsin nesting phenology, also form statistically significant correlations with population trends in Michigan, Indiana, Iowa, and for a short period in North Dakota. A similar correlation for Pelee Island produced a suggestive, but not significant coefficient. Correlations for Nebraska and South Dakota were not significant. The region-wide decline of the 1940's occurred during a 5-year period with predominantly subnormal spring temperatures throughout the Midwest.

Weather probably is the most important single factor causing short-term fluctuations in Wisconsin pheasants, with prenesting temperatures probably the most important, though perhaps not the exclusive, aspect of weather. Weather may operate directly on a population, or indirectly through an interacting, dependent variable.

PART III—MECHANISMS IN DETERMINATION OF LONG-TERM MEAN DENSITY

We now turn from short-term changes in numbers within areas to a consideration of the mechanisms and causes of differences between areas in long-term mean densities. Ideally we should have accurate reproductive and mortality rates for each area, and a knowledge of how each environmental factor influences these. However, what reproductive and mortality data we do have do not lend themselves to comparison between areas. Year-to-year comparison of biased data within an area can be made with reasonable confidence because the biases are sufficiently constant each year. But the variation in bias between areas, and often in observational methods, preclude meaningful inter-area comparisons, even within Wisconsin as we have seen.

Our next recourse is in the use of population trend measurements which represent the difference between reproductive and mortality rates. Potentially a pheasant population can increase at the rate of about 600 percent per year if each pair raises all young from an average clutch of 12 eggs, and no birds die. This same increase rate applies to each sex class individually.

In a shot population where the kill of cocks is used as a population index, the potential, annual increase rate in this index still approaches 500-600 percent, depending on the percentage of cocks harvested, assuming that the hens attain their reproductive potential, and assuming no other causes of mortality to cocks or hens.

A pheasant population also has a potential decrease rate of 100 percent per year. This would occur if all adults died and no young were produced.

These are potential, annual rates of change. Each year a population is potentially capable of changing by a percentage anywhere within this range. Actually most of the annual population changes we observe fall within a narrow part of this range as Hickey (1955:357) pointed out for gallinaceous birds in general, and as seen in Figures 38-40 and 44. They seldom increase or decrease in any one year more than 50-75 percent.

Andrewartha and Birch (1954:33) defined such annual rates of population change as ". . . the *actual* rate of increase . . ." and gave it the symbol **r**. The **r** value for each year is a function of the disparity between number of animals born and the number dying within that year, and is expressed as a percentage. It is positive when births exceed deaths, negative when deaths exceed births, and zero when the two are equal.

In Part III we extend our analysis to a consideration of the mechanisms and causes of differences between areas in long-term mean densities, and use the **r** values as indices of environmental effect on population. Actually we have already used them in the two previous chapters.

Unfortunately, the symbol for actual rate of population increase is the same as that for the correlation coefficient, both of which are used in this report. Since both symbols have become traditional in previous work, we did not feel it desirable to change either. The context in which the symbol is used should make clear which concept is involved.

CHAPTER X. CLIMATE

We previously discussed the relationship between yearly weather patterns and year-to-year changes in pheasant density. In this chapter we explore some of the long-term weather effects on mean pheasant density expressed as climatic influences. Yearly climatic variations, often in an otherwise roughly stable environment, are somewhat analogous to the manipulation of a single variable in a controlled experiment. Population changes can be readily correlated with climatic influences. Effects of some of the other limiting factors, such as hay mowers and predators, seem to be less variable between years, and hence more difficult to detect or demonstrate.

Prenesting Temperatures

Limiting Effect on Pheasant Populations

Limitation in Wisconsin

In our analysis of the correlation between prenesting temperatures and percentage change in estimated kill from the previous fall (annual **r** values) for Wisconsin, temperatures during the period April 21-May 11 seem to be the most influential (Fig. 46).

We concluded previously that the nearness to zero of the mean Wisconsin **r** value (+ 9 percent) implies approximate balance through the 18-year period in which we have measured it. Yearly temperatures average out to the long-term norm somewhere near 53 degrees. If we can assume that the April 21-May 11 temperature mean for this 18-year period represents a long enough period to approximate the long-term norm, then the correlation in Figure 46 implies that the pheasant population is balanced at the local, climatic norm.

If the April 21-May 11 temperature norm were to increase a few degrees to some new higher norm, the frequency of annual temperature above 53 degrees would increase, and that of annual temperatures below 53 degrees would decrease. Accordingly, we could reasonably expect the frequency of years with population increase to be higher, and the frequency of population decrease to be lower. As a result the mean of **r** would increase, and the net trend of the population would be upward although not indefinitely.

Evidently then, Wisconsin spring temperatures exert some limiting influence on pheasant densities. If spring temperatures were higher, pheasant densities would be higher, other things remaining constant. How much higher the populations would be would depend on how much higher the temperatures increased.

As far as we know, the correlation between spring temperatures and pheasant fluctuation is a direct relationship operating through the physiology of the bird. Any long-term increase in mean density through any increase in spring temperature norm could probably occur without any other environmental change. The limiting effect of temperature on pheasant densities seems to be a direct relationship independent of the habitat.

Limitation in Other Midwestern States

If the conclusions we have deduced for Wisconsin are correct, they should also apply in other states where a correlation exists between prenesting temperatures and **r** (e.g. the states represented in Fig. 44). This includes Pelee Island where the populations have not attained a balancing density, but where a correlation exists between temperatures and **r**, and where a higher temperature norm would presumably be associated with a higher, long-term, mean **r** value.

Spring temperatures of any given date are cooler on the average in the northern Lake States (i.e. Michigan, Wisconsin, and Minnesota) than in the next tier of states to the south (cf. McCabe *et al.,* 1956:323). The questions arise

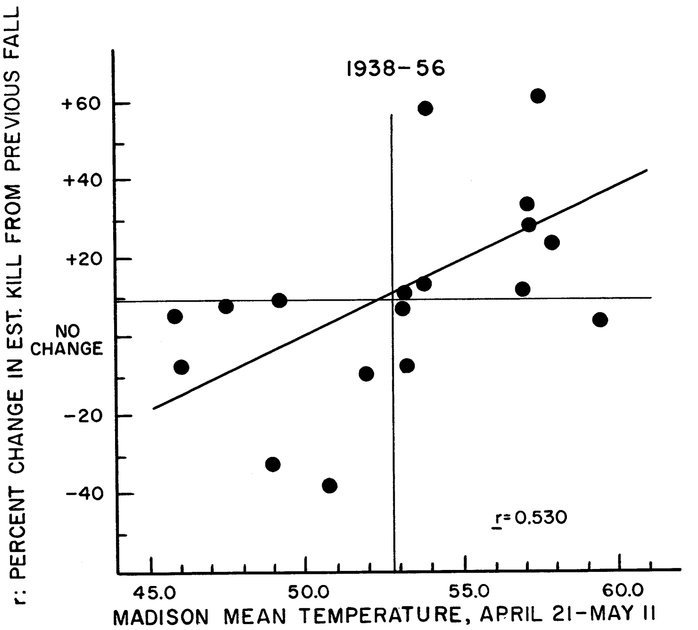


Figure 46. Correlation between Madison mean temperatures for the period April 21-May 11, and the percentage change from one fall to the next in the estimated Wisconsin pheasant kill, 1938-56.

as to (1) whether or not the pheasant populations in the more southerly states within the established midwestern pheasant range derive some advantage over those to the north from this temperature differential, and (2) whether or not these more southerly states are inherently better pheasant areas as a result.

The first question is deceptive because of variation in photoperiod. The nesting season begins earlier in the south: compare nesting phenology reported for Ohio and Illinois by Dustman (1950) and Robertson (1958) with that for Wisconsin in this report and Michigan in Blouch and Eberhardt (1953). This earlier onset of nesting while perhaps partly due to temperatures, is partly due to the longer, pre-equinoxial photoperiod. Consequently the temperatures preceding nesting do not differ greatly in the northern Lake States from those in the next tier of states to the south. (cf. Figs. 44 and 46. Mean temperatures of the period of maximum influence in Indiana are only 1-2 degrees warmer than the later, but phenologically comparable, dates in Michigan, Minnesota, and Wisconsin.) As a result, the more southerly states do not have the temperature advantage that they seem to have at first glance.

Regardless of whether the north-south difference in nesting phenology is a function of temperature or photoperiod or both, several clues suggest that the more southerly populations have an advantage in at least one reproductive characteristic (Dustman and Wagner, 1960). Since the nesting season begins earlier in the south, the total nesting season appears to be longer, as previously pointed out by Westerskov (1955). Consequently there is potentially more time for renesting. And perhaps significantly, pheasant investigators in the more southerly midwestern states consider the contribution of renesting to be greater than do their colleagues in the northern states (Dustman and Wagner, 1960).

In those studies where total nests and total hens were recorded, the comparison of the number of nesting attempts per hen offers some suggestion. During a 5-year study in southern Nebraska, each hen averaged 2.9 nesting attempts per year (Linder *et al.,* 1960). In three areas farther north, the number of nests per hen averaged 1.1 in northern Iowa (Kozicky and Hendrickson, 1951), 1.4 on Pelee Island (Stokes, 1954:23 for estimate of total nests and p. 99 for estimate of hens on February 1, 1949), and 1.9 in southern Wisconsin (John M. Gates, unpubl.) during 5, 1, and 2 years of observation respectively. This is not an unequivocal indication, however, since the number of nests per hen may be a function of nest success and the number of times a hen may be obliged to renest. Nest success in the Nebraska area was lowest of the four studies.

Another reproductive difference between the northern and southern areas is the southward decrease in clutch size (Westerskov, 1955). This partially negates any reproductive gain from a southward lengthening of the nesting season.

Dustman and Wagner (1960) pointed out that pheasants in the more southerly areas appear to be able to maintain their numbers in more adverse habitat (i.e., one with more hay). This may be one indication that the southern populations are more resilient, possibly because of the longer nesting season and greater renesting potential.

If our logic is correct, the prenesting temperatures in any given area, where a correlation exists with r, have some limiting effect on densities within that area.

Relationship to Population Density

Andrewartha and Birch (1954:16-21) have stated that no factors operate independent of density, and hence the distinction between density-dependent and density-independent action is pointless. In their opinion the shrinking remnants of a declining population take shelter in the most favorable habitat niches. They thereby become progressively less vulnerable to weather influences, the factors most often cited as being density independent.

While we have no critical observations to test the temperature relationship in our pheasants, we surmise it is density independent. The day-long ambient temperatures affect the birds, no matter where they are. In April and May they are well dispersed over the landscape.

Other Climatic Influences

While we were not able to demonstrate a correlation between any other weather factor and **r** in Wisconsin pheasant populations, there undoubtedly are some minor influences. These may have some limited depressant effect on mean pheasant density over a period of years.

In the Plains States, where the influence of periodic severe winters can be observed, and farther west where drought may be a factor in population fluctuations, we conclude that these influences have some long-term depressant effect. Where periodic severe winters depress populations (winter of 1958-59 in Wisconsin and elsewhere in the Midwest), and they require several years to recover, the mean pheasant density over a period of years would presumably be higher with a milder winter climate. Hence, climate per se, where associated with population fluctuations, can be considered to exert some limiting effect on mean densities over a period of years.

Summary

The correlation between prenesting temperatures and **r** in Wisconsin seems to imply that the population is balanced at the local temperature norm, and any increase in this norm would be accompanied by a population increase. Hence, prenesting temperatures per se, and independent of the habitat, apparently exert some influence on pheasant densities. This is also true in other states where correlations exist between temperature and **r**. The influence appears to be density independent.

Other climatic factors also influence pheasant population density, especially those which correlate strongly with **r** in year-to-year fluctuations.

CHAPTER XI. FARMING PRACTICES

Influence of Some Specific Farming Practices

Hay Mowing

Between two-thirds and three-fourths of Wisconsin pheasant nests are begun during the month of May in an average year. The peak of nest initiation is usually between May 10-15.

At this time nearly one-half of the land in the primary, southeastern Wisconsin pheasant range has little or no herbaceous cover and is unavailable to pheasants for nesting. Land set aside for corn or miscellaneous cash crops is either being prepared or has recently been planted and offers no cover. Small grains were planted 3-6 weeks earlier and their growth is too sparse to attract hens. Woodlands and permanent pasture, while occuping another 20-25 percent of the land area, seem to be poor cover because they generally are bare due to heavy grazing, lack appreciable new growth this early, and do not seem to be particularly attractive to pheasants for nesting.

The remaining one-third of the landscape is in herbaceous and grassy cover of sufficient density to be considered attractive nesting cover. Approximately 10-20 percent of the land is in glacial marshes and swales, much of which is available for pheasant nesting. In early or mid-May, there is little new growth of vegetation in marshes, but there is a heavy ground cover of dead material from the previous year. Fencerows, railroad rights-of-way, roadsides, and odd corners provide additional small acreages of reasonably attractive vegetation, again mainly dead residue from the previous year. Some 15-20 percent of the landscape is in tame hay crops. Although hay is one of the earliest growing plants on the landscape, it offers little cover to the very early nesting birds. But by mid-May, luxuriant hay growth is 12 or more inches in height (cf. Buss, 1946:44).

Tame hay in southeastern Wisconsin makes up somewhat more than one-third of all vegetative cover in the first half of May, and somewhat more than one-half of what is attractive nesting cover. It inevitably attracts large percentages of nesting hens.

The average Wisconsin hatching date is about June 18. Hay mowing usually begins in the first half of June, and most fields are cut in the ensuing 3-5 weeks. By the time mowing begins, some nests have hatched. When the field is cut, virtually all of the unhatched nests are destroyed, often only a few days before hatching. Some incubating hens, and some chicks and non-incubating hens are killed or badly maimed. Each year this occurs on many, if not a majority of southeastern Wisconsin farms. It is widely reported by farmers. Every Wisconsin nesting study (Leopold, 1937; Buss, 1946; Bell, 1954; McCabe, 1955) has reported such losses.

To many pheasant biologists, it is all but axiomatic that hayfield losses depress pheasant densities to some degree. But to others, the renesting capabilities of the hen and compensatory, self-limiting mechanisms may override the detrimental effects of these losses. Because some hens renest and because most hens alive at the end of summer have broods, Errington (1945:196) concluded: "Thus substantial nesting losses had little influence on final productivity." More recently, Klonglan, Robbins, and Ridley (1959) were not able to see any population response from a 38-percent 3-year reduction in hayfield hen losses with the use of flushing bars. They suggested that some "carrying capacity" principle may cancel any gain from the increased hen survival. If there is a surplus of hens at the beginning of the nesting season in most areas as Allen (1956) and Linder *et al.* (1960) contend, then some loss of hens and reproductive effort might not affect the ultimate, fall population.

Comparative Phenology of Mowing and Nesting

From 1949 to 1951, Wisconsin biologists kept weekly records on hay mowing activities by recording hayfields as uncut, started, half-cut, or completely cut. Between 1952 and 1957, District Game Managers made similar counts as routine, annual surveys. These provided information on annual and regional variations in Wisconsin hay mowing phenology.

These hay mowing observations and the brood data were used to compare the phenology of mowing and nesting. In earlier nesting studies, investigations concluded that nest densities were higher around the peripheries of fields than toward the interiors. Thus, most of the mowing damage to pheasants could be done in the first few swaths cut around the field. Although in recent Wisconsin studies (John M. Gates, unpubl.) there has not necessarily been an edge effect in nest placement, we have compared the statewide, cumulative percentage of broods hatched with the percentage of hayfields completely uncut in order to be conservative (Fig. 47). Since some nests are located in the interior of the fields, the mowing line could be shifted slightly to the right to depict the relationship more accurately.

The hatching curve is based on broods observed in late summer, therefore representing only successful nests. Thus it is not a precise index of total nesting phenology. Because of this bias it is not possible to deduce the actual percentage of nests and hens lost. Figure 47 does suggest that a substantial fraction of the hatch comes off before mowing. According to this figure, approximately one-half of the broods have hatched when mowing begins, and roughly two-thirds are off when one-fourth of the fields are started.

Wight (1950), Dustman (1950), Salinger (1952), and Yeager *et al.* (1956:179) concluded that the severity of mowing loss varies between years, depending on the comparative phenology of nesting and mowing. In years when nesting is late, fewer nests hatch by mowing time, and a higher proportion of nests and hens is destroyed. The annual variation is extreme enough to be associated with fluctuation, according to these authors.

In order to examine this relationship in Wisconsin, we compared the annual, statewide average hatching dates with the annual percentage of hayfields cut by the week of June 24-30 (Fig. 48). Although the variations appear to be parallel, the correlation coefficient of 0.556 is short of significance at the .05 level.

This relationship, if present, might at first glance appear to be an artifact of hay mowing phenology. If mowing is late, nest success in hay could be higher. Since hayfield nests are frequently later attempts of hens whose nests were destroyed in other cover (John M. Gates, unpubl.), greater success of these could produce a later mean hatching date independent of nesting phenology. While there may be some slight tendency in this direction, we previously showed that the average hatching date is probably a valid index of nesting phenology, and the latter in turn varies importantly with prenesting temperatures.

Other information suggests that mowing and nesting phenology tend to be related. Hay mowing information in 1950 from phenologically later Milwaukee County showed that

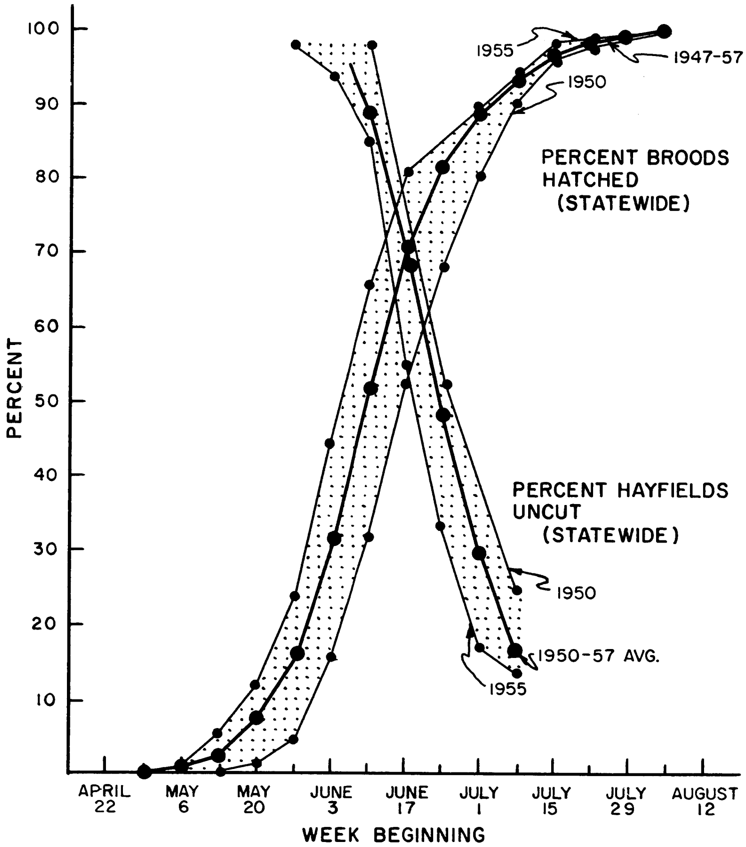


Figure 47. Comparison of the 1950-57 average, cumulative percentage of hayfields unmowed and of broods hatched for the entire state, and for the earliest (1955) and latest (1950) years observed.

TABLE 21

Interrelationships Between Percentage of Nesting Cover in Tame Hay, Percentage of Nests in Tame Hay, and Loss of Nests and Hens

State	Years of Study	Percentage of All Nests in Tame Hay	Percentage of Nesting Cover in Tame Hay[1]	Percentage of All Nests Destroyed by Mowing	Percentage of Hen Population Killed and Maimed by Mowing	Percentage of Hayfield Nests Successful	Reference
Penn.	1949	82	—	61	ca. 27[2]	11	Wight, 1950
Iowa	1950	67	—	56	—	6	Robbins & Hendrickson, 1951
Ohio	1938–41	64	36	38–51[3]	ca. 21[4]	20–40	Leedy & Dustman, 1947
Ohio	1946–47	63	—	38–50[3]	ca. 34	20–40	Ibid., and Dustman, 1950
N. Y.	1953	63	87	50	—	7	Robeson, 1957
Ore.	1937	62	ca. 54	31	38	46	Eklund, 1942
Mich.	—	60	—	37	—	—	Wight, 1945:147
Idaho	1950	59	31	—	31	0	Salinger, 1952
Penn.	1939	51	63	40	22	27	Randall, 1940a
Mass.	—	50	—	17	—	—	Pearce, 1945:46
Iowa	1954	43	33	35	31	7	Klonglan, 1955a
Wash.	1940–42	40	28	11	—	—	Knott, *et al.,* 1943
Wis.	1936–42	35	24[5]	20	3	37	Buss, 1946:38
Colo.	1948–50	33	47	33	17	—	Yeager, *et al.,* 1951
Iowa	1933–35	26	—	23	—	14	Hamerstrom, 1936
Iowa	1939–41	25	20	30[6]	18	25	Baskett, 1947
Iowa	—	—	—	—	10	—	Errington, 1945:196
S. Dak.	1947	ca. 10–15	15[7]	14[8]	—	—	Nelson, 1950
Iowa	1948	12	12	18	0	7	Weston, 1953
Pelee Is.	1949–50	6	6	3	1	26	Stokes, 1954
Mich.	1940–42	1	5	1	1	0	Shick, 1952

[1] Tame hay acreage ÷ (total acreage of area minus acreage in row crops: corn, grain, etc.).
[2] 21 hens killed out of 77 active nests found: 21/77 = 27 percent.
[3] Percentage of nests in hay x (100 - percentage of hayfield nests successful at cutting time).
[4] 3 yr. average no. of pheasant casualties per 100 nests mowed over x percentage of nests in hay.
[5] Fish Hatchery Marsh study area only.
[6] 30 percent destroyed by all agricultural practices.
[7] 15 percent of cover in all types of hay including some wild hay.
[8] 14 percent of nests destroyed by all agricultural practices.

mowing had begun in 20 percent of 49 hayfields under observation during the week of July 8-14. Mowing had started in 76 percent of 90 fields observed in counties west of Milwaukee during the same week. In the following week, mowing was started in 45 percent of the Milwaukee County fields while 99 percent of the fields to the west were partially or completely cut.

Between 1952-57, 49 percent of 9,538 hayfields sampled in the Conservation Department's southern administrative area were uncut during the week of June 24-30; 50 percent of 17,968 fields were uncut in the east and west central areas, while 67 percent (3,175) were uncut in the two northern areas. The difference between the southern and central areas is not statistically different, but both are significantly earlier than the northern areas at the .05 level.

Mowing and nesting phenology in Wisconsin may therefore be influenced by the same factor—spring temperatures. The correlation is not perfect because other variables influence both hay growth and mowing time. One of the most significant of these is rain. Rain affects hay growth and, when it occurs at mowing time, can cause a substantial delay in mowing. For example, not only was 1957 phenologically late, but continued rains delayed hay mowing further (Fig. 48). The spring and summer of 1949 were warm and dry; mowing began early and was completed quickly. Despite these variables, there appears to be a tendency for mowing and nesting to vary together and this would reduce the degree of variation between years and areas of the state in the effect of mowing on pheasant populations.

Limiting Effect on Populations

We compiled data from nesting studies in the literature to learn more about hayfield nesting and related losses (Table 21). A nesting study was included if it contained data pertinent to the columns in Table 21.

Our first objective was to learn what variation exists in the extent of hayfield nesting, and what factors influence it. Information on the percentage of all nests situated in tame hay

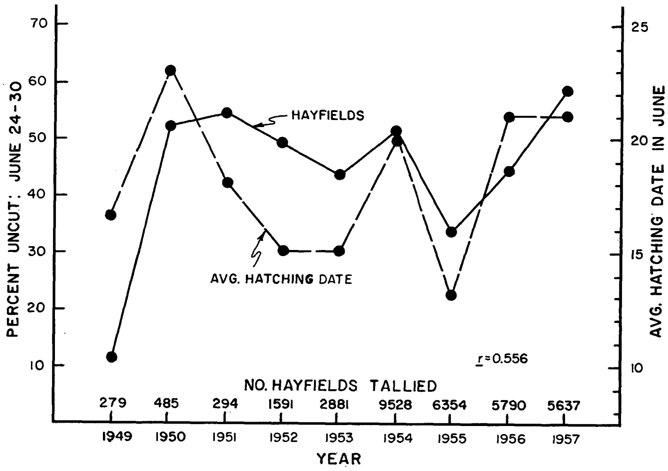


Figure 48. Relationship between the statewide Wisconsin average hatching date and the statewide percentage of hayfields uncut during the week of June 24-30.

was assembled in descending order (Column 3). We restricted our analysis to tame hay because it is usually cut earlier than wild hay, and losses would be more severe. Hence, the values cited in the table vary from the total percentage of nests in all hay in those studies where a substantial part of the study area was in wild hay.

On the assumption that the percentage of nests in tame hay might be largely a function of the hay acreage available to the birds, we first tried to correlate the percentage of nests in hay with the percentage of the total land area in tame hay in each study. In Weston's area in Emmet County, Iowa, Buss' in Wisconsin, and that of Yeager *et al.* in Colorado, the percentages of the total area in hay were 10, 16, and 21, respectively. The percentages of nests in hay were lower than in Salinger's area in Ohio, Klonglan's area in Winnebago County, Iowa, and Dustman's area in Ohio where the percentage of each area in hay was only 7, 9, and 7, respectively. The lack of a correlation was undoubtedly due to our restricting the analysis only to tame hay cover.

We next estimated what percentage hay made up of all the potential nesting cover in each area. Where this statistic was not given directly by each author, we obtained it as follows. The acreage in all row crops (including corn, small grains, and miscellaneous cash crops, but not hay) was subtracted from the total acreage of the study area. We then assumed that the remainder—woodland, marshes, strip cover, miscellaneous rough land, pasture, and tame and wild hay—constituted all potential nesting cover, and we divided this total into the acreage of tame hay (Column 4). Such areas as overgrazed pasture and woodland can only be considered poor nesting cover and carry few nests. However, small grains, particularly winter wheat, have some nests and these were not included in the nesting cover total. Hence, our result is only a crude estimate of the percentage of all nesting cover in tame hay.

The percentage of all potential nesting cover in tame hay (Column 4) was correlated with the percentage of all nests in tame hay (Column 3). The result is significant at the .01 level (Fig. 49). We conclude that the percentage of hens nesting in hay is primarily ($0.791^2 = 63$ percent of the variation) a function of the percentage of all nesting cover in hay. This correlation suggests neither a strong preference for, nor avoidance of, hay as nesting cover. Hens seem to distribute their efforts over the acceptable nesting cover.

The implication is that heavy hayfield nesting does not necessarily occur in areas with large hay acreage, provided there are comparably large acreages of other cover types that will draw a good fraction of the population. And low hayfield acreages do not insure that few hens will nest in hay if there is not enough cover of other types.

Our second objective in analyzing these published data was to learn what variation exists in the extent of nest and hen loss, and what factors influence this variation. We first correlated the percentage of all nests destroyed by mowing (Column 5, Table 21), and the percentage of all hens killed and maimed (Column 6), with the percentage of all nests in tame hay (Column 3). In many cases, these values were reported directly by the authors. In others, we extrapolated them from the information provided (the method is shown in the footnotes to Table 21). The correlations ($r = 0.865$ and 0.829) are significant at the .01 level. This is what one would expect: the percentage of nests and hens destroyed by mowing is simply a function of the percentage of hens that nest in hay.

We then completed the picture by correlating the percentage of all nests destroyed, and of all hens killed and maimed, with the percentage of all nesting cover in tame hay (Column 4). The correlations are significant at the .01 level (Fig. 50).

Figure 50 indicates that we can expect a loss of 25-30 percent of all pheasant nests and approximately 20 percent of all hens from hay mowing in southeastern Wisconsin. While

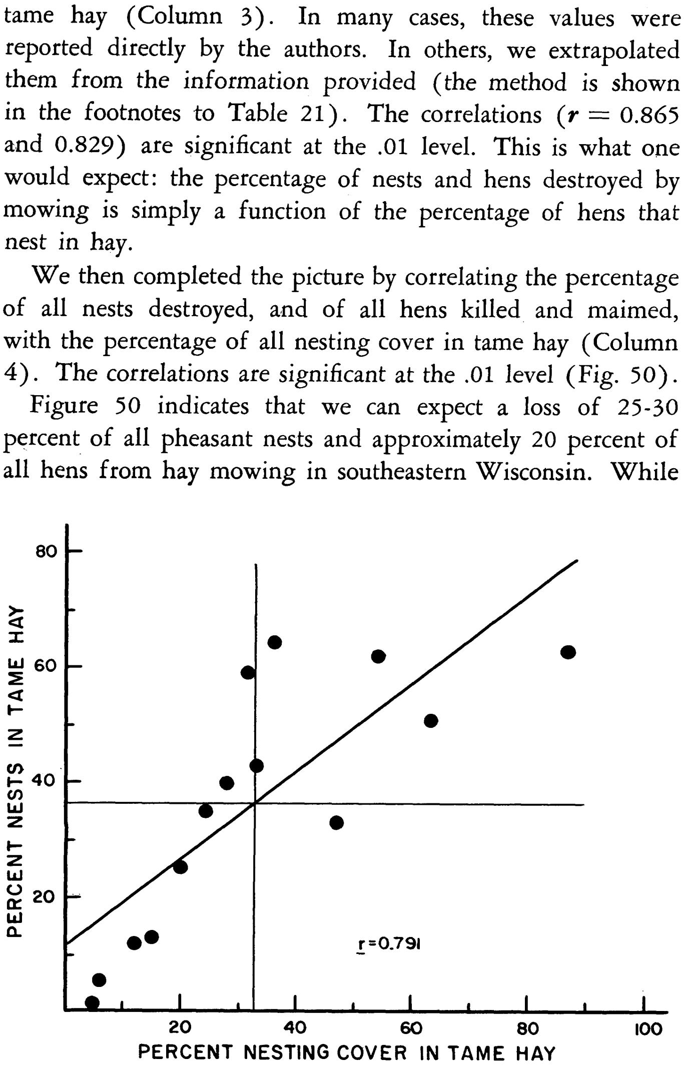
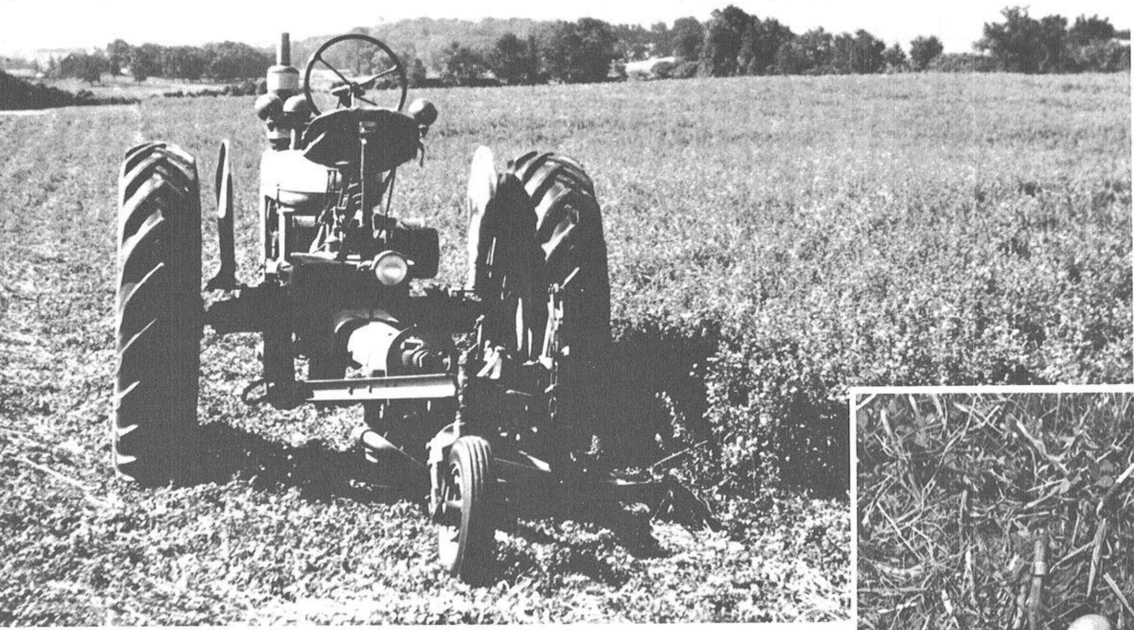


Figure 49. Correlation between the percentage of all potential nesting cover in tame hay, and the percentage of all nests in tame hay in the nesting studies reported in literature. See Table 21 for sources.



Tame hay in southeastern Wisconsin makes up approximately one-third of the available vegetative cover in the first half of May, and substantially more than half of what is attractive nesting cover. It attracts large numbers of nesting hens. Hay mowing begins in early June, well before the peak of hatch. Approximately 25-30 percent of the nests and 20 percent of the nesting hens are lost each year in southeastern Wisconsin hayfields.

we could not determine the extent of chick loss to hay mowing, this could also be a function of the prevalence of hayfields as nesting cover.

The basic question now is whether or not these hayfield losses reduce pheasant densities below what they would be without the loss, and if so, how much? Generally pheasant densities in the areas shown in Table 21 are lower near the top of the table where losses are severe, and higher near the bottom where losses are light. Thus Pelee Island, South Dakota, the Michigan Prairie Farm of the early 1940's, and northern Iowa in the 1930's—all areas with excellent pheasant densities—are situated in the lower lines of Table 21. Several of the eastern states and southeast Iowa—all areas with lesser pheasant numbers—are situated in the upper half of the table.

Kozicky and Hendrickson (1956) analyzed the factors responsible for depressing pheasant numbers of recent years below the level of the 1930's on the Winnebago County, Iowa study area. The shift upwards of this area in Table 21 (data from Klonglan, 1955a for the later years) reflects some of the influences these authors discussed, including increased mowing loss. We do not imply that mowing is the only factor involved in the differences in density between these areas, but the correlation exists, and it may be partially causal.

Another indication comes from the effects of changes in mowing practices on population density. These changes, involving increase in speed of mowing, advance in mowing dates, and increase in hay acreages have been pointed out by Leedy and Dustman (1947), Wight (1950), and Kozicky and Hendrickson (1956). That these changes have been associated with changes in mowing loss is suggested by the data in Table 21. In 7 studies prior to 1946, an average of 25.6 percent of hayfield nests were successful. In 7 studies of subsequent years, the average success of hayfield nests dropped to 11.8 percent, barely short of a significant difference at the .05 level. In 9 studies prior to 1946, 16 percent of all hens were killed by mowing. In 7 subsequent studies, this average rose to 20 percent, but is not significantly greater. Associated with these changes, if real, in severity of loss to mowing is the general failure of pheasant populations to show the vigor of the late 1930's and early 1940's, or to regain the densities of those years despite some recovery following the population declines of the middle 1940's. Our knowledge of population mechanics would indicate that mowing has some effect on population density.

Errington and Hamerstrom (1937) concluded: "It is not necessarily of supreme importance to insure that a given hen pheasant bring off her season's brood from her first clutch of eggs, when any time within the next couple of months may

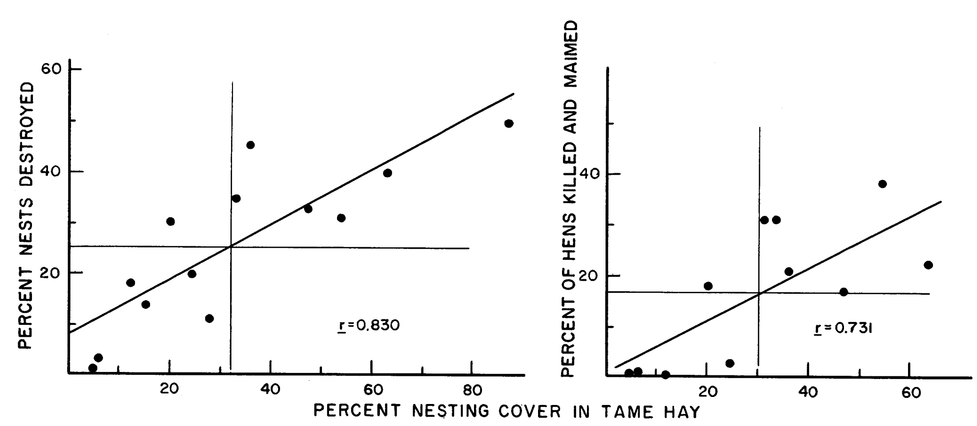


Figure 50. Correlation between the percentage of all nesting cover in tame hay and (1) the percentage of all nests destroyed by mowing, and (2) the percentage of the breeding hen population killed or maimed by mowing. See Table 21 for sources.

serve as well. . . . It appears broadly true that broods brought off at any time during the main season are comparable in size for a comparable age class and enjoy not dissimilar advantages."

However, we now know that clutch sizes and chick survival rates decline in later clutches, that late reproduction usually results in a poor crop, and that there is a terminal date in early July beyond which hens will not renest. Some hay mowing dates in Wisconsin are late enough that many hens, particularly those in the last days of incubation, may not renest following hayfield destruction. In addition to the hen loss in hayfields, summer mortality of hens may be increased by added reproductive stress of renesting (Wagner, 1957).

All of these factors will probably reduce the fall pheasant crop. The available evidence does not bear out the existence of flexible, compensatory tendencies that can override these effects. Thus, we view mowing as a population depressant, the extent of population reduction conceivably being correlated with the severity of mowing loss. The failure of Klonglan *et al.* (1959) to observe a population increase from a 38-percent reduction in hen mortality may have in part been due to the fact that mowing loss on the Winnebago area may have affected no more than about 31 percent of the hens (Table 21). A 38-percent reduction in this loss would mean a savings of 12 percent of the hens. It is possible that many of these hens failed to renest successfully and thus their contribution to the fall population was not detected.

Relationship to Population Density

If certain types of natural cover were preferred over hay and if these types filled up first to some saturation level, then as populations rose an increasing percentage of hens might be forced to nest in hay. The effect of hayfield loss might then be density dependent.

Hens undoubtedly display some preference for nesting cover. Hay, and strip cover such as fencerows, ditchbanks, roadsides, etc., usually carry higher nesting densities than heavily grazed pastures, woodlands, and small grains. However, comparative nesting densities are not always infallible indicators of preference for any given type. Rather, they may often reflect availability at the time hens are ready to nest. For example, Randall (1940), Buss (1946), Baskett (1947), and others observed that the very early nests are established in dead vegetation of the year previous, apparently because hay and other new growth have not yet developed to any degree. Many of the later nests are established in hay. Since many of these areas are intensively farmed, the permanent cover of fencerows, roadsides, etc., constitute a very minor fraction of the total land area, and the early nesters are forced to nest in them in high densities.

Baskett (1947) concluded that fencerows were preferred nesting cover because the number of pheasant nests in fencerows did not increase greatly during a period when the populations on his area more than doubled. At the same time, the percentage of nests in hayfields increased; and he suggested that the fencerows might have been saturated, with an increasing proportion of birds forced into hay as the population increased. However, the increase in percentage of nests in hay and perhaps the failure of any increase in strip cover, at least in the third year, may have been due to substantial increase in the hay acreage on his study area.

Buss (1946) noted that annual changes in population density on one area were paralleled by an increase in number of nests in hayfields. There evidently was no particular density effect, and the number of hens nesting in hay was a function of the population level. Leopold (1937) similarly noted that the density of nests in hayfields in different areas roughly paralleled the population densities in these areas. Although he took this as evidence that hens nested in hay because they were forced to by the inadequacy of other cover, it seems to us that the same interpretation can be applied here as in Buss's study. Linder *et al.* (1960) found roughly constant proportions of nests in the different cover types over a 5-year period when pheasant densities varied nearly two-fold.

We conclude that the birds seem to show some tendencies toward cover preference, primarily in avoidance of sparse cover. Whether or not hayfields are at the top of the preference list, they evidently are quite acceptable and attract hens at all population densities. Hay provides a dense growth of vegetation at a time when much of the landscape is bare, and when many hens are ready to nest. Hens obviously have no prior knowledge that this cover will be cut within a month.

The evidence from Leopold (1937), Buss (1946), Linder *et al.* (1960), and that from Figure 50 suggests that the proportion of a hen population nesting in hay is largely a function of the percentage of all nesting cover in hay. There is no real evidence that this percentage changes with population density. Hence, mowing loss may be largely density independent.

Changes in Hay Mowing Practices

While modern machinery has allowed the farmer to harvest the annual hay crop more efficiently than 10-15 years ago, the advancement in hay cutting dates is one of the most important trends taking place in Wisconsin agriculture today.

Three factors are contributing to this advance. (1) Hay has changed from a predominance of clover-timothy to a majority of faster-growing alfalfas to provide necessary forage for the state's large dairy herd. (2) With new wilt-resistant alfalfa varieties available (Smith, 1956), agronomists are recommending a 3-cutting system for maximum quantity of high quality forage: June 1, July 15, and September 1. (3) There is a trend toward more grassland farming. This trend encourages the growth of more forage crops and less soil-depleting crops such as corn. It is advancing faster in marginal pheasant range.

Dairy farming will in all likelihood continue to be the major enterprise in Wisconsin's agricultural economy. The demand for high quality forage crops will continue and perhaps even increase. This trend cannot be anything but detrimental to the state's pheasant populations.

Wetland Drainage

Role of Wetlands in Wisconsin Pheasant Ecology

While most good midwestern pheasant areas have only fragmentary natural cover, Wisconsin's pheasant densities are correlated with, and seem to depend on, large acreages of glacial marshes (Fig. 10). The Wisconsin range with its dairy economy is also unique in having such a large percentage of land area in tame hay—about two or more times that found in most other midwestern areas. In the past, the view has generally prevailed in the state that the major value of wetland areas is for winter cover. Although pheasants do move into these areas in large numbers in winter, we have doubted at times whether such large acreages were needed for this purpose.

However, the correlation in Figure 10 suggests that our pheasant population density is a function of the total amount of wetland available. The implications of Figures 49 and 50 suggest the possible causal links involved. Wetlands, according to these findings, may be primarily important as nesting cover to balance the extensive hay acreages in the state. The positive correlation between wetland acreage and pheasant density may also imply a negative correlation between hayfield loss and pheasant density.

The total extent is unknown, but Wisconsin pheasants do nest in wetlands. Buss (1946) found about 39 percent of all nests within the Fish Hatchery Marsh portion of one of his study areas. On the basis of the total number of nests found and a winter census of his area, Buss' data (p. 29) suggested that the number of hens nesting in or within several hundred yards of the marsh approached the number of hens wintering in the marsh. No systematic nesting study has been made of the University Arboretum, but nests have frequently been found in it, and its abundance of broods in summer in the 1940's led to its selection as one of the study areas covered in this work.

By the opening of the hunting season in fall, many birds are found in and around wetlands, and these are favorite hunting areas. In order to get quantitative information on the degree to which pheasants are associated with wetland cover in fall, we made surveys in Nepeuskun and Utica Townships in Winnebago County, both excellent pheasant areas. Approximately 20-21 percent of the area of these townships is in wetland cover. In the fall of 1955, we contacted 85 hunters who we knew hunted pheasants in these townships. We sent them maps of the two townships on which the wetland areas were shown. Each hunter was asked to plot the exact location of every cock he shot and record the type of cover in which it was shot. The results showed about 60 percent of the kills were in or on the edges of the wetlands (Fig. 51).

Much of the pheasant kill occurs in the first few days of the hunting season in October and hence the distribution shown in Figure 51 is a rough index of the mid-October population distribution. Since the birds are still in partially fragmented broods as late as the middle or latter part of September, a month or less prior to the season opening, and since over 90 percent of the shot birds are young of the year, this kill distribution may roughly reflect the distribution of young production in these townships

Effect of Drainage on Pheasant Populations

McCabe *et al.* (1956) discussed the problem of wetland drainage in the Lake States. The gravity of this problem is somewhat unique to Wisconsin where wetlands occupy such large acreages (Fig. 52), and where good pheasant densities seem to depend on these acreages.

Many of Wisconsin wetlands have been drained, cleared of marsh vegetation and planted to crops of sweet corn, mint, potatoes, and a number of truck crops. Land so treated loses all value as nesting cover, and most of its value for winter cover and food production.

The extent of drainage since the 1934-39 Bordner Land Economic Inventory was documented for 11 southeastern counties by the 1954-58 wetlands survey of the Wisconsin Conservation Department. Losses from these counties (Table 22) have averaged 26.2 percent. The most severe losses have tended to occur in the counties with the lowest percentage of their areas in wetland. (Correlation coefficient for 1934-39 percentage of county in wetland and percentage loss by 1954-58 is -0.687, significant at the .05 level.)

The importance of these wetlands to southeastern Wis-

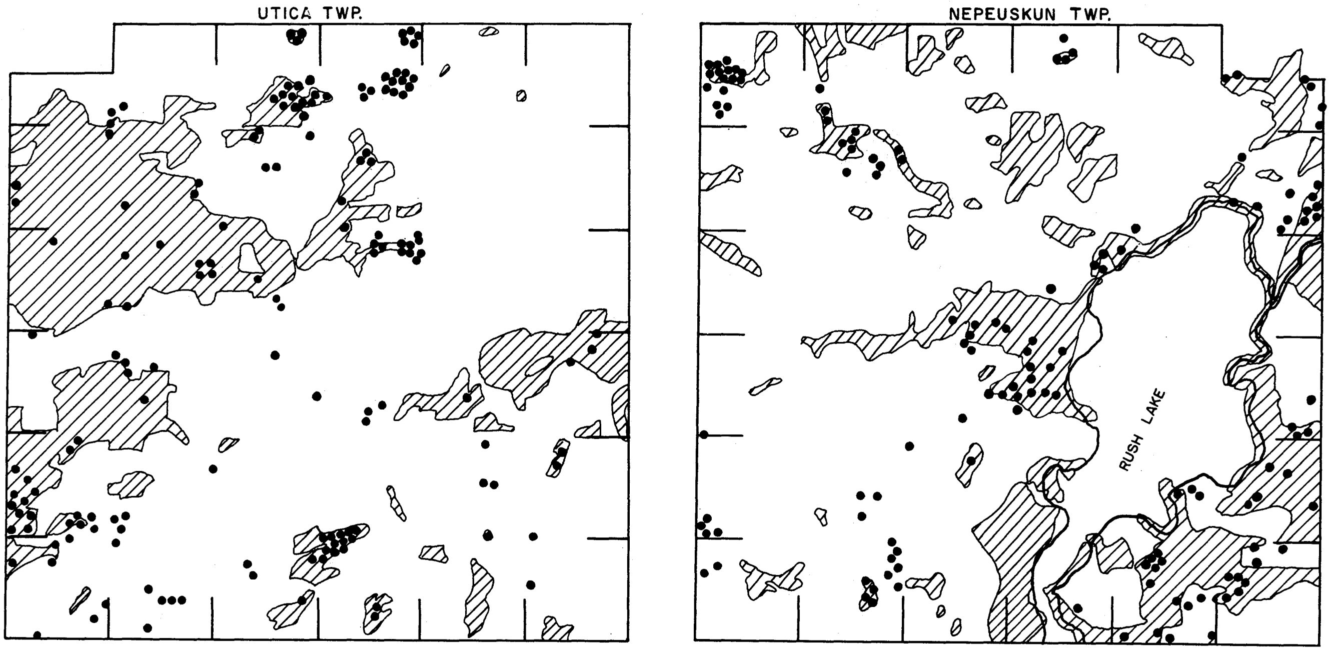


Figure 51. Relationship of pheasant kill distribution to wetlands in Nepeuskun and Utica Townships, Winnebago County, Wisconsin in 1956. Each point indicates where a pheasant was shot, as reported by a sample of hunters. Cross-hatched areas are wetlands.

consin pheasant populations is shown by their effects on population change. During the population decline of 1942-47, the extent of decline in kill in each county shown in Table 22 varied from 50 to 73 percent, and was negatively correlated with the 1934-39 percentage of county area in wetland (Fig. 53). Populations in counties with the highest percentage of land in wetland declined the least. Similarly, during the population recovery of 1947-55, these same counties displayed a positive correlation between the percentage of recovery in the kill and the percentage of land in wetland ($r = 0.775$, also highly significant). Counties with the highest percentage of their areas in wetland experienced the greatest increase.

Evidently the density and general resilience of the populations are a function of the total area of wetland. Any wetland reduction will apparently affect the populations adversely, the greater the reduction the more adverse the effect.

We also correlated the 1947-55 percentage of recovery in the kill with the percentage of wetlands lost between the Bordner and Conservation Department surveys (Table 22). This produced a highly significant negative correlation ($r = -0.773$). Counties with the least wetland loss experienced the greatest population recovery. However, this cannot necessarily be taken as cause and effect because, as noted earlier, the extent of wetland loss is negatively correlated with the amount of wetland in each county. Hence this correlation between population increase and wetland loss may be indirect with the actual wetland acreages being the causal, independent variable.

Other, more subjective evidence of the effects of drainage on population density comes from observing the history of pheasant populations on areas following drainage. McCabe *et al.* (1956:286) mentioned the drainage and removal of 90 percent of the cover in Bird Marsh, Jefferson County. Prior to drainage, this area produced an average kill of about 135 wild pheasants during the hunting seasons of 1940-42 (Buss, 1946:80). Today this area is almost completely bare of natural cover and virtually without pheasants.

During the hunting seasons of 1948 and 1949, 212 and

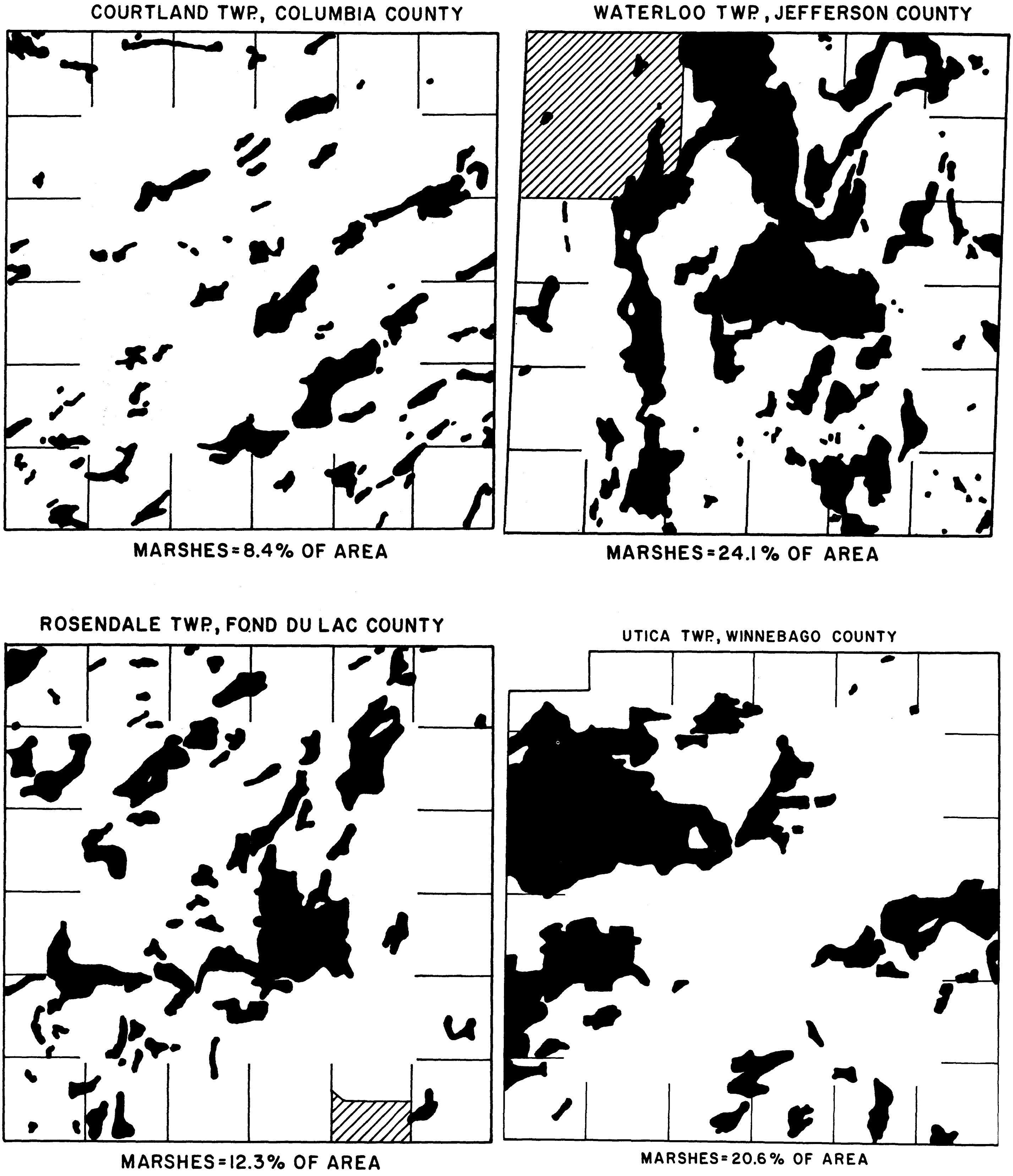
TABLE 22

Changes in Wetland Acreages in Southeastern Wisconsin, 1934-58

		1934-39*		1954-58**	
County	County Acreage	Wetland Acreage	Percent Co. Area	Wetland Acreage	Percent Lost
Green	370,950	15,777	4	8,646	−54.8
Rock	457,286	33,775	7	20,312	−39.8
Racine-Kenosha	385,666	35,546	9	17,899	−49.6
Dane	765,025	67,277	9	44,599	−33.7
Walworth	357,199	36,115	10	27,254	—24.5
Columbia	500,141	63,763	13	55,181	−13.4
Fond du Lac	462,320	63,393	14	52,765	−16.8
Waukesha	354,360	55,491	16	40,891	−26.2
Dodge	572,083	127,279	22	89,378	−29.8
Jefferson	354,013	76,963	22	67,915	−11.7
Total	4,579,043	575,369	12.6	424,840	—26.2

*Bordner Land Economic Inventory.

**Wisconsin Conservation Department Wetland Survey.



COURTLAND TWP., COLUMBIA COUNTY

MARSHES=8.4% OF AREA

WATERLOO TWP., JEFFERSON COUNTY

MARSHES=24.1% OF AREA

ROSENDALE TWP., FOND DU LAC COUNTY

MARSHES=12.3% OF AREA

UTICA TWP., WINNEBAGO COUNTY

MARSHES=20.6% OF AREA

Figure 52. 1956 Distribution of marshes (in black) in four Wisconsin townships having "Good" to "Very Good" pheasant densities.

182 wild cocks were shot on the 4,000-acre Potter's Marsh in Sauk County (Kabat *et al.,* 1955). This area was an island of pheasant range surrounded by wooded hills, and served as a Conservation Department Public Hunting Ground. In the ensuing years, intensive drainage and cover removal laid the area bare for mint farming. Pheasants declined to a small remnant of their previous numbers and it has been abandoned as a Public Hunting Ground.

The 9,900-acre Mazomanie Public Hunting Ground in Dane County is largely lowland, partly in crops and partly in marshy cover. It too is an island of pheasant range surrounded by sandy, wooded river plain and wooded hills. Annual hunting season checks on this area since 1952 showed a peak kill of 314 wild cocks on opening day of the season in 1953. During the 1950's, the marsh was progressively cleared and cropped. Concomitantly, the pheasants declined to where only 12 wild cocks were checked on opening day of the 1959 season.

We conclude that Wisconsin pheasant densities are positively correlated with the percentage of land area in wetland in the heavily farmed areas of southern and eastern Wisconsin. These wetland acreages may be needed to match the large hay acreages and attract a large enough proportion of hens for nesting to bring up the mean nesting success and reduce hen mortality. No doubt there is an optimum beyond which additional wetland is of no value, or perhaps even detrimental. But no southeastern county had more than 27 percent of its area in wetland in 1934-37, and this does not appear to have been excessive. Presumably the optimum is somewhat above this amount, depending on the total acreage of hay also present.

Several exceptions to the correlation between marshes and pheasants need to be rationalized. High pheasant densities occur in parts of Milwaukee, Racine, and Kenosha Counties in the absence of extensive wetland acreages. The greatest densities in the latter two counties are in the easternmost townships around the cities of Racine and Kenosha (Fig. 1). Some of the highest densities in Milwaukee County occur in semi-rural, semi-urban townships surrounding the city of Milwaukee. The habitat supporting these populations seems to be a ragged zone of fallow fields and small scattered wetland areas interspersing the advancing residential and business activities and relaxing agriculture of an expanding city exterior.

At one time there were high pheasant densities in a number of intensively farmed areas in the southern part of the state that had little or no wetland cover. Good pheasant numbers occurred in the early 1940's on the Arlington Prairie in Dane County. In the 1940's, southern Green County had some of the highest pheasant densities in the state, and this was the reason for our selecting it as a study area.

The Arlington Prairie today has very low pheasant densities. It is impossible to say definitely why it was able to carry good numbers at one time without wetlands. We can only speculate that nesting was successful enough and hen mortality low enough during the era of later mowing dates and horse-drawn mowers to permit the population to maintain itself at fairly good levels.

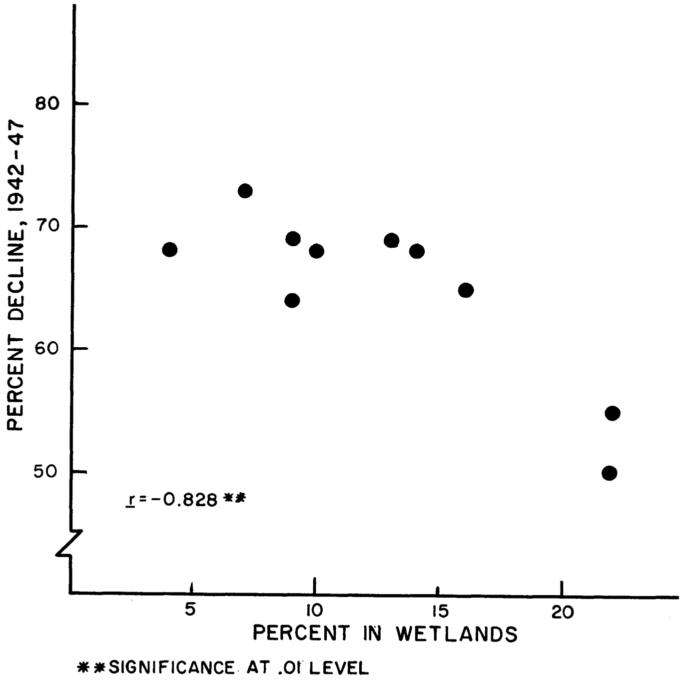


Figure 53. Correlation between percentage of county area in wetland in 1934-39 with percentage decline in kill estimates, 1942-49. Each point represents a southeastern county shown in Table 22.

The Green County pheasant populations maintained themselves well into the 1950's when the newer farming practices were fully entrenched. They began to lose ground in the middle 1950's, and by the end of the decade had shrunk to a small fraction of their previous densities. That this population maintained itself somewhat longer in the modern era without appreciable wetland acreage may have been made possible because southern Green County had an unusually high acreage of improved or rotation pasture in the 1940's and 1950's. Federal-State Crop Reporting Service statistics show that the acreage of grazed cropland made up 35-40 percent of the harvested cropland acreage. In other southeastern Wisconsin counties, this percentage was generally below 25, often below 15.

Miscellaneous Influences

There are several other farming practices which adversely affect pheasant populations. These are widely recognized and we only mention them briefly.

The first is grain harvest. Combining of small grains destroys a few nests and kills an occasional bird. Birds are rarely killed by corn-pickers.

The second influence is spring plowing. Corn is preceded by hay in the Wisconsin crop rotation, and is the last rotation crop planted in spring. When the spring work schedule is delayed by inclement weather, plowing of sod for corn land may be quite late, and fair numbers of nests and rarely hens

The density and general resilience of the Wisconsin pheasant population are a function of the total area of available wetlands. Any wetland reduction will adversely affect the population. Large, undisturbed wetland acreages are needed as secure nesting areas to maintain a high nesting success and reduce hen mortality. Extensive drainage and overgrazing of wetlands have placed increased pressure on pheasant populations.

are plowed under (cf. Eklund, 1942; Knott *et al.,* 1943; Buss, 1946; Robeson, 1957). The hens forced to renest are now delayed, and those moving into hay have less chance of succeeding before mowing than if they had begun their first clutch in hay. Although fall plowing is generally considered unfavorable for pheasants because of the reduction of winter food and cover, some workers (e.g. Paul J. Moore, pers. comm.) question whether it may be less undesirable than having the same land plowed in spring.

A third influence is livestock grazing. Cows occasionally destroy nests (cf. Eklund, 1942; Buss, 1946). But their most serious effect, aside from demanding large hay acreages for forage, is the removal of cover from pastured areas. Most southwestern Wisconsin woodlands and many wetlands, are used for pasture. These are often overgrazed and appear to be voids in pheasant habitat.

The practice of maintaining the dairy herd in small feed lots, rather than in large permanent pastures is increasing. Removal of cows from grazed marshes would be an asset unless such removal discontinued the need for such pasture, and encouraged drainage for cropland. In that case, a grazed marsh would be preferred to no marsh.

One of the unfavorable aspects of the feed-lot practice is the daily cutting of a few swaths of hay from cropland and transporting this fresh feed to the dairy herd. This practice begins early in May and is another factor which advances hay mowing dates.

Other influences such as fencerow removal, roadside spraying, burning of cover in spring and fall, and increased use of pesticides cannot be expected to have many favorable effects on pheasants. Thus, the dairy farming pattern, with all its various ramifications, is probably one of the strongest influences preventing Wisconsin from being more than a mediocre pheasant state by midwestern standards.

Relationship of Farming Trends to Pheasant Populations

To examine the gross changes occurring in the pheasant population, perhaps as the result of the sum-total influence of agricultural changes, we plotted the annual Wisconsin pheasant kill estimates. Figure 54 shows the levels to which the population has risen and the extent of fluctuation.

Several features of this curve seem to be significant. First, the 1942 high exceeded the 1955 high, the latter attaining only 70 percent of the former. Furthermore, the 1960 low dropped below the 1947 low. The mean kill of the 1938-47 period (502,000) exceeded the mean kill of the 1948-60 period (440,000), although the difference is short of statistical significance. Actually the disparity between the two highs and lows may be greater than indicated because of the increased nonresponse bias in the kill figures. The mean population level may therefore have slipped below that of the earlier years.

Another related feature of the curve is the comparative rates of increase (**r** values) in the 1938-42 and 1948-55 periods. The kill roughly tripled in the 1938-42 period but it increased less than 100 percent from 1948 to 1955, and then took 8 years to achieve this gain. During the early increase period, the mean **r** value (21.3 percent) was sig-

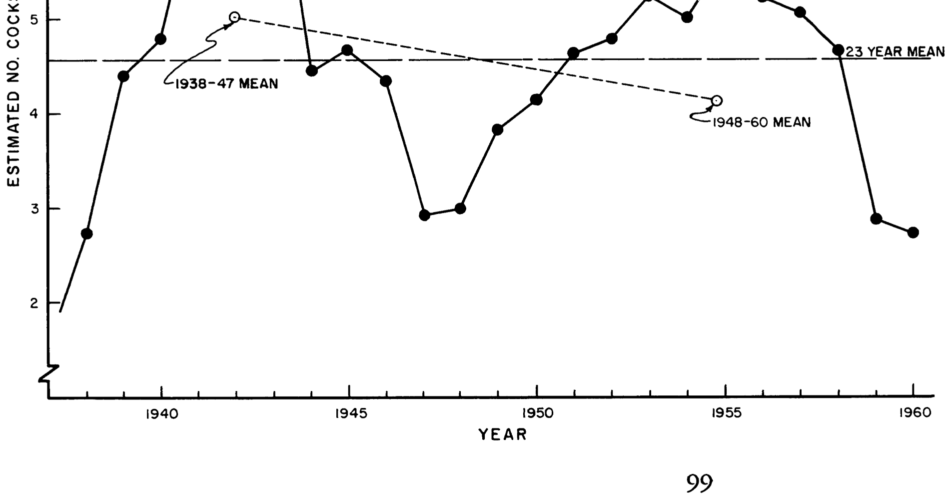


Figure 54. Wisconsin pheasant kill estimates, 1938-60.

nificantly larger than in the later period (10.7 percent). This suggests a smaller margin of reproduction over mortality.

The environment may have exerted a heavier, long-term pressure on the populations in the period 1948-60 than in the late 1930's and 1940's because of the various changes discussed in this chapter. Mean r values were lower, and these may ultimatively have resulted in lower, mean population levels. If present farming trends continue, we can look for further declines in population density in the decades ahead.

Summary

In early May, when hens are ready to nest, no more than half of the landscape in southeastern Wisconsin is in potential nesting cover. Tame hay makes up one-third of this cover and over half of the desirable nesting cover. It attracts large numbers of hens for nesting, and many nests are destroyed by mowing, although in some years a portion of the nests hatch before mowing. Mowing phenology, like nesting, may be correlated with spring temperatures.

The percentage of nests in tame hay in different areas is correlated with the percentage of all potential nesting cover in tame hay. The percentages of all nests and hens destroyed by mowing are closely correlated with the percentage of nests in hay. Consequently, the percentages of all nests and hens destroyed by mowing in different areas are correlated with the percentage of potential nesting cover in hay in each area. The percentages of nests and hens lost in southeastern Wisconsin hayfields may be on the order of 25-30 and 20 percent respectively.

Generally those areas on the continent with low hayfield losses have higher pheasant densities than those with high hayfield losses. The proportion of hens nesting in hayfields may be largely a function of the percentage of all nesting cover in hay. Mowing losses may be density independent.

The density and general resilience of the Wisconsin pheasant populations are a function of the total area of wetland. Any wetland reduction will apparently affect the populations adversely. Large wetland acreages are needed to match the large hay acreages and attract a large enough population of hens for nesting to bring up the mean nesting success and reduce hen mortality.

More intensive farming, especially the advancement of hay mowing dates, and continued wetland drainage have placed increased pressure on pheasant populations. Population densities and rates of population increase (r values) have been lower in the period 1948-55 than in the period 1938-42. With a continuation of current trends, we look for further declines.

CHAPTER XII. PREDATION

The published data on pheasant predation fall into three disproportionate groups: (1) many observed instances of predation on pheasants; (2) very few studies simultaneously measuring predator and pheasant populations and the fraction of pheasants taken; and (3) an extremely small number of studies involving predator removal in most cases involving only a single species of predator.

Several hypotheses on the effects of predation have been proposed by various investigators on the basis of their findings or on the basis of principles operating in other species. While the available data do not permit many positive generalizations about predatory effects on pheasant population levels, we surveyed the published data and included Wisconsin findings to attempt to gain some insight into predator-pheasant relationships.

Pheasant Predators

Types

Predators on Adults and Young

Species in the Wisconsin fauna which have been observed here or in other states to prey on adult or young pheasants total 24 (Table 23): 13 mammals, 2 owls, 7 hawks, and 2 reptiles. Less than half of these can be considered even remotely effective predators on Wisconsin pheasants, either because of their proficiency and/or their abundance in pheasant range. However, each species need take only a small fraction in order for all predators to be potentially capable of removing a material percentage of a population. On the other hand, no single species, such as the red fox, should be magnified out of proportion to its importance. Any one species is only part of the total predator community.

Predators on Nests

The potential predators on pheasant nests in the state total 20 species (Table 24): 15 mammals, 3 birds, and 2 reptiles. The gray fox is probably a potential nest predator, but we are not aware of any specific literature reference. There are 7 species listed in Table 24, not included in Table 23, which bring the total list of known pheasant predators in Wisconsin to 31.

Again in Table 24, the species listed vary in importance as nest predators. The skunk and crow are probably the most important, followed by the foxes, raccoon, opossum, dog and cat. Still others on the list must have very little, if any, significance as pheasant predators.

Distribution

Variations in Wisconsin

Game Division kill estimates and bounty records were consulted to learn what regional variations exist in mammalian predator densities. We calculated the mean number of each mammal taken annually during the period 1952-57 for each county. The 5-year averages were then divided into the area of each county to get square-miles-per-animal values. Species included were red and gray foxes, raccoon, skunk, weasels (three species combined), badger, opossum, and mink.

The biases in this type of data are unknown. Species with high pelt value (mink) or sport value (fox and raccoon) may be taken in higher numbers in the heavily populated

TABLE 23

Wisconsin Species Reported to Have Preyed on Pheasants

Predator Species	Physical Competence as a Pheasant Predator*	Occurrence in Wisconsin Pheasant Range	Reference
Red fox (*Vulpes fulva*)	1	Common	Richards and Hine, 1953; MacMullan, 1954; Findley, 1956
Gray fox *(Urocyon cinereoargenteus)*	1	Rare	Hatfield, 1939; Latham, 1950; Richards and Hine, 1953
Domestic dog	1	Common	Leedy and Hicks, 1945
Coyote *(Canis latrans)*	1	Rare	McKean, 1948; Fichter *et al.,* 1955
Badger *(Taxidea taxus)*	3?	Moderate	K. Hamilton, pers. comm.
Mink *(Mustela vison)*	2	Common	Shick, 1952; This study
Weasel *(Mustela spp.)*	3	Moderate	Shick, 1952
Striped skunk *(Mephitis mephitis)*	3	Common	Bishop, 1944
Raccoon *(Procyon lotor)*	2?	Common	Stuewer, 1943; Klonglan, 1955a
Domestic cat	1	Common	Leedy and Hicks, 1945; Rasmussen and McKean, 1945
Norway rat *(Rattus norvegicus)*	3 (on young)	Common	Stokes, 1954
Opossum (*Didelphis virginiana*)	3	Common	Hamilton, 1958
Greathorned owl *(Bubo virginianus)*	1	Common	Errington *et al.,* 1940; Orians and Kuhlman, 1956
Snowy owl *(Nyctea scandiaca)*	2?	Rare in winter	Gross, 1944; Latham, 1950
Red-tailed hawk *(Buteo jamaicensis)*	1	Common	Errington & Breckenridge, 1938; Orians and Kuhlman, 1956
Red-shouldered hawk *(B. lineatus)*	3	Moderate	Latham, 1950; Craighead and Craighead, 1956
Rough-legged hawk *(B. lagopus)*	3	Common in winter	Errington and Breckenridge, 1938
Cooper's hawk *(Accipiter cooperi)*	1	Common	Shick, 1952; This study
Goshawk *(A. gentilis)*	1	Rare in winter	Bump *et al.,* 1947; Latham, 1950
Peregrine falcon (*Falco peregrinus*)	1?	Rare	Sharp and McClure, 1945
Marsh hawk *(Circus cyaneus)*	1 (on young)	Common	Breckenridge, 1935; Bump *et al.,* 1947; Shick, 1952
Fox snake *(Elaphe vulpina)*	3 (on young)	Moderate	Grange, 1948
Snapping turtle *(Chelydra serpentina)*	3	Common	Edminster, 1953

*Our subjective rating of competence is based on physical capabilities and published proclivity for preying on pheasants. Descending scale of proficiency: 1, 2, 3.

eastern and southern counties while species of no commercial value may only be taken incidentally. Hence these distribution data must be used cautiously.

As previously shown by Richards and Hine (1953), foxes are most numerous in the southwestern and western parts of the state (Fig. 55). The partly wooded, partly cultivated, dissected western landscape seems to be ideal red and gray fox habitat. Foxes occur in the primary southeastern Wisconsin pheasant range, but in nowhere near the densities of the southwest and west.

Raccoons occur over the entire state (Fig. 55), but the region of abundance partially coincides with the fox distribution of the west. This is a species that prefers some woodland in addition to water sources. The large numbers of raccoon taken in several southeastern counties may reflect heavier hunting pressure or higher raccoon populations especially in the Kettle Moraine region.

Skunks also occur over the entire state (Fig. 55), although they seem to be most abundant in the west and northwest. Skunks prefer semi-open country with brush patches and marshes, but they can adapt to heavily forested areas or wide-open country.

Weasels apparently are most abundant in northern Wisconsin (Fig. 55). This distribution is undoubtedly weighted by the short-tailed weasel which is primarily northern in distribution (Jackson 1961:340) and outnumbers the more southerly long-tailed weasel.

TABLE 24

Wisconsin Species Reported to Have Preyed on Pheasant Nests

Predator Species	Significance as a nest Predator*	Occurrence in Wisconsin Pheasant Range	Reference
Red fox	1	Common	Nelson, 1950; Grondahl, 1956
Domestic dog	1	Common	Randall, 1939; Shick, 1952
Coyote	1	Rare	Nelson, 1950
Badger	1	Moderate	Carlson, 1953; Grondahl, 1956
Mink	3?	Common	Buss, 1946
Weasel	3?	Moderate	Randall, 1939; Carlson, 1953
Striped skunk	1	Common	Carlson, 1953; Grondahl, 1956
Raccoon	1?	Common	Klonglan, 1955a; Grondahl, 1956
Domestic cat	1?	Common	Randall, 1939
Opossum	2	Common	Allen, 1940
Franklin's ground squirrel *(Citellus franklinii)*	3	Rare	Klonglan, 1955a
Striped ground squirrel *(C. tridecemlineatus)*	3	Common	R. Labisky, pers. comm.
Norway rat	3	Common	Randall, 1939; Stokes, 1954
Fox squirrel *(Sciurus niger)*	3	Common	Randall, 1939
Crow *(Corvus brachyrhynchos)*	1	Common	Most studies
Blue jay *(Cyanocitta cristata)*	3	Common	Randall, 1939
Bronzed grackle *(Quiscalus quiscula)***	3	Common	Randall, 1939; Stokes, 1954
Fox snake	3	Moderate	Stokes, 1954
Bull snake *(Pituophis sayi)*	3	Rare	Sharp and McClure, 1945

*Our subjective rating of potential significance is based on physical capabilities and published proclivity for marauding nests. Descending scale of proficiency: 1, 2, 3.

**Suspected of destroying nests.

While not shown on the maps, coyote data show a pattern that coincides closely with the weasel distribution. Badgers are distributed similarly as the skunk with the largest harvests reported outside the primary pheasant range. This distribution has been reported previously by Jackson (1961: 365). The mink data showed a statewide distribution with no evident centers of abundance, but possible scarcity in the water-deficient southwestern region.

The opossum is one of the few mammalian predators that is most abundant in the primary pheasant range (Fig. 55). Here it finds ideal habitat in farm country interspersed with woodlands and marshes.

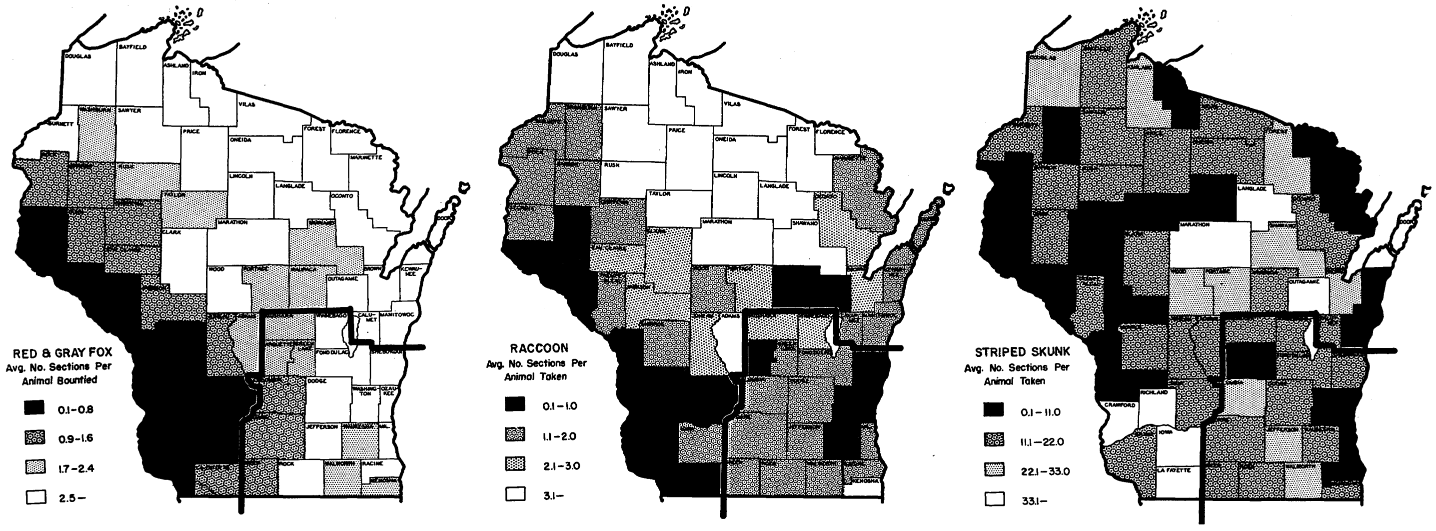
We have very little information on raptor distribution. Such forest-inhabitating species as the great-horned owl and accipiters may be less numerous in southeastern and eastern Wisconsin than in the other, more heavily wooded parts of the state. Distribution of the more open-country species such as the red-tailed and marsh hawks is more uncertain.

On the whole, the total predator pressure may be lower in southeastern Wisconsin. This appears especially likely for the more significant predators of pheasants and their nests—foxes, skunks, raccoon, and the forest-inhabiting raptors—which probably find better habitat in other parts of the state. The converse may be true of red-tailed and marsh hawks, opossum, and of domestic dogs and cats.

Long-term trends in the density of different predators in Wisconsin vary between species. Red fox populations have increased in the past 10-20 years as have the continent-wide fox populations. While the rise of the foxes in the 1940's coincided with the general pheasant decline, the subsequent pheasant recovery occurred while fox populations were high, or increasing further (Arnold, 1951; Richards and Hine, 1953; McCabe *et al.*, 1956). Raccoons (Woehler, 1956) and opossums (Knudsen, 1953) have been increasing in the state but harvest records show skunks and gray foxes on the decline. The skunk decline may reflect low pelt values. We have no long-term information on raptor populations for Wisconsin but findings from Illinois (Graber and Golden, 1960) show a decline of wintering raptors during 1903-55, and this same trend may have taken place in Wisconsin. The collective effect of these changes in predator populations on the state's pheasant population is unknown.

Variations Between Areas in Other States

In order to correlate pheasant and predator numbers in other areas, we compiled predator densities from the literature for areas where pheasant numbers were reported, or where we could approximate the pheasant density rank relative to the other areas. We then listed the areas in approximate decreasing order of pheasant density (Table 25).



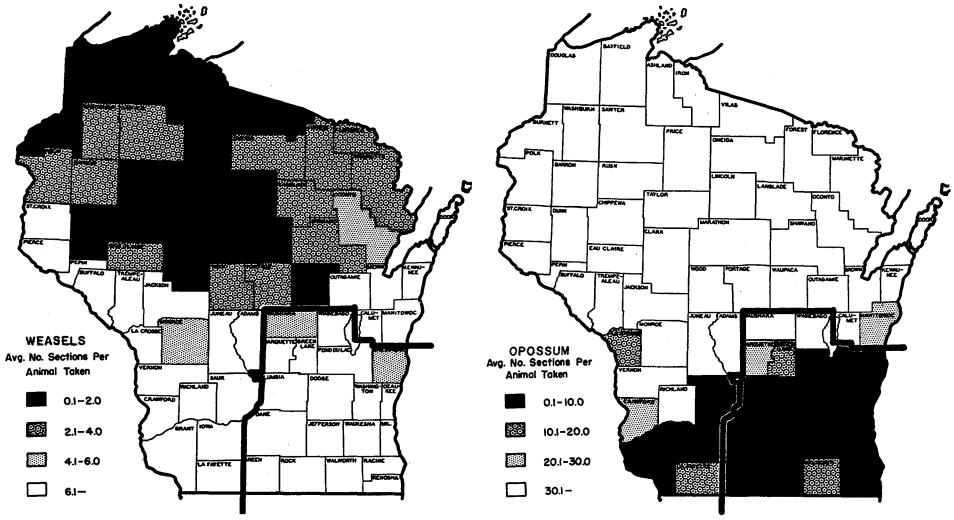


Figure 55. Distribution of red and gray foxes, raccoon, striped skunk, short- and long-tailed weasels, and opossum in Wisconsin. Fox densities based on bounty records, other densities based on Game Management Division kill estimates. The values are annual means for the period 1952-57. The heavy line in the southeast is roughly the limit of the primary pheasant range.

In those cases where we supplied the pheasant density ranking, it was subjective on the basis of how we believed those areas compared with the others in the list. Scott and Selko (1939) gave no information on the pheasant density of their northwestern Iowa area, but this is excellent pheasant range, as they indicated, and surely belongs near the top of the list. Their central Iowa area was marginal for pheasants. The position of the west-central and central New York areas is conjectural on our part. Errington and Stoddard's (1938) area is today a poor pheasant area, and must also have been poor in the early 1930's before pheasants were well established. The Connecticut Hill grouse area in New York must be completely submarginal for pheasants.

The predator densities shown in the table do not all represent the same season, a source of variation in the data. Where possible we have tried to use winter or spring densities. Also, these values only represent a single year, in most cases, and some of them may deviate from the typical, mean densities for the areas.

The comparisons in Table 25, while considered very crude, suggest an inverse correlation between pheasant densities and predator densities. As pointed out by other workers, certain land characteristics which make for good habitat for the different predatory species are not typical of most good pheasant range. Foxes in Michigan reach highest densities where soils are light and well drained, topography dissected, land use intermediate in intensity, and woodlands numerous. They are less numerous in the better pheasant areas where cultivation is intensive, land flat, and soils heavy and fertile (Arnold, 1956). Allen noted a similar distinction between skunk habitat (1939) and pheasant habitat (1938) in Michigan.

Scott (1947) described one area in central Iowa in which topography was rough, land partly wooded, foxes fairly numerous, and pheasant populations sparse. In a second area, topography was gentle, cultivation intensive, foxes only one-fourth as dense as in the former area, and pheasants more than ten times as numerous.

Scott and Selko (1939) demonstrated the importance of topography alone on fox and skunk density in two Iowa townships. Land use and natural vegetation were very nearly the same, but one area in west central Iowa had three times as many acres of slopes predominantly 5-10 percent or more as the other area in northwestern Iowa. The central area had 3 times the number of fox dens, 2.5 times the number of skunk dens, and was marginal for pheasants. The northwestern area had excellent pheasant densities.

Horned owls prefer large blocks of mature woodlands (Hagar, 1957). Lack of extensive woodlands may have limited horned owl populations in the Michigan study area used by Craighead and Craighead (1956:86). In Wisconsin, pheasant densities are inversely correlated with percentage of land area in woodland (Fig. 9).

Red-tailed hawks prefer small woodlands for nesting, and even occasionally nest in isolated trees (Hager, 1957). However, the more open pheasant areas may support lighter hawk populations than somewhat more extensively wooded areas (Table 25).

Thus, predator densities are probably determined by habitat characteristics: effect of soil, topography, vegetation, and land use on denning and nesting sites, and these probably affect the densities of the various prey species that form their stable food supply. Pheasant densities are also influenced by habitat characteristics, and if an inverse predator-pheasant correlation does exist, we do not suggest that it is simple cause and effect. Nevertheless, the weight of predation pressure on pheasants conceivably is heavier in marginal range, and may contribute to that marginality and to some degree of pheasant population reduction.

TABLE 25*

Relationship Between Pheasant and Predator Population Densities

Areas Studied in Approximate Decreasing Order of Pheasant Density	Square Miles Per Predator Fox	Skunk	Great Horned Owl	Red-tailed Hawk	Reference
Eastern Michigan	3.1	—	—	—	Shick, 1952
Northwestern Iowa	4.9	0.6	—	—	Scott & Selko, 1939
Central Iowa**	2.5	—	—	—	Scott, 1947
Southern Michigan	3.0	—	—	—	Arnold, 1956
Southern Wisconsin	—	—	2.8	1.4	Orians & Kuhlman, 1956
Southeastern Michigan	3.6	0.3	2.6	3.0	Craighead & Craighead, 1956:78, 392
Southwestern Michigan	None	0.1	1.1	—	Allen, 1938
Western New York	0.1	—	—	—	Robeson, 1950
Central Iowa	1.6	0.3	—	—	Scott & Selko, 1939
Central Iowa***	0.9	—	—	—	Scott, 1947
West Central New York	0.2	—	—	—	N. Y. State Cons. Dept., 1951
Central New York	—	—	1.8	1.0	Hagar, 1957
South Central Wisconsin	0.2	0.1	0.9	1.0	Errington & Stoddard, 1938
South Central New York	0.3	0.1	0.2	—	Bump *et al.,* 1947:330

*Where observations were reported for more than one year, the value in the table represents the mean density for the period of study.
**Wall Lake Area.
***Moingona Area.

Effect of Predation on Pheasant Populations

Predation on Adults and Young

Relationship of Pheasant Density to Frequency in Predator Diets

In an attempt to learn what relationships may exist between pheasant density and the frequency with which individual predators take pheasants, we summarized food-habits data from the literature on five of the more effective and widely distributed pheasant predators (Tables 26 and 27). The objective was to compare the frequency of predator food samples containing pheasant remains with pheasant density.

Most predator food-habit studies have biases. Fragments of fur or feathers in the stomach or droppings are positive evidence that a prey species was eaten, but there is no proof that it was killed by the predator. An animal may make several meals from a large prey item, and stomachs, droppings, or pellets may show a given species several times when in fact only one individual is involved. On the other hand, remains around dens (and this seems logical for raptor nests as well) may also over-represent the larger prey items (Errington, 1935) because portions of them lay about and are fed upon for days.

TABLE 26

Relationship of Frequency of Pheasant in Fox Diet to Pheasant Density*

Area Studied in Approximate Decreasing Order of Pheasant Density	Season Studied	Percentage of Stomachs or Scats (**) with Pheasant		Reference
		Red Fox	Gray Fox	
Eastern South Dakota	Winter	65	—	Findley, 1956
North Dakota	Winter-spring	13–23	—	McKean, 1947
Eastern Michigan	Year-round	47***	—	Shick, 1952
Central Iowa	Winter-spring	9**	—	Scott, 1947
Southern Minnesota	Winter-spring	14	13	Hatfield, 1939
Iowa	Spring-summer	6**	—	Errington, 1935
Iowa	Winter	6–7	—	Errington, 1937
Southeastern Pennsylvania	Winter-spring	14	16	Latham, 1950
Southeastern Pennsylvania	—	2**	6**	Latham, 1950
Southern Michigan	Winter	8***	—	MacMullan, 1954
Central Iowa	Winter-spring	11**	—	Scott, 1947
Pennsylvania	—	0	1	Latham, 1950
North Central New York	Year-round	4	—	N. Y. State Cons. Dept., 1951
New York	Fall-winter	1	—	Hamilton, 1935
Indiana	Winter-spring	2	—	Haller, 1951
Eastern Iowa	Winter	4	2	Scott, 1955
Central Massachusetts	Fall-winter	0	0	MacGregor, 1942
Southern N. Y. & Catskills	Year-round	1	—	Darrow, 1944
Southern New Hampshire	Year-round	0**	—	Eadie, 1943
Eastern New York	Winter-spring	0	—	Cook and Hamilton, 1944
Southwestern Wisconsin	Winter	2	2	Richards and Hine, 1953
South Central Wisconsin	Fall-winter	0	0	Errington, 1935
North Central Pennsylvania	Fall-winter	0	0	Latham, 1950
South Central Pennsylvania	—	0	0	Latham, 1950

*Where studies were carried on for more than one year, the value in the table represents the average for the period of study.
**Results from scats.
***Percentage of pheasants in all prey items.

Smaller animals such as mice, shrews, small birds, and insects are usually swallowed whole and leave no traces around nest or den. Since stomach, dropping, and pellet analyses would seem to be less biased than observing remains around nests or dens, we have restricted our discussion to these.

We attempted to arrange the data in Tables 26 and 27 in decreasing order of pheasant density in the same manner as in Table 25. The same state was placed at different levels of the table when studies were conducted in different parts of it with varying pheasant densities (e.g. in Table 26: Scott, 1947; the various New York studies; etc.).

Pheasants are taken, both by raptors and foxes, most frequently in spring, second most often in winter, and less frequently in summer and fall (Errington, 1938; Scott, 1947; McKean, 1947; Latham, 1950, and others). Samples from different seasons are not comparable, and we have not included summer and fall results where it was possible to omit them. This was not possible in some cases, where material from several seasons was combined. In several cases, we separated information from the same study by season, and placed spring data above winter or year-round material (cf. Errington, 1938; Craigheads, 1956 in Table 27).

We gave some consideration to the chronology of the studies. Errington's (1932, 1933) data in Table 27 from south central Wisconsin were taken in 1929-32 when pheasants were barely gaining a foothold in the state. Grange's (1948) were taken from central Wisconsin in the winters of 1940-1942 at the population high, and so were ranked above Errington's.

These and other potential variables make this a subjective comparison. Nevertheless, the tables suggest a rough correlation between pheasant density and frequency of occurrence of pheasant remains in the predator's diet. Less extensive data for other predators show roughly the same relationship. Fichter *et al.* (1955) demonstrated a correlation between pheasant density and frequency of pheasant in coyote diets. Errington (1933) found only one case of marsh hawk predation on pheasants in south central Wisconsin between 1929-33, and Latham (1950) showed none for New York, Maine, and several samples from Pennsylvania. Breckenridge

TABLE 27

Relationship of Frequency of Pheasant in Raptor Diet to Pheasant Density

		Percentage of Stomachs or Pellets[1] with Pheasant[2]			
Areas Studied in Approximate Decreasing Order of Pheasant Density	Season Studied	Great Horned Owl	Red-tailed Hawk	Cooper's Hawk	Reference
S. Minn. & E. S. Dakota	Fall-spring	—	31	1	Errington & Breckenridge, 1938
E. Michigan	All year	41[3]	—	100?[3]	Shick, 1952
N. W. Iowa	Spring-summer	30[1]	—	—	Errington, 1938
N. W. Iowa	Winter	15[1]	—	—	Errington, 1938
Iowa	Fall-winter	—	0	—	Errington & Breckenridge, 1938
S. E. Michigan	Spring-summer	17[4]	7[4]	10[4]	Craighead & Craighead, 1956:400-401, 403
S. E. Michigan	Winter	6[1]	0.4	—	Craighead & Craighead, 1956:131, 133
Pennsylvania	All year	1	2[5]	3[5]	Latham, 1950
Pennsylvania	All year	6[1]	—	—	Latham, 1950
New York	—	4	2	9	Bump *et al.,* 1947:339
W. Indiana	Winter	1[1]	—	—	Kirkpatrick & Conway, 1947
N. E. U. S.	—	—	—	4[5]	Latham, 1950
Central Wisconsin	Winter-spring	2[1]	—	—	Grange, 1948:129-131
S. Central Wisconsin	All year	0	0	0	Errington, 1932, 1933; Errington & Breckenridge, 1938
Maine	—	0	0	—	Mendall, 1944

[1] Results from pellets.
[2] Where studies were carried on for more than one year, the value in the table represents the average for the study period.
[3] Percentage of observed kills.
[4] Percentage "of diet".
[5] Total for all studies listed.

(1935) observed several cases in east central Minnesota (mediocre pheasant range). Randall (1940) and Shick (1952) reported numerous cases of marsh hawk predation on their dense pheasant populations.

Chronological changes in pheasant density suggest a similar pattern. Pheasants occurred in 21 and 37 percent of horned owl pellets collected in northwestern Iowa in the winter of 1933-34 and spring and summer of 1934, respectively (Errington, 1938). The following year pheasants were fewer and their frequency in pellets dropped to 6 and 23 for the same season.

Between 1929-31, Errington (1935) found no pheasant remains in red and gray fox stomachs in the Wisconsin unglaciated region. Some 16-18 years later, and after pheasants were established, Richards and Hine (1953) found pheasant in 2 percent of red and gray fox stomachs in winter.

Hamerstrom and Hamerstrom (1951) observed a number of pheasants among prey items at Cooper's hawk nests in the George Reserve in Michigan in 1941-42 near the pheasant peak. In 1946 near the population low, they found no pheasants among prey items.

The suggested relationship between pheasant density and frequency of occurrence in the combined predators' diet coincides with the general principle of availability that is widely operative in predator-prey relationships. A predator tends to distribute its efforts over the entire base of prey animals that fall within the limits of its physical capabilities and are available to it. Species which are abundant are taken frequently, and ones that are scarce make up only a minor part of the diet. This has been shown for the horned owl (Errington *et al.*, 1940), the European sparrow hawk, *Accipiter nisus* (Tinbergen, 1946; Hartley, 1947), the red fox (Scott, 1955; Besadny, 1961), a collective raptor population (Craighead and Craighead, 1956), the total complex of Nearctic birds (McAtee, 1932), and others. In a general review of predation principles, Latham (1951) concluded: "The frequency of occurrence of a prey species is often . . . closely proportional to the size of the prey population . . . ."

Frequency of a prey species in a predator's diet is often assumed, and erroneously so, to indicate the degree to which that predator affects the prey population. Latham (1950) emphasized the fallacy of this assumption, and Bump *et al.* (1947:338) pointed out that the removal of a small number of prey animals may be sufficient to have an important effect on that prey population.

The important statistic in determining the degree of effect on a prey population by a predator is the percentage of the prey population taken (Leopold, 1933:232; Solomon, 1949; Latham, 1951). This percentage depends not only on the frequency of kill per predator, but also on the number of predators and of prey. Frequency in the predators' kill may bear no relationship to the percentage of pheasants taken.

Pheasants were found to constitute 8 percent of the prey items in southern Michigan fox studies (MacMullan, 1954). However, the total kill in this "average" pheasant range was only about 3 percent of the winter pheasant population. In southwestern Wisconsin, where pheasants are scarce and foxes abundant, Richards and Hine (1953) found remains of pheasant in only 2 percent of fox stomachs examined. Yet their estimates indicated that foxes took approximately 14 percent of the winter pheasant population.

The frequency of pheasant in the winter fox diet in two Iowa areas was roughly similar (Scott, 1947). But since one area had less than one-tenth the pheasant densities and four times the fox densities as the other area, the effect on the pheasant populations probably was much more severe in the poorer pheasant area.

In summary, the frequency of pheasants in predator diets is roughly correlated with pheasant density, being higher in good pheasant range. However, this frequency cannot be considered indicative of the degree of effect on pheasant populations. In fact, the reverse was true in the Michigan-Wisconsin comparison above. Since predator pressure apparently is higher in marginal pheasant range, pheasants in marginal range may generally make up a smaller proportion of predator diets, but be affected more severely.

Percentage of Pheasant Populations Taken

This is one of the most difficult statistics to get in predation studies, and requires an estimate of the pheasant population for a given area and an estimate of the total number of pheasants taken on that area. There are few such statistics available. We present the available estimates to give some idea of their order of magnitude (Table 28).

Since these estimates give no indication of the loss to mink, weasels, badgers, raccoon, cats, dogs, and others, total losses undoubtedly exceed the values at the bottom of the columns to some degree, perhaps considerably. The Craigheads' (1956) findings suggest material differences in the extent of losses in different years.

Predation on Nests

Predation ranks second to agricultural activities, primarily mowing, as a cause of nest destruction in most nesting studies (Allen, 1953; Stokes, 1954). Where hayfields are few, predation usually becomes the most frequent cause of nest loss (Nelson, 1950; Stokes, 1954).

In order to learn the magnitude of nest destruction by predators, its relationship to land use intensity, and the extent of nest loss from farming activities, we compiled data from published nesting studies (Table 29). The percentage of nests destroyed by predators and by land-use activities falls into about the same range; the means for the two are fairly similar.

For any one area, however, the percentage of nests destroyed by agricultural activities and by predation tend to be roughly inverse to each other. In order to visualize this graphically, we plotted the values in Table 29, and included the values for total percentage of nests successful (Fig. 56).

In areas where a small fraction (20-60 percent) of the land is under cultivation, presumably because soils and/or topography are unfavorable, nest destruction by predators is high. This probably is due to the higher predator densities in these types of areas discussed earlier. Nest destruction by farming practices, and total nest success, are low.

In areas where more than 85-90 percent of the land is cultivated, nest destruction by predators is nominal, probably because predator densities are low. Nest destruction by farming activities is severe, and total nest success is low.

In the range of 60-85 percent cultivation, nest destruction both by predators and farming practices is low enough so that total nest success is fairly high. Although not included, Pelee Island, with about 75 percent cropland, falls in this range. Stokes (1954:41) pointed out that the exceptionally high nest success on this island results to a big extent from the light predation and mower loss.

Nelson (1950) showed a similar pattern for several areas within South Dakota. Nesting success was low in areas with the lowest and highest cultivation intensity. Predators destroyed most nests at the low intensity range, and land-use activities destroyed many in the upper part of the range. Total nesting success was highest between the extremes.

The destruction rate due to farming practices will vary significantly at a given cultivation intensity depending on the amount of mowed hay present. Other sources of nest loss, especially desertion, may be important variables in the total success picture (Stokes, 1954; Linder *et al.*, 1960). The nest-success rate alone is not an entirely valid criterion of reproductive success because of renesting.

Areas with roughly 50-70 percent cultivation carry the highest densities in Wisconsin, and in the Plains States (Norstog, 1951; Kimball *et al.*, 1956:213). This range may be importantly influenced by the extent of predation at one extreme, and disturbance from farming practices on the other.

Evidence from Predator Control Experiments

Among the few predator control experiments conducted in pheasant range, the New York fox studies (Robeson, 1950; N. Y. State Conservation Dept., 1951) are best known. Robeson concluded, after controlling foxes on one area and not on a second, that pheasant populations on the trapped area were not measurably greater at the end of the 4-year study than at the start. On the Seneca Area (N. Y. State Conservation Dept., 1951) similar fox control neither increased the survival of game farm releases nor the native population level. However, the study was only run for two years.

Lauckhart and McKean (1956:65) reported on a Washington study in which "winged nest predators" were controlled. No population response was noted.

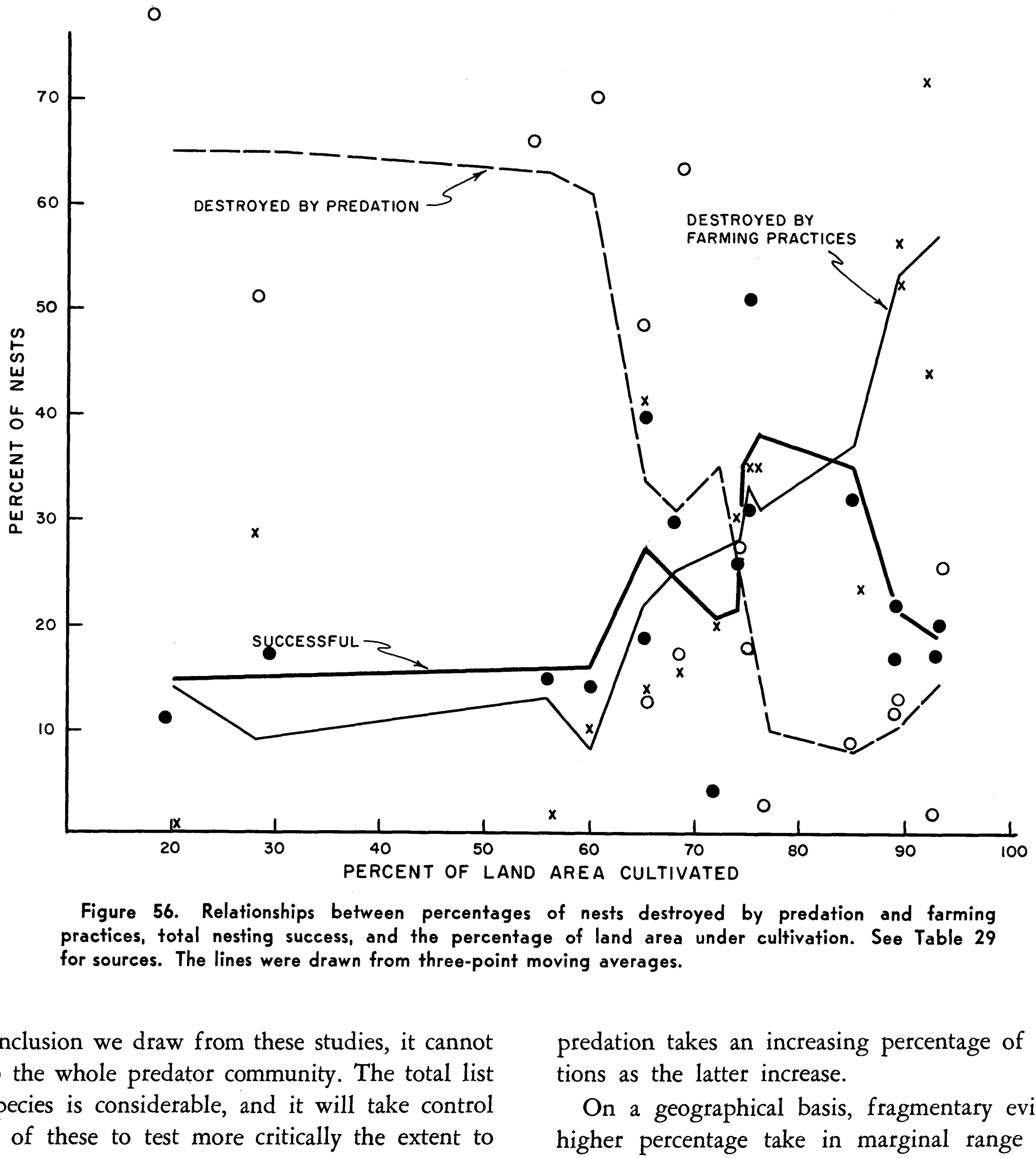


Figure 56. Relationships between percentages of nests destroyed by predation and farming practices, total nesting success, and the percentage of land area under cultivation. See Table 29 for sources. The lines were drawn from three-point moving averages.

Whatever conclusion we draw from these studies, it cannot be projected to the whole predator community. The total list of predatory species is considerable, and it will take control of all or most of these to test more critically the extent to which predation may or may not depress pheasant populations.

A few total predator-control studies have been carried out. A number of pheasant releases were made with and without general predator control on Eliza Island (Einarsen, 1950). Under control conditions, more hens survived and more young were produced than where predators were not controlled. Hart, Glading and Harper (1956:145) showed marked reduction in nest destruction following intensive predator control on one California area. Although no data were given on population response, these authors concluded that fall populations could be increased if nest success and/or survival were increased through predator control.

Relationship of Predation to Pheasant Population Density

Predation is generally considered to be a density-dependent limiting factor by population ecologists (Nicholson, 1933; Lack, 1954). In order to learn whether or not this is true of pheasant predation, we must ascertain whether or not predation takes an increasing percentage of pheasant populations as the latter increase.

On a geographical basis, fragmentary evidence suggests a higher percentage take in marginal range where pheasants are scarce than in good range where pheasants are numerous. This may be due to higher predator densities in marginal range, and the higher predator: prey ratio. Hence it is not truly evidence of what we want. Foxes took a higher percentage of dense pheasant populations at the Fennville State Game Area in Michigan than over the less-populated Michigan range at large (Arnold, 1956). However, Arnold did not state whether or not fox populations were higher at the Fennville Area. As pheasant densities increase, they make up an increasing proportion of predators' diet. But this does not necessarily indicate an increasing percentage take of the pheasant population.

Actually there are no critical data that can definitely answer the question, but some brief speculation based on the Craighead and Craighead (1956) findings might suggest some possible hypotheses. Although Hamerstrom (1958) has criticized the shortcomings of these findings, it is difficult to attribute to chance the strikingly close correlation (p. 426, Table 98) between the percentage that each prey species

TABLE 28

Percentage of Pheasant Populations Taken Seasonally by Various Predatory Species

		Percentage Loss of Population Alive at Start of Season				
Predatory Species	Area Studied	Winter	Spring	Summer	Fall	Reference
Red fox	S. Michigan	3–7	3	1	1	Arnold, 1956
Red fox	SW. Wisconsin	14	–	–	–	Richards and Hine, 1953
Cooper's hawk	S. Michigan	6–12	–	–	–	Allen, 1938
All raptors	S. Michigan	3	6	–	–	Craighead & Craighead, 1956
All predators	SE. Penn.	3	–	4*	–	Randall, 1939a
Cooper's Hawk	S. Michigan	–	4–5	–	–	Craighead & Craighead, 1956
Marsh hawk	E. Michigan	–	–	10*	–	Shick, 1952
Marsh hawk	SE. Penn.	–	–	1	–	Randall, 1940
Cooper's hawk	SE. Penn.	–	–	1	–	Randall, 1940
Red-tailed hawk	S. Michigan	–	–	3	–	English, 1934
All predators	SE. Penn.	–	–	4*	–	Randall, 1940
Extreme limits**		3–26	9	4–15	–	

*Chicks only

**Lowest and highest possible by the combined individual species listed in the column.

comprised in the total prey population, and the percentage that each prey species made up in the total raptor kill. We combined both years' data and tested the correlation. This produced a correlation coefficient of 0.994. On the basis of these results, very nearly all of the variation in the frequency occurrence of a given prey species in the collective raptor diet was associated with the relative abundance of that species in the total prey population. If each occurrence in the predator diet of a given species represented one individual of that species, as the Craigheads assumed, it would follow from this almost perfect correlation that in any one year the raptors were taking about the same fraction of each prey species.

The estimated percentages of prey populations killed (Craigheads' Table 96, p. 425) do not show the same fraction of each population taken. However, these estimated percentages involve all the sources of bias, assumptions, and corrections of the entire study. In spite of the potential danger of compounding these sources of error, the maximum variation between the percentage killed of the various species was nowhere near the order of magnitude of the variation in the dietary frequencies. In 1941-42, an estimated 4 percent of the small birds and 47 percent of the rabbits were taken, a 12-fold variation. On the other hand, the maximum variation in the dietary frequency was by a factor of more than 1,000 (meadow mice constituted 84 percent of the diet while fox squirrels and rabbits each made up about 0.08). Perhaps this is the best evidence we can expect from these data of the conclusion we have deduced. Even though meadow mice were more than ten times as frequent in the diet as white-footed mice in 1941-42, the estimated percentage taken of each population was 26 and 22, respectively. In 1947-48, the same percentages for these two species were 22 and 24, again despite a big difference in frequency in the diet.

In any event, the raptor kills were evidently spread over the total prey population in proportion to their relative abundance, the frequency of each prey species in the collective diet correlating almost perfectly with the proportion that it made up in the total prey population. While the Craigheads' estimates did not clearly confirm it, the conclusion follows that predation in a given year removed roughly the same proportion of each prey species.

If we accept this provisionally for the purposes of speculation, several pertinent implications follow from fluctuations in (1) the nonpheasant prey species, (2) the predator populations, and (3) the pheasants themselves.

(1) Let us consider a hypothetical example in which meadow mice constitute the majority of the prey resource and the staple food of the raptors. When they decline, the other prey species represent an increased proportion of the total prey resource and are taken in greater numbers by the raptors which continually redistribute their predatory effort over the entire prey base.

This, of course, is the buffer effect, and was observed by the Craigheads in the second year of their study. Meadow mice populations fell to less than a fourth of the density observed in the first year. With similar raptor densities, more predation pressure was shifted to the other species, most of which were taken in greater numbers. Those that had the same or lower densities in the second year, including pheasants, lost a higher fraction of their populations. Scott (1947) noted very little fox predation on pheasants on one of his study areas, apparently because foxes were concentrating on a muskrat population exposed by drought.

TABLE 29

Relationship of Nest Destruction by Predation and Agricultural Activities to Percentage of Land Under Cultivation[1]

Area Studied	Percentage of Land Under Cultivation	Percentage of Nests Destroyed By Agricultural Activities	Percentage of Nests Destroyed By Predation	Reference
Pennsylvania	93	43	25	Randall, 1940a
Pennsylvania	93	74	3	Wight, 1950
Iowa	89	52[2]	13[7]	Robbins, 1953[3]
Iowa	89	56	12	Klonglan, 1955a
Ohio	75-95	23[4]	9	Dustman, 1950
Washington	76	35	3	Knott *et al.,* 1943
Colorado	75	35[4]	17	Yeager *et al.,* 1951
Iowa	74	30	27	Baskett, 1947
South Dakota	72	20	64	Nelson, 1950
Michigan	68	14	16	Shick, 1952
Wisconsin	65[5]	41	12	Buss, 1946
South Dakota	65	13	47	Nelson, 1950
South Dakota	60	10	71	Nelson, 1950
South Dakota	56	2	66	Nelson, 1950
Iowa	28	28	51[6]	Weston, 1953
South Dakota	20	0	78	Nelson, 1950
Mean	—	29.6	32.1	—

[1] Where a study was carried on for several years, the values in the table represent the average for the period of study.
[2] Loss from mowing alone.
[3] Based only on 97 nests described in fencerows, hay, and grain. Percentage in cultivation taken from Klonglan, 1955a.
[4] Crop harvest activities only.
[5] From this study. Nest success data cited by Buss were composite data from several study areas. Hence we used an average cultivation value for southeastern Wisconsin.
[6] 37 of 45 nests described in natural cover (51% of all nests) were destroyed. Many, though undoubtedly not all, of these must have been destroyed by predators. Weston did not give the exact value.
[7] The fencerow nests, which comprised 13% of the total, were destroyed by predation. Undoubtedly other nests were destroyed by predators, although the number was not given.

Evidently the percentage of pheasant populations taken by predators not only can, but does, vary with fluctuations in the buffer populations and independent of pheasant densities. Predators could conceivably take a higher fraction of a low pheasant population than of a high one if there were a marked reduction in buffers as did occur in the Craighead's study.

(2) If the raptor population changed, it would require a proportionately greater or lesser amount of food, and would therefore take a greater or lesser fraction of the prey populations. Such migratory species as goshawk and snowy owl vary in abundance from year to year. Resident raptor populations might adjust their numbers to changes in staple prey populations such as mice and rabbits, and in the process vary their pressure on pheasants. And variations in raptor numbers could occur with changes in plant succession, woodland cutting and clearing, and periodic eradication campaigns.

Hence, predator populations probably undergo variations independent of pheasant densities and in the process vary the pressure on pheasants irrespective of the density of the latter. Hence, as Milne (1957) pointed out, predation can only be imperfectly density dependent at best.

(3) One could imagine a third situation in which buffer and predator numbers remained stable while pheasant numbers increased. In a simplified situation with a prey population of 90 meadow mice and 10 pheasants, the total raptor kill might be 9 mice and 1 pheasant, true to the Craighead's correlation between relative prey abundance and proportions of each in the kills. If the population increased to 90 mice and 30 pheasants, the new relative prey ratio is 75:25. With the raptor population constant, the total number of prey individuals would remain constant at 10, and hence the new take would be 7.5 mice and 2.5 pheasants. But although the number of pheasants taken increased 2.5 times, the percentage of the population taken would fall from 10 to 8.

This of course assumes stability in the raptor population and its food needs. One might question whether increase in pheasant numbers might not be followed by an increase in predator numbers. This does not seem to be a strong possibility except in extreme cases. Pheasants rarely constitute a major fraction of any predator's diet (Tables 26 and 27). Mice and rabbits are the staple foods in most cases, and are probably the chief resources to which raptors adjust their numbers. It seems problematical whether predators would make delicate adjustments to what often are minor changes in a minor food item, especially when the main prey species may be changing independently. Hence, under some circumstances, predators might take a lower percentage of a larger pheasant population than of a smaller one.

In conclusion, the percentage of a pheasant population taken by predators may vary with changes in buffer populations, with changes in predator numbers, and with changes in pheasant densities, all of which may occur partially or largely independent of the other. Hence, it is difficult to visualize predation operating as a sensitive density-dependent factor on pheasant populations, if in fact it has any marked tendencies in this direction at all. At best, it probably is what Milne (1957) has termed imperfectly density dependent.

Discussion

The collective views of predation in the field of wildlife management have been profoundly influenced by the views of Errington (1935a, 1936, 1946, and 1946a) which, in turn, were strongly influenced by his experience with the bobwhite (Errington and Hamerstrom, 1936; Errington, Hamerstrom and Hamerstrom, 1940; Errington, 1941).

According to Errington, a given area has a number of protective covey sites that will shelter a fairly constant and well-defined number of quail through winter. As Lack (1954: 159) pointed out, he termed this level the "carrying capacity" in earlier papers, but later he referred to it more often as the "threshold of security." When quail numbers are at or below this threshold, they suffer little from predation. But when they exceed it, predators assist in removing this "surplus," and their numbers are reduced to the threshold level. Hence, the maximum effect of predators on the populations is to reduce the surplus. Furthermore, Errington believed that the kinds and numbers of predators make little difference, because any that are available are able to reduce the vulnerable surplus.

The most significant extension of these views (Errington, 1936; 1946a) was that, if predators do not remove the surplus, some other environmental influence will. The carrying capacity is determined largely by the interactions between social intolerance, which permits only a limited number of birds in each covey site, and with the nature of the habitat. Excess birds are evicted, and if predators do not kill them, they are lost to some other factor or simply emigration. Hence, a given area can carry only so many birds, and this is affected little, if at all, by the presence or absence of predators. Predators therefore have little or no influence in determining the numbers of birds on a given area.

Roughly similar generalizations have been made for the pheasant by several authors. Lauckhart and McKean (1956: 61-62) visualized an annual surplus following breeding that was reduced each year to the constant winter carrying capacity level. MacMullan (1954) concluded: "As long as predators eat only this surplus, they don't seriously affect the pheasant populations." Arnold (1956) visualized fox predation on pheasants as operating on an annual surplus.

What has generally been overlooked is that Errington was reluctant in his writings to extend these principles to the pheasant (Errington, 1946; Errington and Breckenridge, 1936; Errington, Hamerstrom and Hamerstrom, 1940). He noted that winter pheasant populations, unlike the bobwhite, are tolerant of crowding; and that there is no similar tendency toward eviction to marginal habitat of all but a well defined threshold number.

Our findings have shown that spring pheasant densities are correlated with population levels of the previous fall. Severe winter predation could conceivably reduce spring densities below what they would be without predation.

Similarly, fall levels in an area are a function of the breeding density and reproductive success. Predation is one influence on reproductive success. It operates differently from mowing in that mowing wipes out all nests in part of the nesting cover in a short period of time; predation operates throughout the nesting season and takes only a part of the nests in all types of cover. But their effect on the population is similar: both reduce reproductive success by forcing renesting with smaller clutches and higher juvenile mortality, by preventing some hens from being successful because of repeated failure, and by killing hens. If we are to conclude that mowing is a limiting factor, seemingly we must conclude the same for nest predation, although the latter may not be as severe as mowing.

However, predation operates at all seasons of the year. In good pheasant range, its action is probably less severe than mowing, although some degree of population limitation by predation is within the realm of possibility. In marginal range, it may be a factor of some significance.

Summary

Some 24 Wisconsin species (13 mammals, 2 owls, 7 hawks, and 2 reptiles) have been reported at one time or another to prey on adult and juvenile pheasants. At least 20 Wisconsin species (15 mammals, 3 birds, and 2 reptiles) have been reported to destroy nests.

In Wisconsin, highest densities of foxes, raccoons, skunks, badgers, and weasels occur outside of the primary pheasant range. The opossum reaches its greatest numbers within the primary pheasant range; mink are generally distributed. Some raptors are less numerous in southeastern Wisconsin than in the remainder of the state. Predator densities are also roughly inverse to pheasant densities in areas of different states. Such habitat features as intensive cultivation, flat topography, heavy soils, and a minimum of woodland that are associated with first-class pheasant range do not encourage high densities of predators which prefer rougher topography, lighter soils, and waste or wooded land.

Red foxes, raccoons, and opossums have been increasing in Wisconsin in the past 15-20 years while gray foxes and possibly skunks have been declining. There is no information on raptor changes in the state. Information from Illinois suggests a general decrease in wintering raptors during 1903-55.

The frequency of pheasants in the diet of several predators is roughly correlated with pheasant densities suggesting the importance of availability. Frequency of pheasant in predator diets is not evidence of predation severity in terms of the proportion of the pheasant population taken.

Estimates of the percentage of pheasants taken in winter range from 3 to 14 percent for foxes and 3 to 12 percent for Cooper's hawks, and are about 3 percent for all raptors according to one estimate. Total loss might range from 3 to 26 percent. Foxes in spring took another 3 percent on one area, and raptors 3 to 6 percent. Summer mammal pressure on adults and young is lower. Marsh hawks may take from 1 to 10 percent of young; red-tailed hawks took 3 percent on one area. In one estimate, all predation took 4 percent of the young; in another, raptors alone reduced a theoretical fall population by 16 percent. Fall predation is light.

Predators have been reported to destroy from 3 to 78 percent of all nests in various studies. Predation loss tends to be roughly inverse to nest loss from farming activities, the former being most serious where land use is least intensive, and the latter most serious under intensive land use. Mean nest success is highest in the intermediate range where loss from both factors is light to moderate.

In one study where general predator control was practiced, released hens survived better and produced more young than in another where no control was used. In another, general predator control reduced nest losses. In two studies in which only foxes were controlled, and one in which only winged nest predators were controlled, no population changes resulted.

Variations in buffer populations have been noted to cause variations in pheasant losses to predators independent of pheasant or predator densities. Observed changes in predator populations, occurring independently of pheasant densities, may cause variations in pheasant losses. Pheasant population changes occurring independently of buffer densities and predator densities could result in a negative rather than positive density dependent predator effect. Hence, predation on pheasant populations, at best, may be what Milne (1957) has termed imperfectly density dependent if it has any material tendencies in this direction at all.

Although extended to the pheasant by other workers, Errington has always been reluctant to extend to this species his principles of thresholds of security, population surpluses, and predation. He conceded that pheasant densities could be depressed by predation below what they would be without it. The strong correlation between fall densities and those of the following springs, and the weather-induced variations in fall densities without any habitat changes precludes any definite or precise threshold or carrying-capacity phenomenon.

Predation operates at all seasons of the year, and therefore probably influences pheasant population levels to some degree particularly in marginal range.

CHAPTER XIII. ILLEGAL AND LEGAL HEN KILL

During each Wisconsin hunting season, hen pheasants are shot although the law does not permit it under present regulations. Some are shot deliberately, some are shot through carelessness, and some are shot by accident, usually where shooting ranges are extreme and/or light conditions are unfavorable. A few hens are shot by hunters who actually claim they do not know the difference between sexes.

We obtained estimates of the extent of illegal and accidental hen kill to get some clue to its effect on the population. These estimates also shed light on the practical question of whether or not we can shoot hens legally without detrimentally affecting the population.

Magnitude of Illegal Hen Loss

Use of Fluoroscopy to Gauge Shooting Pressure

After examining under a fluoroscope some 21,000 birds that survived hunting seasons in North America and Europe, Elder (1955) concluded that the incidence of body shot could be used to determine the relative shooting pressure on two or more populations of a species. This conclusion was obtained through indirect means including comparison of body shot incidence with band recovery rates, body size, and average number of body shot for several species of ducks, geese, coots (*Fulica americana*), and pheasants.

The pheasant is an ideal species for testing the validity of this conclusion because postseason sex ratios provide an estimate of the percentage of cocks shot with which the body shot incidence can be compared. Elder first fluoroscoped winter-killed pheasants in South Dakota. Subsequent to the report of these results (S. Dak. Dept. Game, Fish and Parks, 1953), we asked all Wisconsin Conservation Department field personnel to pick up and save car-killed cocks and hens they saw along roads during their regular work activities. Collections were begun each year immediately following the hunting season, and were continued until early summer. Roadkills were collected for 7 consecutive years from 1953-54 through 1959-60, the sample for the 7 years totaling 495 hens and 132 cocks.

The number of shot found in individual cocks varied from 1 to 8, and averaged 1.9 for the cocks with shot. Of the 132 cocks examined, 33 percent contained one or more shot. This compares with 34 percent for a California sample (Hart, 1957), and 27 percent for Elder's South Dakota sample. The estimated percentage of cocks shot in these populations is 74 (This study: 1953-60 mean), 74 (Hart, 1957), and about 50 percent (S. Dak. Dept. Game, Fish and Parks, 1953), respectively.

Comparison of body shot incidence in primary Wisconsin pheasant range (with about 70-82 percent mean cock harvest) with that in marginal range (65 percent harvest) shows 38 percent (84 cocks) and 26 percent (38 cocks) with shot, respectively, in 122 cocks where location was reported. Comparison of body shot incidence in adult cocks (which have been through two or more hunting seasons) with that in juveniles (survivors of one season) shows 40 percent (15 cocks) and 33 percent (105 cocks), respectively, of the 120 birds in which age was determined.

We compared the annual percentage of cocks shot in Wisconsin (cf. Table 5) with the annual body shot incidence in cocks (Fig. 57). The correlation coefficient (0.630) is short of statistical significance, but the comparison looks suggestive. Elder (1955) concluded that extremely large samples are necessary to demonstrate anything by major year-to-year differences in shooting pressure. This seems to be the case since the adults which have shot from the previous year dilute each year's sample and damp the annual changes in body shot incidence. This must have little effect in our cock pheasants, however, because adults only constitute 5-10 percent of the fall cock population. With a third of hunting season survivors carrying shot, no more than 2-3 percent of all cocks go into any one hunting season with shot. In order to avoid this damping influence completely, we tabulated the annual shot incidence in juvenile cocks. The year-to-year trends and the actual percentages in the juveniles were quite similar to those shown for the entire cock samples in Fig. 57.

These findings suggest a correlation between hunting pressure and body shot incidence, and lend further support to the use of body shot incidence as an index of shooting pressure on pheasants.

Estimated Percentage of Hens Killed

Of the 495 hens examined, 36 or 7 percent, contained body shot. The number of shot in these hens varied from 1 to 4, and averaged 1.3.

The percentage of hens killed can be estimated from these values if we assume that the percentage of hens carrying shot bears the same relationship to the percentage of hens killed, as the percentage of cocks carrying shot bears to the percentage of cocks killed (S. Dak. Dept. Game, Fish and Parks, 1953). With an estimate of 74 percent of cocks harvested during the period 1953-60, we set up the following ratio:

$$\frac{\text{7 percent hens with shot}}{X} = \frac{\text{33 percent cocks with shot}}{\text{74 percent of cocks killed}}$$

$$X = \text{16 percent of hens killed}$$

Varying the percentage of cocks killed to correct for possible errors in the sex ratios changes the result only slightly. A 15-percent hen kill follows from a 70-percent cock harvest, while a 17-percent kill follows from an 80-percent cock harvest.

Because the silhouette area of the cock is one-fourth larger than that of the hen, Elder (1955) suggested that the body shot incidence should be corrected upward by 25 percent. This would increase the body shot percentage to 8.8 and the indicated kill of hens to about 20 percent. Also, it may take fewer shot to kill the smaller hen; and the ratio of number killed to number surviving and carrying shot may therefore be higher in the hen. This would lead us further to underestimate the percentage of hens killed. However, hens may not be subjected to the same quality of shooting pressure as the cocks, a possibility suggested by the lower body shot incidence. Hens may be shot at more frequently at extreme ranges were the visibility problem leads to the mistakes, and where the percentage of mortal wounds is lower.

These latter two factors would offset to some degree the two former ones. The percentage of hens shot may therefore approximate 16. This loss applies only to shot gun kill which occurs in fall, winter, and spring.

Factors Influencing Magnitude of Loss

Hunting Season Length

Since 1950, our pheasant hunting seasons have been extended from the 10-day to 2-week seasons of the middle and late 1940's, to between 3 and 5 weeks in the 1950's. There has been occasional concern that such lengthened

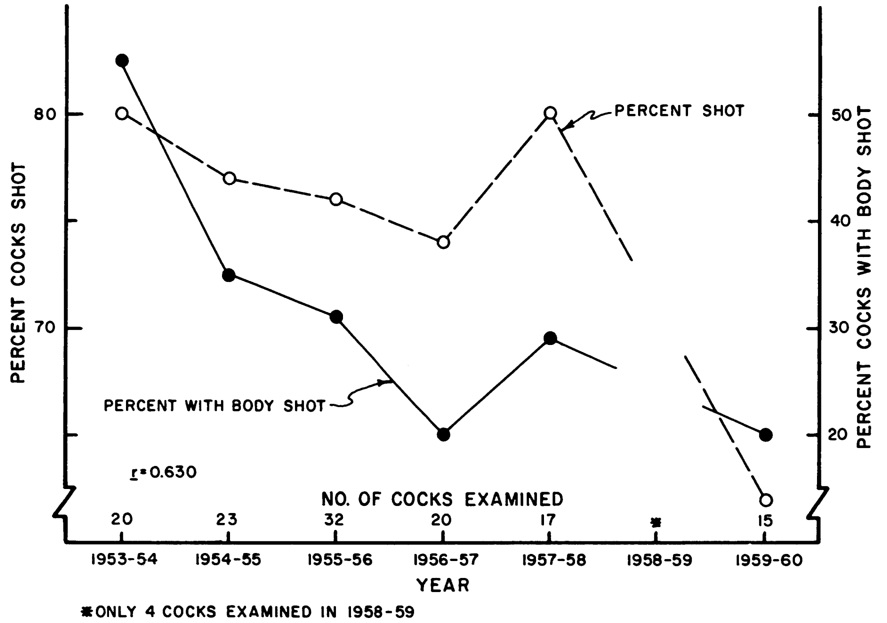


Figure 57. Comparison between percentage of cocks shot in Wisconsin (as shown by postseason sex ratios) and percentage of postseason, road-killed cocks carrying shot.

During each hunting season, hen pheasants are shot deliberately or accidentally. Fluoroscopy studies utilizing the incidence of body shot to determine the relative shooting pressure on hens indicate about 16 percent of the hens are killed each year. While there is no evidence that this loss varies with population change, it is another drain on the pheasant resource.

seasons encourage hen shooting, the logic being that in the latter weeks of a long season, when cocks are scarce and hard to find, hunters occasionally shoot hens out of irritation. Allen (1956:458) has reported similar concern elsewhere. In order to learn whether or not this is the case, we tabulated information from the arrest records of the Law Enforcement Division to determine at what time most arrests for shooting hens are made.

The results (Table 30) show a pronounced tendency for most of the hen kill to occur in the first, and to a lesser extent the second, week of the season. Loss in the third and fourth weeks is much lighter. Even after the season closes, losses still occur which may approach half of the losses in the last 2 weeks of the season.

Hence, some loss does occur in the latter weeks of a long season, but there is no evidence of a severe upswing. Actually the loss is fairly light, and one cannot assume that it stops when the season closes. Since 14 and 12 percent of the hunting season loss occurs in the third and fourth weeks of 4-week seasons, and if we assume that the entire 16-percent estimated loss of the hen population takes place in the hunting season, about 2 percent of the entire, fall hen population is lost in each of the third and fourth weeks of the season. Since all hen shooting does not occur during the season, the proportion of hens lost in the last 2 weeks of the season is somewhat less than 2 percent each week.

These conclusions rest on the validity of the assumption that the arrest records are a reliable index of the trends in hen kill. We asked several Conservation Wardens in the primary pheasant range about this question. They believed the level of law enforcement effort is fairly constant through the hunting season, and that these trends probably reflect the actual trends in hen loss (pers. comm. from K. L. Beghin, L. Oshesky, and H. A. Pederson). If anything, the percentage of violations apprehended may be higher in the latter part of the season when there are fewer hunters, and therefore more law enforcement effort per hunter afield.

Further evidence that an additional 1-2 weeks added to the season length has little effect on the total hen kill comes from the fluoroscopy data. In 1953, 1956, and 1959, pheasant hunting seasons were 26, 23, and 19 days in length, respectively. In 1954, 1955, 1957, and 1958 they were 30, 30, 37, and 44 days long. A total of 208 hens was collected after the three shorter seasons, and 287 hens after the four longer seasons. The percentage of hens with body shot was 7 percent in both groups, indicating no difference in shooting pressure.

Hunting Pressure

Since a major part of the illegal and accidental hen kill occurs in the early part of the season when hunting pressure is at its peak, hen kill may be a function of hunting pressure. This suggestion may be supported by the fluoroscopy data. Of 368 hens from the primary range, 7 percent contained shot, while 5 percent of 111 hens from marginal range contained shot. The difference between these two percentages is not statistically significant.

Further evidence is supplied by comparing the percentage of hens lost in states with varying hunting pressure. In approximately decreasing order of hunting pressure: some 60 percent of hens may be lost in Massachusetts (Pearce, 1945:43); about 22 percent in Ohio (Leedy and Hicks, 1945:82) and perhaps a comparable value in Michigan (Wight, 1945:162); 16 percent in Wisconsin; and 8-10 percent in South Dakota (S. Dak. Dept. Game, Fish and Parks, 1953). If the magnitude of hen kill is a function of hunting pressure, it will probably increase in the future if the number of pheasant hunters in Wisconsin increases.

Calibre of Hunters

During our hunting season checks, the hunters afield in the latter part of the season appear to be the more experienced hunters, those who are more likely to own and use dogs, and individuals who perhaps display more sportsmanship. Much of the early season pressure is from less experienced hunters who are more easily discouraged and do not hunt through the season. This may account partly for more hen shooting early in the season, and Conservation Wardens have reported this same belief.

Relationship to Pheasant Density

As pheasant populations increase and hunting improves, hunters may hunt more often in the latter part of the season with a consequent increase in total hunting pressure. With hunting pressure an evident influence on the extent of hen loss, more hens could conceivably be shot when densities are high. The body shot incidence in hens averaged 7 percent following the 1953-57 period when populations were up. It averaged 8 percent in 1958-59 after the population had declined, and was 7 percent following the very low 1959 population and poor hunting season.

Some hen loss apparently occurs at all densities, as suggested by the body shot incidence reported for marginal Wisconsin range. There is no evidence at present that the loss rate changes with population fluctuation within any given class of range, although the loss may be lower in poor areas than in good ones because hunting pressure is heavier in the latter.

TABLE 30

Chronological Distribution of Arrests for Shooting Hens Before, During and After the Hunting Seasons

			4-week Seasons	
Week	No. Arrests 2-week Seasons*	No. Arrests 3-week Seasons**	No. Arrests†	Percentage of Season Total
Before season:				
Third week	4	1	3	—
Second week	8	0	6	—
First week	3	3	5	—
During season:				
First week	74	46	47	52
Second week	37	4	19	21
Third week	0	5	13	14
Fourth week	0	0	11	12
After season:				
First week	5	1	6	—
Second week	3	5	5	—
Third week	1	0	3	—

*1937-38, 1940, 1944-50.

**1939, 1941, 1956.

†1942-43, 1951-55.

Effect of Hen Losses on Populations

Evidence from Areas with Legalized Hen Shooting

Wisconsin

The taking of hens or cocks in equal numbers was permitted in nine northwestern Wisconsin counties during the hunting seasons of 1946 and 1947 (Fig. 58).

In order to use kill estimates to determine any population response in these marginal pheasant counties, we made adjustments in the county kill figures to compensate for the large numbers of birds stocked each year and for inflation of the kill estimates discussed earlier. The resulting kill figures were used as indices of the number of wild-reared cocks shot in the hen and control county groups in each of the two years.

Prior to the hen seasons, the kill of wild-reared cocks in the hen counties was generally higher than in the control counties by some 10-30 percent (Fig. 59). The total area of the control counties is slightly greater than that of the hen counties (6,950 and 6,600 square miles, respectively). Thus the higher densities in the hen-season counties suggest the superiority of their pheasant range over that of the control counties.

Following two hen seasons, the wild cock kill in these counties declined to a level about 40 percent below that of

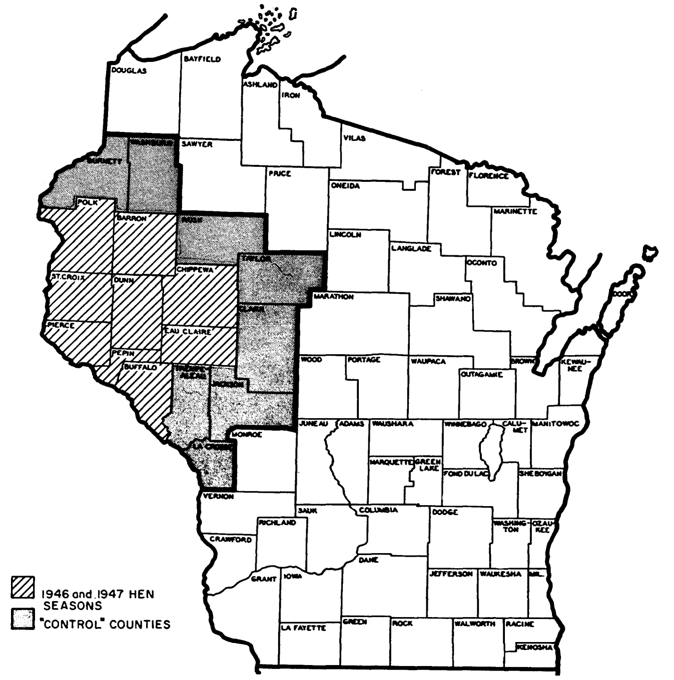


Figure 58. Counties in which an open season was held on hens in 1946 and 1947, and a surrounding zone with which the estimated cock kill is compared in Figure 59.

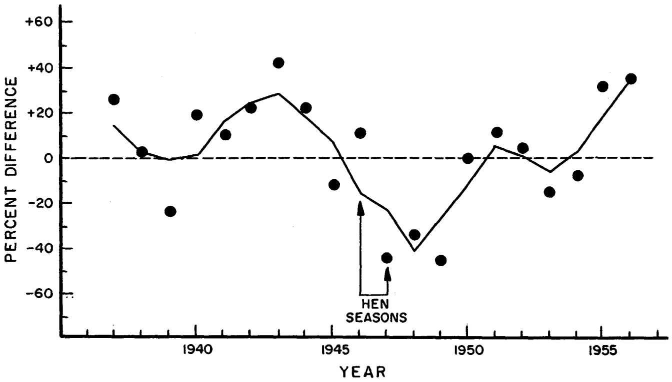


Figure 59. The annual percentage by which the wild-reared cock kill in the hen-season counties (Fig. 58) has differed from that of the control counties.

the control counties. The hen counties eventually regained their superiority over the control counties (Fig. 59), but it took 10 years of hen protection to do so.

The percentage of hens taken during the two liberal seasons is not known exactly, but its order of magnitude can be estimated. In 1946 the first hen season, the actual kill estimate in the combined hen counties rose to 44,952 from 19,595 of the previous year. The kill estimate in the control counties was almost the same in 1945 and 1946. In 1948, when regulations returned to cocks only, the kill in the hen counties dropped to 15,979 from 28,735 of the previous year. The control county group dropped less than 1,000. Hence, the kill during the hen seasons was about twice the kill of the cocks-only years. Evidently about as many hens were taken as cocks. Approximately 65 percent of the cocks are normally taken in marginal counties (cf. sex ratios in Table 7). With a slight excess of hens in the population before the season, approximately 50-60 percent of the hens may have been taken.

In view of the decisiveness with which the hen-county populations were forced below the level of the control counties, these populations obviously could not maintain themselves under a continued hen harvest of 50-60 percent.

Minnesota

One hen was allowed in the daily bag during the Minnesota hunting seasons of 1933, 1935-37 inclusive, and 1941-43 inclusive (Schrader, 1944). The pheasant kill declined every year following hen shooting except in 1935 (Schrader, 1944 and Fig. 60).

Decline in kill in the first year of hen protection following a hen season may not always imply a population reduction. The decline may result from the absence of hens in the bag, while the number of cocks taken, and the population level, remain the same in the two years. The only good evidence is the kill trends during two or more consecutive hen seasons wherein both sexes are present in the bag. Thus the population trend following liberalization can only be judged in Figure 60 by the 1936, 1937, 1942 and 1943 kills. In all four cases these show decline. Population decline might have occurred naturally in some of these years, but it is unlikely that it would have occurred by chance in all four.

Examination of the kill estimates (Erickson *et al.,* 1951; and Erickson, in litt.) showed that in 3 hen-season years (each following a year in which hens were protected) the kill increased between 20 and 52 percent. Similarly, in years when hens were protected (following hen seasons) the kill ranged from +11 to −34 percent. These data suggest that usually less than half as many hens as cocks were taken when hen shooting was allowed.

Erickson *et al.* (1951) reported winter sex ratios of less than three hens per cock suggesting a harvest of approximately two-thirds of the cocks in 1946 and 1947 when hens were not shot. If we assume (1) an average harvest of two-thirds of the cocks, (2) a maximum of half as many hens shot as cocks, and (3) near-equal numbers of hens and cocks in the population before the season, it follows that during the seven hen seasons the maximum take of hens was about 33 percent. The kill estimates suggest that Minnesota populations were not able to maintain their numbers with seasons that remove up to one-third of the hens.

Indiana

In 1940 and 1941, one hen was allowed in the daily, two-bird bag in Indiana (Ginn, 1955 and in litt.). Ginn calculated separately the number of cocks and hens killed in these two years and found that the cock harvest declined 18 and 27 percent in 1941 and 1942, respectively (Fig. 61) — years in which the pheasant population was increasing in other, nearby midwestern states. In 1942, the Indiana cock kill was 60 percent below that of 1940.

Ginn's estimates show that the hen harvest in 1940 equalled 55 percent of the number of cocks taken while in 1941,

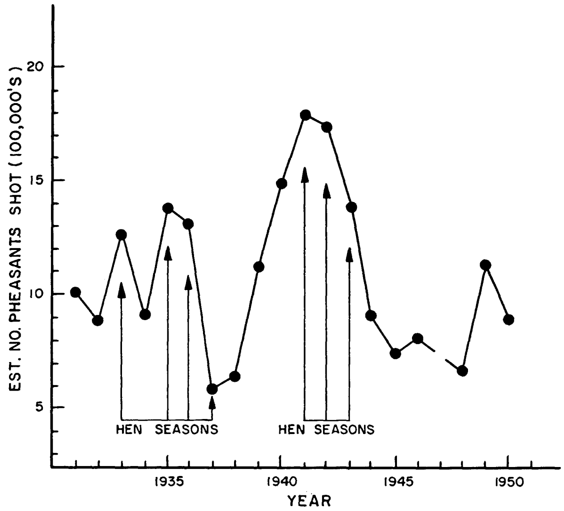


Figure 60. Annual estimated pheasant kill in Minnesota and years in which hens were allowed in the bag. Data from Schrader (1944), and Erickson *et al.* (1951).

39 percent as many hens were taken as cocks. Ginn (1955) stated that postseason sex ratios do not vary from 50:50 following cocks-only seasons, although he suggested this results partly from high illegal hen loss. Thus, if we use a conservative harvest of 50 percent of the cocks and balanced preseason sex ratios, it follows from the above sex composition in the bag, that about 28 and 20 percent of the hen populations were taken during the 1940 and 1941 seasons, respectively. The observed population declines, during years when the adjacent states were experiencing pheasant increases, suggest that the Indiana pheasant populations were not able to maintain their numbers with hen kills of this magnitude.

Washington

Prior to 1941, one hen was allowed in the three-bird daily bag (Lauckhart and McKean, 1956:68-70). Hunting was taking 69 percent of the pheasant populations based on data from study areas. Since hens made up 45 percent of the bag, and assuming a balanced preseason sex ratio, between 50 and 60 percent of the hens were being taken. It was not reported whether a hen take of this magnitude was general throughout the Washington range.

On the two study areas, populations increased 370 and 96 percent in the 5 years following closure of hen seasons. These increases occurred during a period of population decline elsewhere in the Northwest (p. 56). Statewide population increases apparently were less marked.

Iowa, Nebraska, and South Dakota

Some hen shooting was permitted in Iowa in 1930-32, inclusive (2-5 half-day seasons), 1935 (7-day season), and in the spring and fall of 1943 (Faber, 1948). While no population indices are available for years prior to 1936, roadside counts (Kozicky *et al.,* 1952) showed higher populations in 1944 than in 1943.

One hen was legal in the daily bag in Nebraska from 1937 to 1941 (Mohler, 1959:83). Population indices were not begun until 1941 (pp. 24-26). These show a population peak reached in 1942 followed by decline. Whether or not the peak would have been higher without the hen shooting is an open question, but at least the shooting did not prevent the build-up to the peak.

Hens were legal game in South Dakota in 1945 and 1946 (Kimball, 1948). The populations declined in the 2 years following these seasons, but the regional population decline was underway at this time.

California

California had limited (one hen per hunter per season) statewide hen shooting in 1955-57, inclusive; 5 hens per season per hunter in 1951-54 and up to 10 since 1954 in southern California; and either-sex shooting since 1939 on licensed pheasant clubs.

Harper (1960) summarized available information on the California hen seasons. From the evidence in his report, the percentage of hens shot varied widely. For the entire state,

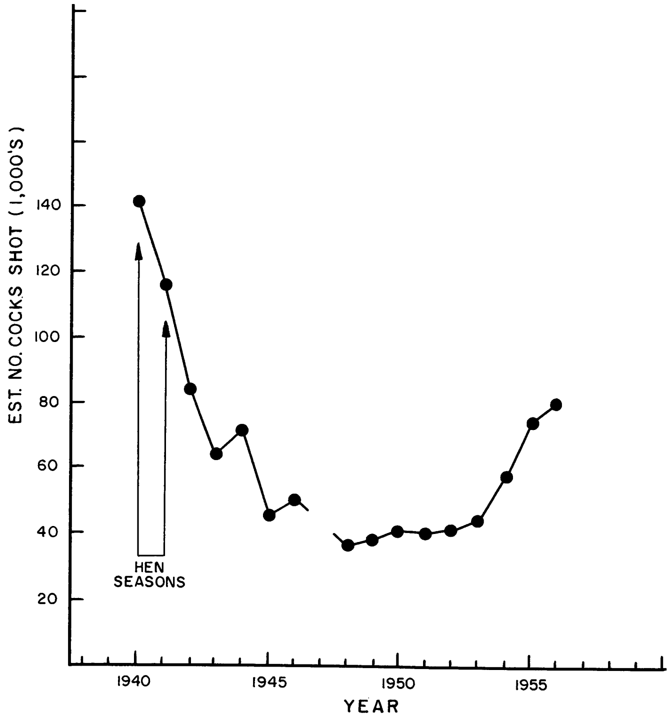


Figure 61. Annual estimated kill of pheasant cocks in Indiana and years in which hens were allowed in the bag. Data from W. E. Ginn (in litt.).

we estimated the reported hen kill at approximately 10-11 percent of the hen populations during the 1955-57 seasons (based on cock:hen ratios in the kill in Harper's Table 8, an assumed 75 percent cock harvest, and a 40:60 preseason cock:hen ratio). On 15 heavily hunted State Cooperative Hunting Areas, the percentage of hens shot varied from 10 to 46, and averaged about 22 during the 1955-57 seasons (Harper's Table 2). On licensed pheasant clubs in the Sacramento and San Joaquin Valleys, we estimated the annual hen kill at more than 50 percent (and perhaps approaching 68 percent, based on the cock:hen ratios in the kill in Harper's Table 3, an assumed 75 percent cock harvest, and a 40:60 preseason cock:hen ratio).

Fluoroscopic examinations of hens on two of the study areas (Sutter Basin and Honey Lake) showed increases in body shot incidence indicating that shooting pressure on hens increased during the 1955-57 seasons. There are no comparable data on statewide populations to indicate whether or not the estimated 10-11 percent hen kill represented an increase over previous illegal and accidental kill levels. This figure probably underestimates the total hen kill because it makes no provision for illegal kill and crippling loss.

The population responses apparently varied with the level of hen kill. The statewide kill estimates remained steady during the 3 years of 10-11 percent estimated hen harvests, suggesting no effect. The total kill at the Knights Landing Sportsmen's Association, with an estimated 10-percent hen kill, and at the Gray Lodge Refuge, where the hen kill was 32, 13, and 17 percent in the 3 years, held up well.

On four Delta Areas where we estimated that 35-47 percent of the hens were shot, both the cock and hen kills declined during the 1955-57 period. The kill also declined on licensed pheasant clubs in the Sacramento and San Joaquin Valleys where the annual hen kill exceeded the cock kill during 1952-59.

Liberal hen shooting in roughly the southern third of California has taken about equal number of cocks and hens since 1951 (Glading, in litt.). In this marginal region, the number of pheasants stocked has about equalled the total kill. Although the percentage of hens shot was not reported, it has evidently been substantial. Glading concluded on the basis of hunter questionnaire surveys: "There is no evidence to indicate either-sex pheasant hunting during the past 11 years in southern California has caused a reduction in the resident pheasant populations in this area."

Hart (1955) and Harper (1960) concluded that two compensatory responses occurred in the Sutter Basin populations. Hart first estimated the survival rate of cocks and hens at 20 and 35 percent, respectively, in the years prior to the general hen seasons. The respective mortality rates, then, were 80 and 65 per cent. Hunting took 56 percent of the cocks and 9 percent of the hens (due to limited kill by licensed clubs). Hart stated that the nonhunting loss therefore was 24 percent in cocks (80-56), and 56 percent in hens (65-9) and concluded "... it appears that nonhunting mortality of hens was approximately equal to the hunting mortality suffered by cocks ... to increase the hunter harvest of hens ... would be based on the assumption that some increased hunting mortality of hens could be substituted for nonhunting losses without appreciably raising the total mortality rate."

The unstated inference here seems to be that the population responds to varied degrees of hunting take with changes in the nonhunting mortality *rate,* and thereby tends to maintain the crude annual mortality rate at about the same level. However, the crude annual mortality rate cannot be derived by adding the mortality rates due to exploitation and to natural causes (Ricker, 1958:25), nor can the latter be obtained by subtracting the mortality rate due to hunting from the crude annual mortality rate, as was done here. The mortality rate due to natural causes must be calculated by dividing the number of hunting-season survivors into the number dying from nonhunting causes during the rest of the year. These develop as follows:

$$\text{For cocks: } \frac{(100 - 56) - 20}{100 - 56} \times 100 = 55 \text{ percent nonhunting mortality rate}$$

$$\text{For hens: } \frac{(100 - 9) - 35}{100 - 9} \times 100 = 62 \text{ percent nonhunting mortality rate}$$

Hence, the nonhunting mortality rates were actually quite similar in the two sexes despite the 6-fold difference in hunting take. At best, these nonhunting mortality rates may be slightly different and imply slight compensation, although even this may not be true because natural hen mortality appears to be slightly higher than that of cocks possibly due to the stresses of reproduction.

Harper (1960) continued this approach to include the 1955-57 period of hen shooting. The percentage of hens shot increased from 9 to 14 and the crude annual survival rates continued at the previous 35-percent level. The nonhunting losses dropped from 56 to 51 percent, and the inference again was present that this represented compensatory decline in the nonhunting mortality rate.

The actual nonhunting mortality rates for hens can be calculated as above, and these become 62 and 59 percent for the 1952-54 and 1955-57 periods, respectively, again quite similar. The validity of these values rests on the accuracy with which the crude annual survival rates were measured.

The second indication of compensation was a rise in the Sutter Basin hen age ratio from 1.3 in 1955 before hen shooting, to 2.3 and 1.9 in 1956 and 1957 (Harper, 1960). This may have implied a compensatory reproductive response to hen shooting, although more years of observation before the seasons, and some after, would permit a more convincing comparison.

Pelee Island

We plotted the percentages of hens shot each year on Pelee Island against the annual percentage change in hen population from the beginning of one hunting season to beginning of the next (Fig. 62). The value of **r** represents the difference between reproductive and mortality rates, and is our only measure of population economy in the absence of estimates of reproductive and mortality rates. If the population were compensating in order to absorb hunting kill, it would respond with reduced mortality due to other causes and thereby keep its mortality rate constant; or, in any one year, it would respond with a higher reproductive rate to offset the effects of a higher mortality rate imposed by hunting. In either case, **r** would have to remain stable if the population were not to change.

The strong correlation between **r** and the percentage of hens shot (Fig. 62) implies that either the reproductive rate is reduced in a year with heavy hen kill, or the mortality rate is increased. We see no reason why reproductive rate should decline in a year with heavy hen shooting—an effect opposite to compensation — but the mortality rate would logically increase in such a year. Hence, the correlation probably implies a correlation between percentage of hens shot and the annual mortality rate.

This can be subjected to a limited test with Stokes' (1952) data by correlating the annual hen mortality rates with the percentages of hens shot in those years in which he calculated hen mortality rates (Fig. 63). The correlation, with only 2 degrees of freedom, is barely short of significance, but the extremely high coefficient suggests that a major part of the variation in annual mortality rate is associated with variations in the percentage of hens shot.

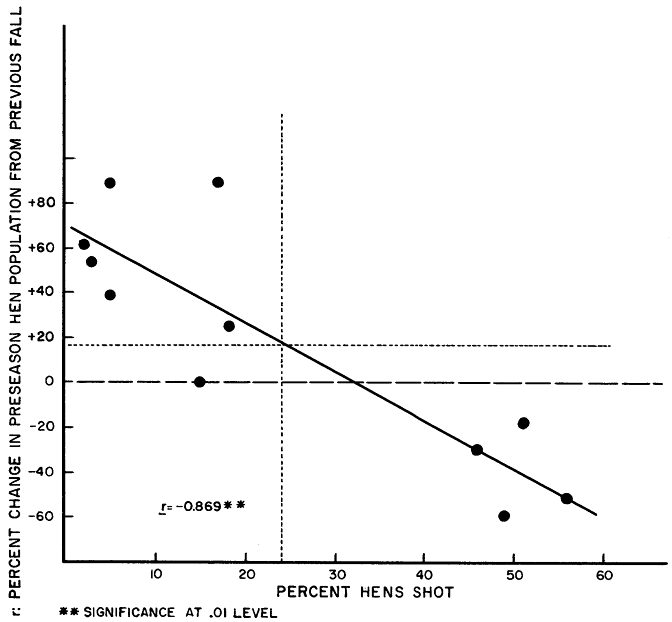


Figure 62. Correlation between percentage of hens shot in previous fall and *r*, the percentage change in preseason hen population from one year to the next on Pelee Island. Data from Stokes (1952), and C. O. Bartlett and H. G. Lumsden (in litt.).

The apparent strength of this relationship probably is partly fortuitous. Obviously the variation in total mortality rates is roughly twice as great as the variation in the percentage of hens killed. Unless the hen kill was severely underestimated, the annual mortality rates overestimated, and/or a heavy, unaccounted-for crippling loss took place, the variation in mortality rate cannot all be ascribed to hunting kill. Actually, substantial variations occur in nonhunting mortality of Pelee Island hens (Wagner, 1957). Of the 4 years reported by Stokes (1952) in which hen mortality (or survival) rates were estimated, the highest natural mortality occurred between 1949 and 1950 (Wagner, 1957), the year during which the highest hen kill took place. Despite these variables, the probability that the relationship in Figure 63 resulted by chance is less than .10. This, plus the pattern shown in Figure 62, leaves little doubt that the total hen mortality rate on Pelee Island increases as a function of the percentage of hens shot.

As noted previously, the Pelee Island populations are not naturally balanced. The sources of natural mortality are not strong enough to balance the reproductive rate, **r** remains positive, and the population increases in most years, at least in the density ranges that have been tolerated on the island. Without hen shooting, the population increases on the average of about 70 percent each year (Fig. 62).

Hen shooting increases the mortality rate and reduces **r**, the extent of reduction depending on the extent of hen kill. The regression line in Figure 62 crosses the **r** = 0 line at about 30-percent hen kill. Evidently, the Pelee population could be balanced with a mean annual kill of about this magnitude. Over a prolonged period, mean annual kill of less than 30 percent of the hens would allow population increases, and mean hen kills in excess of this amount would induce population decline.

With an annual 30 percent hen kill there would be year-to-year fluctuations as **r** varied with weather-induced reproductive success. A more refined approach to stabilizing the population would involve preseason measurement of weather and reproductive success, and adjustments of the hen kill above or below the 30 percent mean to allow for these variations.

Discussion

As Hickey (1955a) pointed out, if a population is to absorb hunting kill and maintain its level without decline, it must respond within the year in one or both of two ways. (1) The first is through a compensatory or density dependent relaxation of fall-to-spring mortality complete enough to absorb the hunting loss (the annual surplus effect). The mortality rate and subsequent spring density must remain the same as they would be without hunting. Implicit in this relationship is complete flexibility in winter loss and the absence of any correlation between posthunting population level and spring density. These relationships may be seen hypothetically set forth in the upper half of Table 31.

The presence of density dependence in overwinter mortality does not necessarily assure that hunting loss can be absorbed. For it is possible to have some density dependent tendencies in a population and still not have complete compensation necessary to fully absorb that loss (lower half of Table 31). Posthunting population level would then be correlated with spring density, and any reduction in the former would have some depressive effect on the latter.

TABLE 31
Fall and Spring Characteristics of a Hypothetical Population Compensating in Winter Loss for Varying Hunting Kills

Fall Population	Percent Shot	Post-hunting Population	Percent Natural Mortality	Percent Total Fall-to-Spring Mortality	Spring Population
With Total Compensation					
400	0	400	50	50	200
400	25	300	33	50	200
400	50	200	0	50	200
With Partial Compensation					
400	0	400	50	50	200
400	25	300	40	55	180
400	50	200	30	65	140

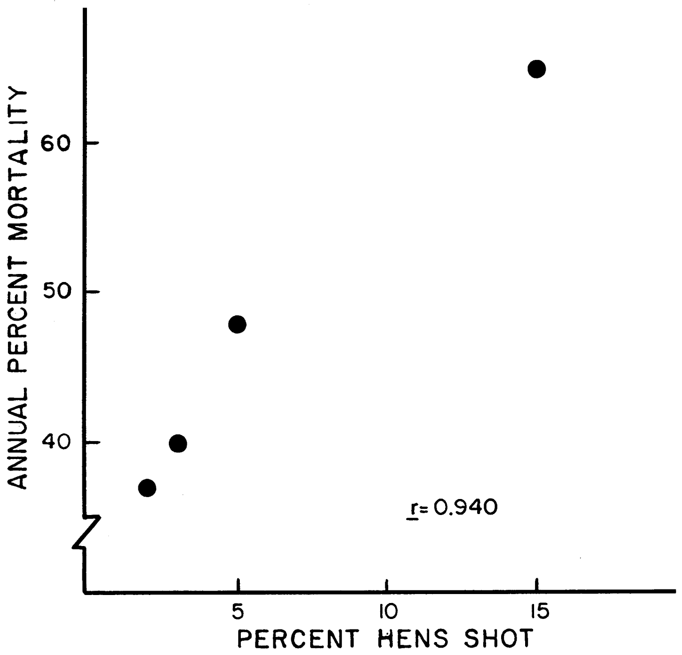


Figure 63. Correlation between annual percentage of hens shot on Pelee Island, 1947-50, and annual hen mortality rates for the same years. Data from Stokes (1952).

The second way in which a population could absorb hunting is in the inversity process; an inverse correlation between reproductive rate (and/or juvenile survival) and density. But here again, the compensation would have to be complete. The spring-fall increase rates would have to be flexible enough to make up for any variation in spring numbers and build the fall density up to the level it would attain without hunting (upper half Table 32). And here again, the implication follows that no correlation would exist between spring and fall numbers.

Again, inversity or density dependence in the spring-to-fall increase rates could exist without fully compensating for the differences in spring numbers (lower half of Table 32). In this event, fall densities would be correlated with, and partially determined by, spring density and those factors affecting spring density.

Regardless of which of these processes operates, the **r** values measured from fall-to-fall would have to remain at zero if hunting losses were fully compensated for. This is simply another way of stating that the populations would not decline.

We do not have measures of fall-to-spring mortality and hence cannot determine whether this is density dependent or not. It is fairly clear, however, that if there is any density dependence in overwinter loss, it is only partially compensatory. For as we saw in Chapter VIII, correlations between fall and subsequent spring numbers seem to be the rule in those populations examined. In Wisconsin, this is a strong correlation, and any reduction in fall numbers could be expected to reduce the subsequent spring levels.

We shall see in a later chapter that some density dependence is present in spring-to-fall increase rates. But here again, the compensation appears to be only partial because correlations still exist between spring numbers and subsequent fall populations.

Hence, we would expect the imposition of a hen kill to increase the mortality rate of a population, to reduce **r**, and to occasion some population decline if **r** were zero at the time. The empirical evidence we have examined bears out this expectation to some degree. On Pelee Island, where **r** is positive, the annual **r** values were correlated with the percentage of hens shot, and with the annual mortality rate during 4 years. Hen kill levels below about 30 percent do not prevent the continued increase on Pelee, but they slow the increase rate. Given the same starting densities, a population on Pelee will have a lower mean density during a 5-year period with hen shooting than during a similar period without such shooting. Any amount of hen shooting, therefore, seems to have some depressing effect on Pelee populations even though that population continues to increase.

In instances where an added legal hen kill of about 25-30 percent or more was imposed on continental populations (northwestern Wisconsin, Minnesota, and several California areas), and in Indiana where an estimated 20-28 percent of the hens were taken, **r** became negative and populations declined.

In those areas where an added legal take of less than 25 percent of the hens was imposed (mostly in California), the evidence did not point to population decline. This may have been due to one or more possibilities: (1) Compensation made up for this amount of loss and held **r** = 0. (2) Population decline resulting from the added hen kill was so slight and/or gradual that it could not be measured with available evidence, and in the time periods involved. (3) The added kill partly or largely replaced previous illegal and accidental hen kill without materially increasing the mortality rate, **r** was not altered from 0, and the populations continued balanced in the face of this degree of hen loss.

TABLE 32

Spring and Fall Characteristics of a Hypothetical Population Compensating in Rates of Spring-Fall Increase for Varying Hunting Kills

Spring Population	Percent Spring-Fall Increase	Fall Population
	With Total Compensation	
300	33	400
200	100	400
100	300	400
	With Partial Compensation	
300	33	400
200	50	300
100	100	200

(4) Where measured on restricted study areas, population processes are often damped or masked by ingress or egress.

It is pertinent here to mention briefly the mathematical effect on a population of hunting season kill which somewhat resembles compensation in net effect. The addition of a given percentage mortality (as with hunting) is not additive with the existing annual mortality, but increases the latter by a considerably smaller percentage than the actual percentage of individuals removed (Thompson, 1928). The formula for calculating the crude annual mortality rate (Ricker, 1958:25) is:

$$a = m + n - mn$$

where "a" is the crude annual mortality rate, "m" the mortality rate from fishing (or hunting), and "n" the natural mortality rate.

In a population with a natural annual mortality rate of 70 percent, addition of a 20-percent hunting kill would only increase the crude annual rate from 70 to 76 percent:

$$a = 70\% + 20\% - (70\% \times 20\%) = 76$$

In other words, hunting removes some animals that would otherwise die from natural causes, not because of any Erringtonian compensation, but simply because an animal can only die from one of the two types of causes to which it is exposed. The natural mortality rate remains the same with or without hunting, although the actual number of animals dying from natural causes is less where hunting first removes a fraction of the population. This may have been the case with Hart's (1955) and Harper's (1960) survival results discussed earlier.

Furthermore, a given percentage harvest increases a small annual mortality rate more than a large one. A 20-percent harvest raises a 40-percent annual mortality rate to 52 percent (30 percent increase) whereas it only raises a 70 percent annual mortality rate to 76 percent (9 percent increase). This undoubtedly is partly involved in our ability to see the effects of hunting more clearly on low mortality species such as ungulates and geese, and in Hickey's (1955a) conclusion that the harvestability of a species is some function of its annual mortality rate.

Consequently, the addition of a given degree of illegal hen kill will increase the annual mortality rate, and lower **r**, more than a second addition of the same amount of legal hen kill. If an additional legal hen kill partly replaced illegal kill that was already occurring, the increase in the annual mortality rate from the legalized hen kill would be even less pronounced. The resulting change in **r** might be so minor that little or no population change would occur, or it might be so slight as not to be measurable in a few years with our methods of measurement and the inherent natural variability in populations. Resulting population reduction might occur imperceptibly over a series of years.

Except where the take is so extreme that it exceeds any density dependent leeway in the population, the decline occasioned by hen kill apparently would not be indefinite. As we shall see in a later chapter, **r** increases as a population declines, probably because of increase in the reproductive rate. As **r** is made negative by hen kill, the population begins to decline. As it does so the density responses begin to increase **r**. Eventually the population declines to the point where **r** is restored to zero and the population is balanced at a new, lower density at which it sustains the hen loss without further decline.

Whether or not the California population mechanisms are similar to those in the Midwest is not clear. Ben Glading (pers. comm.) has suggested that they probably are not. The earlier California nesting season, the importance of rainfall for a successful hatch, and the possible, annual surplus effect reported by Hart *et al.* (1956) and Hart (1957) may be evidence of dissimilarity.

In any event, removals above 20-25 percent have apparently effected some degree of population reduction in a number of areas. The evidence does not suggest reduction from removals below this level, but some effect is possible and this includes the 16 percent illegal hen loss in Wisconsin. Hence the Wisconsin illegal hen kill could have some depressant effect on the populations.

Summary

Postseason body shot incidence appears valid as an index of shooting pressure on pheasants because of a correlation between percentage of cocks shot in different areas and percentage of survivors with shot, and a correlation between annual percentages of cocks shot and postseason body shot incidence in Wisconsin cocks. Within a 7-year winter-spring sample of car-killed hens, 7 percent carried shot, indicating about 16 percent of the hens were killed annually during the 1953-59 hunting seasons. There is no evidence that it varies with pheasant population changes.

The percentage of hunting season arrests made specifically for shooting hens in Wisconsin has averaged 52, 21, 14, and 12 for successive weeks of a 4-week season. This distribution is correlated with the seasonal distribution of hunting pressure. This, plus evidence from other states of a correlation between hunting pressure and hen loss, suggests that hunting pressure may be an important influence on the extent of loss.

Legal kills exceeding about 20-25 percent of the hens in Wisconsin, Minnesota, Indiana, and some areas in California appear to have reduced population levels. Legal kills below this level, mainly in some sections of California, had no perceptible effects implying that compensation was taking place, or the legal kill was partially replacing illegal kill. Or, the added kill, only being partially additive with the previous annual mortality rate, may have become lost in the population complexities and our abilities to measure slight effects in short periods of years. The 16-percent illegal hen loss in Wisconsin could have some depressing effect on populations.

CHAPTER XIV. MISCELLANEOUS ACCIDENTS

Highway Mortality

Phenology of Loss

As part of their regular routine duties, county highway patrolmen in Jefferson County remove from roadsides and bury all car-killed animals they see along state and federal highways. L. R. Jahn (unpubl.) asked these men to keep a record of all animals found between April, 1950 and March, 1951 along the 180 miles of such highways. The monthly distribution of the 313 pheasant kills observed (Table 33) shows a high in April and May coincident with the height of mating activities, and again in the latter part of the summer when the population is bolstered by reproduction, and broods commonly frequent the roadsides. This is almost identical with the monthly distribution found by McClure (1951) in Nebraska, and fairly similar to that reported by Hein (1941).

Our own Department road-kill collections for fluoroscoping were made primarily during the late winter and early spring months, and are not well enough distributed through the year. to provide similar indices. They do, however, give some clue to the sex break-down in the kill during much of the year. During the winter months, the sex ratio of 241 kills was 5.5 hens per cock, quite similar to our statewide sex ratios. But in March and April, the sex ratio in a sample of 139 kills dropped to 1.9 hens per cock. Although the kill of both sexes increases during this period, the cocks become considerably more vulnerable. It is not unusual to see cocks fighting in roads in spring, almost oblivious to passing cars. This may be responsible for the increase in percentage of cocks in the spring kills. In May and June, the ratios in the kill revert to higher values approaching those of the winter.

Effects on the Populations

Magnitude of Loss

On the basis of the above sex ratios, hens make up about 80 percent of the loss in late fall, winter, and late spring. They make up about 66 percent of the March and April kill. On the assumption that most of the October kill occurs before the hunting season, hens would make up one-half of the October kill. Using Jahn's data (Table 33), about 136 hens were picked up during the months of October through June on Jefferson County federal and state highways.

The mileage of county highways in Jefferson County, most of which are hard surfaced and carry fairly high-speed traffic, equals or slightly exceeds that of the state and federal highways. The mileage of township roads, some of which are only gravelled, probably equals or exceeds the combined mileage of the federal, state, and county roads. Hence the federal and state highways constitute less than one-fourth of the total road mileage in 24-mile-square Jefferson County.

In view of this, the entire car-kill of pheasants for the county may be three or more times that occurring on the state and federal highways. Based on our derived loss of 136 hens in Jahn's sample, the total loss would be 408 hens. This is low for several reasons: (1) Some hens probably were thrown off the roads into heavy vegetation and not seen; (2) some undoubtedly were eaten by scavengers and predators, especially since the patrolmen only picked up the animals 4 days of the week; and (3) some hens undoubtedly were killed in July, August, and September. We did not include kills for these months because most of the kills are probably young birds, and we had no way of knowing the percentage of hens in the kill.

Thus, the total hen loss probably exceeded the 408 calculated, and possibly reached 500-600 or more. The 1950 estimated kill in Jefferson County was about 17,000 cocks. Assuming the number of hens present before the hunting season was roughly similar to the number of cocks, and making slight provision for crippling loss of cocks, unharvested residue, and overestimate of the kill, a loss of 500-600 hens approached 3-4 percent of the hen population alive on October 1. In a survey of highway mortality in Wood County, Ohio in 1936 and 1937, the observed pheasant loss was about 2.4 percent of the population (Leedy and Hicks,

TABLE 33

Monthly Distribution of Pheasant Road Kills Observed by Jefferson County, Wisconsin Highway Patrolmen, 1950-51

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	No.											
Kills	9	13	16	39	54	29	35	46	37	20	8	7

1945:76). The total loss in that county was estimated at more than 3,000 birds per year.

Actually, its effect is somewhat more serious than a simple 3-4 percent loss of the October hens. According to our estimates, about 97 hens, or 71 percent, of the total hen loss between October and June occurred in the months of March through June. Since hunting season, predation, and other factors take a toll between October 1 and March 1, the hen population in March is obviously lower than it is on October 1. Hence, the highway loss from March through June constitutes more than 71 percent of 3-4 percent of the hen population going into the breeding season—a time when we can least afford to lose hens. Furthermore, the loss of chicks in July, August, and September has not been reckoned with in our calculations which adds somewhat more to the importance of these losses.

Relationship to Pheasant Density

Generally, there are numerically more car-kills in good pheasant areas than in poor. From 1952 to 1958, highway maintenance workers in Pierce County (a northwestern county quite marginal for pheasants) picked up and kept a record of all pheasants found along 25.5 miles of state and federal highway (E. L. Larson, in litt.). These averaged about 3 per year, or roughly 1 kill per 8 miles, in contrast to the near 2 kills per mile reported by Jahn in Jefferson County. On repeated trips from Madison, Wisconsin to Freeport, Illinois over an 18-year period, Schorger (1954) observed most pheasant road-kills in Green County, Wisconsin, an area of high populations.

What is not known is whether the percentage kill bears any relationship to density changes in a given area. Under the stress of high densities, birds might conceivably move around more, be exposed more often to highway loss, and thus lose a higher percentage of their numbers.

Schorger (1954) noted an increase in the number of pheasant kills over his 18-year period of observation irrespective of chronological changes in population levels. He logically attributed this to the increase in traffic during the period. As our traffic increases in volume and speed and as more roads are improved, highway loss will probably continue to increase. While car-kills are not a serious source of loss, they may be one more factor limiting pheasant populations.

Other Miscellaneous Accidents

Other well-known, miscellaneous accidents take a small, undetermined fraction of birds. We have seen a number of railroad kills which Leedy and Hicks (1945:77) reported to be surprisingly high in Ohio. This appears to be especially true in winter when railroad rights-of-way often provide excellent cover and a good source of gravel. One railroad official told us that during a period in which he was engineer on a train running from Green County to Milwaukee, one or more pheasants were killed daily on this run during winter.

As is well known, some birds are killed by flying into wires, fences, and buildings. A small fraction of our "road-kill" collections comes from this type of accident.

Summary

Some 313 car-killed pheasants collected on about 180 miles of state and federal highways in Jefferson County for one year by highway patrolmen showed greatest losses in spring and late summer. Our Department road-kill collections show a winter and late spring sex ratio similar to that observed in the field, but the March and April ratios appear to be biased toward cocks.

Using the sex ratios in Department road-kill collections to calculate the number of hens in the Jefferson County sample, the October 1 to July 1 observed kill was about 136 hens. Allowing for kills on county and town roads, kills not seen, loss to scavengers, and a small kill in July, August, and September, the loss may have reached 500-600 hens in 1950 and represented 3-4 percent of the October 1 population. The loss was somewhat more serious than this since much of it occurs in spring and no provision has been made for the loss of young in July-September.

Some loss occurs at all densities, but it is impossible to say whether or not it tends to be either negatively or positively density-dependent. It appears to be increasing as traffic volume and speed increase.

Other minor causes of loss are train kills and flight accidents.

CHAPTER XV. PHEASANT POPULATION BEHAVIOR

Intra-specific Intolerance

Effect of Density on Reproductive Behavior of the Hen

Observations on Reproductive Behavior

Captive hens, when penned at high densities, drop more eggs, abandon more nests, incubate fewer clutches, and eventually nest later than hens penned at lower densities (Kabat and Thompson, 1963). Other studies have produced similar evidence on wild populations. The prevalence of egg dropping and laying in dump nests increased as the Protection Island populations increased (Einarsen, 1945). Stokes (1954: 35-36) surveyed nesting studies reported in the literature, and found a positive correlation between pheasant density and the percentage of nests abandoned by hens. His own observed abandonment rate was the highest of any reported in the literature for wild populations. Linder and Agee (1961) suggested that, for any given cover pattern, the nest abandonment rate of hens may increase as the population increases.

Chicks also become independent of hens at earlier ages in areas of high pheasant densities than at lower densities (Stokes, 1954:52). Wisconsin broods do not begin to break up until 10-12 weeks of age. On Pelee Island, chicks were entirely independent of hens by 8 weeks. And on Old Hen, a small island 6 miles west of Pelee which had even higher densities (30 birds per acre), chicks were occasionally seen to wander away from broods as early as 4 weeks of age.

Mechanism of Density Effect on Reproductive Behavior

Information on the actual psycho-physiological links between pheasant density and reproductive behavior is not available for the pheasant. However, data primarily from studies of mammals suggest a working hypothesis.

In a number of species, crowding or high densities constitute a source of stress eliciting adaptive response from the pituitary-adrenal system which was first described in detail by Selye (1946, 1949). Subsequent studies and literature review by Scharrer and Scharrer (1963:167-173) led them to conclude that the stress response involves a more complex relationship. "A direct feedback relationship may exist between the pituitary gland and the adrenal cortex, but it is no longer assumed to be an important factor in corticoid secretion. There is every indication that such a feedback includes the central nervous system where hormonal influences are integrated with all other afferent stimuli."

The above interrelationship results in a host of accelerated or inhibitory neuroendocrine changes, including the suppression of gonadotrophin reported by Christian and Davis (1964) in their studies on mice. They suggested also that the increase in the secretion of adrenal androgens occurring under high densities might be sufficient to suppress gonadotrophin, thus the reproductive function would decline. This hypothesis may explain in part observations made by other authors on density relationships in small mammals. Strecker and Emlen (1953) found atrophy of reproductive organs in dense house mouse populations that had stopped reproducing. Frank (1957) reported reduction in fertility and increased resorption of embryos in peak populations of the European vole. Chitty (1952) concluded that field voles were deranged physiologically by density-induced strife, and their offspring were less viable and suffered heavier mortality as a result. Louch (1956) found abandonment and killing of young by overcrowded meadow mouse females.

Finally, Christian and Davis (1964), on the basis of their studies and literature review on voles, Japanese deer, woodchuck, Australian rabbit and dogs concluded that the basic stimulus to endocrine changes are socio-psychological not physical. Further they stated that environmental factors may control populations but when they don't, the endocrine feedback mechanism will.

Density-related changes in reproductive behavior of the pheasant may be analogous. These changes apparently occur in the broody phases of the hen's reproductive cycle, and are readily demonstrated during the egg-laying and incubation stages. Once her brood is hatched, she also is less attentive to the chicks, and they become independent at an earlier age. The possible impact of these behavior-physiology relationships on pheasant populations is discussed in the following section.

Effect of Density on Population Dynamics

Effect of Behavior Variations on Reproductive and Mortality Rates

As population densities increase, increase in the nest-abandonment rate might eventually reduce nesting success to the point where it was barely adequate to balance the mortality rate (Stokes, 1954:35-36). Stokes' evidence shows quite well that the abandonment rate is correlated with density but because other variables enter into nesting success, and probably the abandonment rate, we were not able to demonstrate an inverse correlation between density and nesting success with the data in the literature.

Linder *et al.* (1960) found that in years of higher population levels there was more nesting effort, about equal laying effort, but less incubation effort. From controlled pen studies, Kabat and Thompson (1963) concluded that density had a measured effect on the different phases of reproduction. When the number of cocks was increased, the reproductive success was proportionately lower due mainly to perpetual harassment of hens. When hen pheasants were penned under high densities, they dropped many eggs at random, laid in each others' nests, and incubated nests in which 2 or more hens had laid eggs. This type of behavior greatly reduced productivity and prolonged the reproductive stresses.

The possibility exists that density-related behavior variations could influence the juvenile mortality rate. As the abandonment rate increased, the clutch which is ultimately incubated would probably come relatively late in the hen's sequence of egg laying. As discussed earlier, the eggs might be of lower quality with consequent low vigor and high mortality rate of chicks. The earlier abandonment of broods, as Stokes suggested, might also contribute to higher chick mortality rates.

Stokes (1954:65) did show high loss of chicks: 33-50 percent of the chicks between hatching and 9 weeks of age. However, he pointed out that this is similar in magnitude to other chick loss rates reported: e.g. 37-44 percent loss through brood shrinkage reported by Errington and Hamerstrom (1937) and Baskett (1947). Our Wisconsin data show 6-week broods averaging about 7 chicks—a decline of 30 percent or more after hatching. Since brood shrinkage gives no clue to sudden loss of entire broods, these values are conservative.

Pelee Island chick losses therefore may not be a great deal lower than in many continental areas. However the latter are subject to such limiting factors as hay mowers, predation, highway loss, etc., which are negligible on Pelee. Hence, the loss rates on Pelee may result from compensatory (density-dependent) effects, as Allen (1953:62) suggested. One significant point is Stokes' (1954:29-30) observation of exceptionally high embryonic mortality of chicks on Pelee and Old Hen Islands. This was occurring just prior to hatching, perhaps was a prehatching symptom of the lower chick vigor we postulated, and possibly was a portent of the posthatching fate of the chicks.

The delay in nesting resulting from increased nest abandonment might delay the normal, autumnal buildup of body fat (Kabat, Thompson and Kozlick, 1950). As a result, hens would be forced to go into winter without normal fat stores, and this would place them at a handicap in surviving weather extremes. Such delayed nesting behavior might also increase late summer hen loss (Wagner, 1957). Wagner noted circumstantial evidence of a relationship between hen mortality rates and density on Protection Island (Einarsen, 1945) where the percentage of males in the population increased as density increased.

Effect of Density on r

Since fall-to-spring mortality may be fairly constant in most years and fall densities are correlated with densities of the following springs (Fig. 41), any fall population index could presumably serve as an index of the subsequent spring level. We therefore plotted yearly **r** values against indices of the previous autumns which we assume represent correlations between **r** and breeding density. Tests were made for Wisconsin and Michigan (Fig. 64) using annual changes in the kill to estimate **r**, and the kill estimates of the previous falls as breeding density indices. For example, the percentage change in kill between 1954 and 1955 (**r**) was plotted against the 1954 kill.

We similarly tested data from three other states and Pelee Island (Fig. 65). Minnesota and Indiana **r** values were plotted against kill estimates of the previous years using the same data as in Figure 44. Pelee Island **r** values were based on changes in between-hunting-season hen populations (Fig. 44) and plotted against postseason hen numbers of the previous autumns.

The test of South Dakota populations was based on data in Dahlgren (1959). In order to make these data comparable with the kill estimates for Michigan, Wisconsin, Indiana, and Minnesota, we used Dahlgren's preseason total population estimates (P_1 in his Table 3), divided these in half to estimate the number of cocks, and then multiplied by 70 percent to simulate a 70-percent kill of the total South Dakota cock population. Annual percentage changes in these values were calculated to provide **r** values, and then correlated with their respective previous fall cock indices.

Both linear and curvilinear tests were run, and in all cases the curved lines provided the better fit as indicated by the uniformly higher correlation coefficients. The Wisconsin test is significant at the .01 level while all of the others except the Pelee Island test are significant at the .05 level. All are negative.

Evidently **r** decreases as density increases. The observed variations in **r** may largely be due to variations in the reproductive rate, and perhaps to variations in spring-to-fall mor-

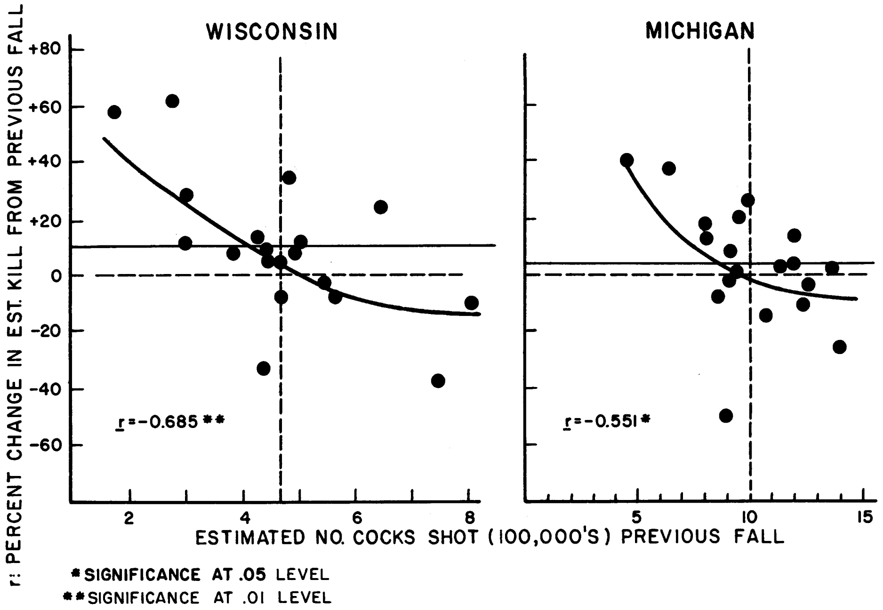


Figure 64. Correlation between breeding population density, as represented by the estimated kill of the previous fall, and *r*, the percentage change in kill between successive years, 1938-56 in Wisconsin and 1937-56 in Michigan. The lines were fit with the formula $Y = a + bX + cX^2$.

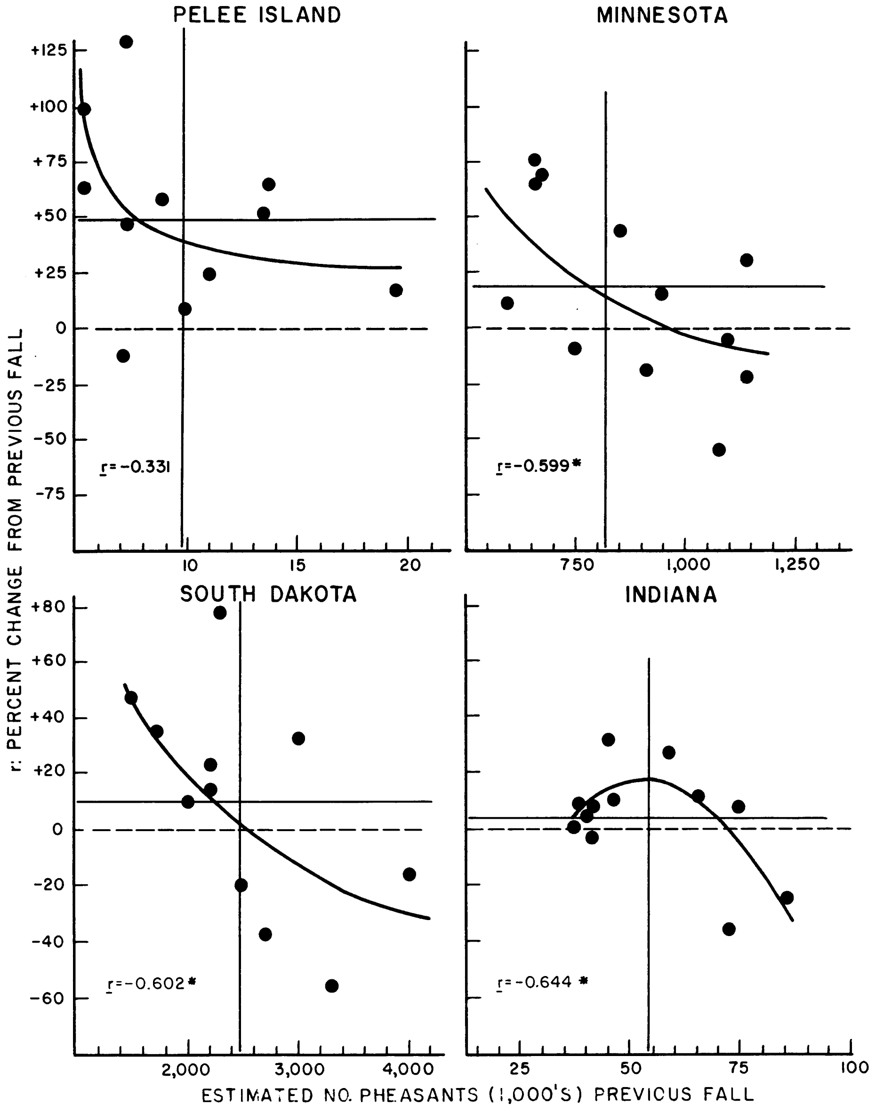


Figure 65. Correlation between breeding population density, as represented by population indices of previous autumns (see text for sources), and *r*, the percentage change between successive years, in Pelee Island, Minnesota, South Dakota and Indiana. The lines were fit with the formula $Y = a + bX + cX^2$.

tality. This suggests an inverse correlation between breeding population level and the percentage increase between spring and fall. This is Errington's (1945a) inversity principle, and something essentially similar was previously suggested to occur in pheasants by Allen (1953:81; 1956:436-437) and Linder *et al.* (1960). While this correlation could occur from any density dependent influences undetected by us, we assume that most of the correlation with **r** results from density related changes in reproductive behavior, and consequent changes in reproductive rate. Einarsen's (1945) Protection Island data showed a declining rate of spring-fall gain as his population increased. The winter censuses on the University of Wisconsin Arboretum (McCabe, 1949) show a negative correlation between **r** and the census of the previous winter.

The existence of the correlations throughout the range of density between those of Indiana and those of South Dakota and Pelee Island—varying perhaps by a factor on the order of several times 10—suggests that the **r**-depressing influence of density may be continuous through all densities. The curvilinear relationships imply that the function is an exponential one which is perhaps to be expected. The addition of 50,000 birds to the Indiana population would represent a substantial increase—perhaps twofold—and would probably incur noticeable reduction in **r**. Addition of the same number of birds to the South Dakota population would hardly be noticed and would probably have no noticeable influence on **r**.

In three of the six cases (Wisconsin, Michigan, and South Dakota) the regression line crosses the **r** = 0 line approximately at the intercept of the latter with the vertical, mean density line. As described previously, the Minnesota points represent a selection of years when hens were not shot, and were preponderantly increase (**r**-positive) years. With a more random selection of years, the position of the regression line would probably be similar to that of the other three states. The Pelee Island population is not balanced as pointed out previously. The **r** values are almost all high in the positive range, and hence the regression line does not cross the **r** = 0 line. The Indiana line differs from the others in attaining its highest value approximately at the population mean. Whether or not this implies a minimum density below which **r** declines, or whether this is a chance array of points and the Indiana situation is basically similar to the others cannot be said at present. The straight line fit to these points is simply an inverse regression line with its midpoint approximately at the **r** = 0 and mean density intercept.

With the exceptions and reservations noted above, these regressions imply that above-average density for any given area is a condition predisposing a population to decline as surely as unfavorable weather, adverse land-use changes, and other influences that lower reproductive and survival rates. And conversely, below-average densities allow **r** values to increase and permit population increase.

We make the distinction between "above-average" and "high densities" because, except for the extremes, "high" and "low" are concepts relative only to the mean density of any given area. The correlation between density and **r** is a continuous relationship spanning all densities between those of Pelee Island and South Dakota on the one hand, and Indiana on the other. What is a high density that forces **r** below zero in Wisconsin, is a low density that permits strong population increase in South Dakota.

Two final implications follow from this relationship. First, if this correlation results from increasing social strife as a population increases, in a sense it represents competition for space. Andrewartha and Birch (1954) examined critically the concept of competition, and Andrewartha (1961:174) further advocated restriction of the term to Birch's (1957) definition: "Competition occurs when a number of animals (of the same or of different species) utilize common resources, the supply of which is short . . . ." This definition fits the present situation except for the further stipulation that we are dealing with intra-specific competition. This is also the one limiting influence in pheasant populations that we have found to be clearly density dependent. Hence, this situation fits Milne's (1957) contention that competition is the only factor which can be perfectly density dependent since it is the only factor that can respond solely to changes in density.

Secondly, this is the one density-dependent or self-limiting influence we have been able to find in pheasant population phenomena. But it does not involve a threshold effect in which the birds interact with the habitat to adjust densities by themselves to some specified level. It is an influence which operates continuously at all levels and, as we shall see in the next chapter, only enters into density determination in combination with the other limiting factors.

Dispersal

The role of dispersal in pheasant population dynamics could serve indirectly as a limiting influence on population density. According to Andrewartha and Birch (1954): (1) the tendency toward dispersal is an innate characteristic of most animals studied; and (2) while many ecologists assume that it is associated with high densities, dispersal occurs at all densities in many species, and the dispersal rate in a number of species may not be markedly influenced by density. Among higher vertebrates, particularly birds, movement is more prevalent in the juvenile segments of the population.

Although several studies have provided information on pheasant movement (Taber, 1949; McCabe, 1949; Grondahl, 1953; Weston, 1954; and others), we need considerably more data before we can visualize the general patterns. However, Thompson (1948) and Kabat and Thompson (1963) have drawn some important generalizations on the effects of movement of bobwhite quail populations and certain aspects of movement patterns may be similar in the pheasant. Based on banding of winter coveys and subsequent movement observations, Kabat and Thompson (1963) found almost explosive, unoriented movement in spring at the time of covey break-up. Movement of banded birds off of, and ingress of unbanded birds onto, their study area showed that a generalized redistribution of the population was taking place throughout the quail range of the region. They also found a differential movement between adults and juvenile quail with more mobility in the juvenile segment of the population in spring.

Northern pheasant populations are well known to undergo some degree of spring movement. McCabe (1949 and pers. comm.) trapped pheasants annually throughout the winter on the University Arboretum. By the end of winter, most birds were banded and repeating in the traps. With warm temperatures in early spring, large numbers of unbanded birds began appearing in traps, and pheasant tracks appeared in the snow in many coverts that had not wintered birds. This suggests something analogous to Kabat and Thompson's spring shuffle in bobwhite. Taber's (1949) observation of the juvenile hens being more prone to move away from the wintering area than adults is reminiscent of the greater mobility in juveniles of other species.

The important implication of Kabat's and Thompson's (1963) quail findings was that, for any limited area, egress is a normal occurrence each year. Where an area is surrounded by comparable quail range, ingress occurs from the adjacent territory, and the gains balance the losses. But in a limited area not surrounded by equally good range, losses exceed gains, and dispersal becomes a limiting influence just as effective as some agent that removes birds from the population by killing them.

Another more subtle effect (also reported for quail by Kabat and Thompson, 1963), may take place in areas with variations in uniformity of habitat quality. Where habitat is uniformly good over large regions—e.g. one county, or more—dispersing birds can move to good range and be as successful as those that remain in the areas of origin. But where habitat varies in quality, dispersal from good to suboptimum areas, with consequent reduction in success of the emigrants, could serve as a means of attrition from a population that would not be experienced in uniformly good areas. The absence of dispersal loss from either of these two types is probably a third factor (along with near-absence of losses from hay mowers and predators) accounting for the high densities on Pelee Island (Stokes, 1956:371).

Summary

At higher densities under both penned and natural conditions hens drop more eggs, abandon more clutches, and eventually nest later than at low densities. Chicks become independent of hens earlier at high densities than at low. The physiological mechanisms are unknown although one possibility is suppression of normal reproductive physiology by density-induced stress and consequent pituitary-adrenal activity.

These behavioral variations may reduce mean nesting success and increase chick and hen mortality rates. Annual rates of population change in Wisconsin and Michigan, South Dakota, Minnesota and Indiana show statistically significant inverse correlations with density; a similar test for Pelee Island shows a negative but not significant coefficient. These tests suggest an inverse correlation between breeding population levels and the percentage increase in the populations between spring and fall. This density-induced reduction in **r** values presumably results from reduction in reproductive and survival rates through the effects of intra-specific intolerance and density-related behavior changes. Social strife represents competition for space, and this is the one truly density dependent function in pheasant populations that we have been able to find.

The role of dispersal in the population dynamics of the pheasant can serve indirectly as a limiting influence on population density. Absence of dispersal loss may be one of the main factors responsible for the high densities on Pelee Island.

CHAPTER XVI. GENERAL POPULATION PRINCIPLES

In order to establish perspective for evaluating the mechanisms and causes of variation in density in Wisconsin pheasants, it seems desirable to bring clearly into focus the questions for which we are seeking answers. We continue to rely upon regional population data for comparative purposes because our own Wisconsin data are not extensive enough to permit a thorough analysis. Pheasant population curves for South Dakota, Michigan, Wisconsin, and Indiana were plotted (Fig. 66). The curves for the latter three states are annual cock kill estimates used previously. The South Dakota curve is an estimated cock kill derived from Dahlgren (1959) as described in the last chapter.

These four populations appear to fluctuate within a limited range around a long-term mean. Numerically, the extent of fluctuation differs, but the magnitude of change is comparable for all four populations. These ranges of variation and their means are roughly horizontal in time without marked, progressive increase or decrease toward the ranges or means of the other populations.

Three basic questions arise from these population curves: (1) Without regard to the density at which this leveling takes place, what keeps these population trends horizontal in time, or in balance? (2) Why and how do these populations fluctuate? (3) What environmental factors and population mechanisms determine the mean density at which any one of these populations is balanced, and why do they differ? In attempting to answer this question, we give special attention to one of the most important questions, both basic and practical, in population ecology today: to what extent are populations self limiting and to what degree do factors external to the animal influence their density?

In undertaking this analysis, we do so with the full realization that we have so far examined only some of the factors that potentially influence pheasant numbers. We have no evidence on such factors as disease, nutrition, genetic lethals, and others. Hence we attempt the following synthesis with only part of the data needed, and recognize that it may well be revised when more knowledge is available.

Population Balance

We have already described subjectively the characteristics of the populations in Figure 66 which imply balance: fluctuation within a limited range around a long-term mean, and without progressive increase or decrease in the range or mean.

In terms of **r**, balance implies a long-term equating of positive and negative **r** values (increases and decreases) with a consequent mean near zero. The density at which **r** reaches zero ultimately becomes the long-term mean density of the population. Deviations from mean density are corrected by changes in **r** which direct the populations back toward its mean (Figs. 64 and 65). In this way, the population is kept varying about its mean without long-term increase or decrease. Other evidence we cited previously for the possible existence of balance includes: (1) The long-term mean reproductive rate is associated with no population change (Chapter VIII); and (2) the spring temperature norm is also associated with no population change (Chapters IX and X).

Andrewartha and Birch (1954) have questioned the validity of the concept of balance. Their skepticism is perhaps understandable in view of the vast range of densities through which insects, their prime consideration, fluctuate. The concept may be of questionable value in species which fluctuate seasonally and annually by factors in the hundreds or thousands, although some entomologists have even stressed the validity of this concept in insects (cf. Nicholson, 1933, 1954, 1954a). However, in our pheasants and other higher vertebrates, the range

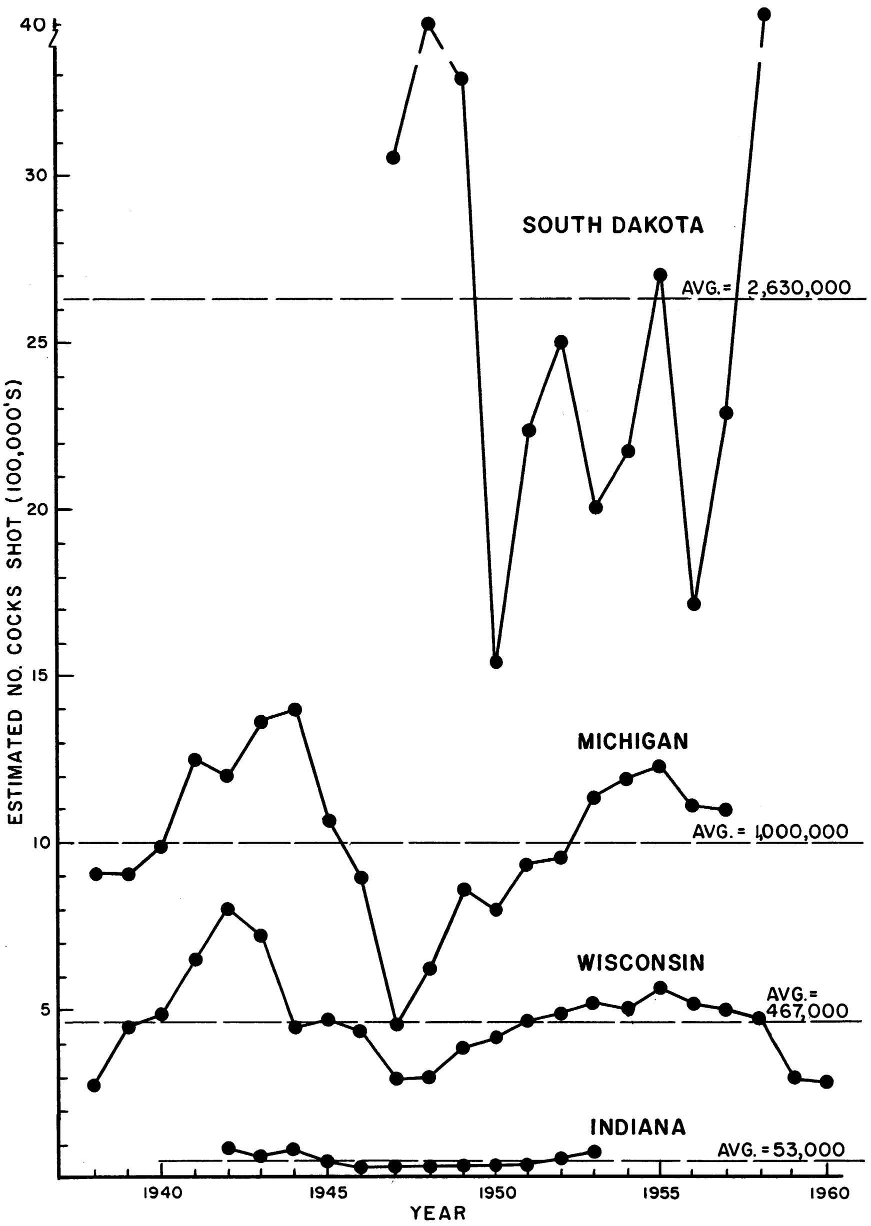


Figure 66. Estimated annual cock kill in South Dakota, Michigan, Wisconsin, and Indiana.

of variation is much more restricted, and the concept has some importance, particularly because of its implications to fluctuation.

Actually, the concept of population balance is somewhat theoretical because it necessitates a constant environment. Environments do experience long-term changes from climatic trends, plant succession, shifts in agricultural practices, human influences, etc. As a result, most mean population densities undergo gradual long-term changes. Where the environment is altering continuously in one direction—as in Wisconsin from changes in haying practices, wetland drainage, predator densities and illegal hen kill—a long-term modification in mean density may be occurring. Nevertheless, a tendency toward balance and the approximate achievement of it for short periods of time seem evident from the data we have examined.

Population balance seems to occur at all densities we have observed (Figs. 64 and 65) except on Pelee Island. Here, without hen shooting, r remains positive. The addition of periodic hen shooting has prevented indefinite population increase, and has imposed an artificial balance.

Cole (1948), Ricker (1954), Lack (1954), Nicholson (1954a), and others have observed that a population solely under the influence of density-independent factors can vary without limit, and eventually will vary by chance to extinction or prodigious densities. Populations are limited in their variations far short of these extremes, and this limitation must come about through the action of density-dependent factors.

Our findings are in accord with these views. The populations in Figures 64-66 are not only kept in existence (cf. Andrewartha, 1961:168) by density dependence, but their long-term trends are kept horizontal by it. Thus the objections of Andrewartha and Birch (1954) and Andrewartha (1961) that the concept of balance is largely deductive are not valid in the case of the pheasant and the empirical evidence in Figures 64-66.

Population Fluctuation

Role of Weather

Year-to-year population fluctuations result from r varying between positive and negative values. These, in turn, result from some influence on the population that varies from year to year, and changes the balance between reproduction and mortality.

Of the various environmental factors we examined, weather was the only conclusive one which experiences marked year-to-year changes. In several north central states, mean prenesting temperatures appeared to be the dominating variable operating through the reproductive rate, and perhaps hen mortality rate. Although prenesting temperatures were not shown to be involved in the South Dakota population changes represented in Figure 66, we surmise that these fluctuations might be associated with some aspect of it.

Role of Intra-Specific Intolerance

Relationship between Fluctuation and Balance

Since annual r values are correlated with density as well as prenesting temperatures (weather), we must clarify the relationship between these two factors.

If the population fluctuated solely with weather, it would take on the same degree of randomness inherent in weather. By chance, it could eventually fluctuate to zero. However, the r-density relationship is the balancing cushion preventing this. When weather is favorable, r becomes positive on the average, and the population increases. In doing so, it will incur more density pressure during the following breeding season, and this will tend to lower r. Only if the weather is favorable enough to override this, will further increase occur. Eventually density pressure will increase to the point where it will force r to become negative and press the population back toward its mean almost irrespective of weather.

This effect can be seen in Figure 67 where we correlated r and prenesting temperature for years when the population was above and below average in Wisconsin. As the population increases, the individual values of r and the regression line are forced downward. Consequently, an increasing percentage of the points falls below $r = 0$ (are negative), an increasingly large (and less probable) deviation from the mean temperature is needed to permit population increase, and the probability of population increase is reduced.

Conversely, with unfavorable weather the population declines below the mean, and density pressure is relaxed to allow mean of r and most of the individual values once again to become positive. Thus, below-average densities are followed by increases, and above-average densities are followed by decreases. In this way density dependence introduces a measure of oscillation into the population, and prevents the full degree of randomness that would characterize a population fluctuating solely under the influence of weather. This randomness is further reduced by the serial correlation shown in Chapter VIII.

Is the Pheasant Cyclic?

Grange (1948:89) asserted that the pheasant is cyclic in Wisconsin. During 1932-50 pheasants and ruffed grouse followed parallel population trends (McCabe *et al.*, 1956: 317).

Since the term "cycle" has been used with widely varying connotation, our first need is definition. The usual dictionary definition (cf. *Webster's New Collegiate Dictionary*) implies a series of phenomena or events that recur regularly and in the same sequence. Andrewartha and Birch (1954:642) sharpen the concept further with the mathematical and physical connotations involving not only a recurring pattern of events, but recurrence in constant phase and amplitude. They cite Kendall (1948:398) who also specifies this distinction.

These authors distinguish between the term "cycle" and a related concept: that of "oscillation". The latter implies variations in a phenomenon alternately between two extremes, but not necessarily with equal phase and amplitude. We use these two terms as defined here.

The recurrence aspect is present in pheasant fluctuations. Increases follow lows, and decreases follow highs because of the correcting influence of density dependence on deviations from the population mean. This feature qualifies these fluctuations at least for the term "oscillation".

The amplitude of fluctuation varies within and between the populations (Fig. 66), being most pronounced in the South Dakota curve. However the amplitude of variation

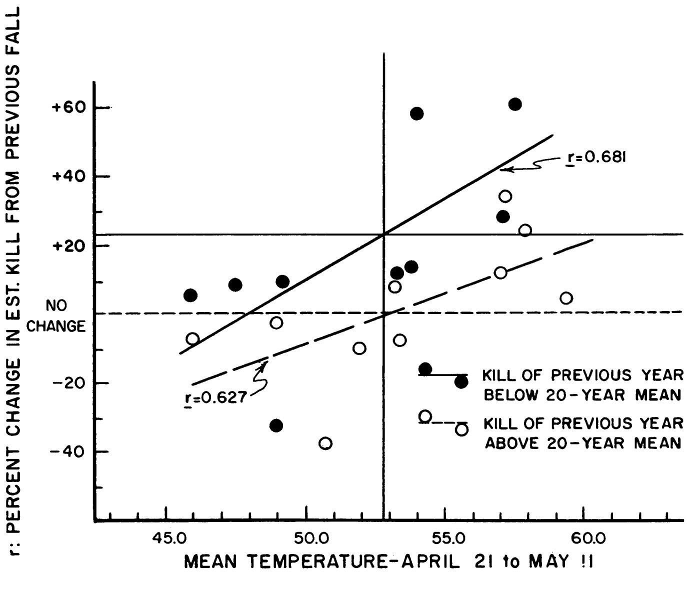


Figure 67. Correlations between prenesting temperatures and r in Wisconsin in years when the kill of the previous year was above the 20-year mean, and years when the kill of the previous year was below. The data are the same as those shown in Figure 50.

Weather probably is the most important single factor causing short-term fluctuations in Wisconsin pheasant populations. While severe winter weather can locally depress pheasant numbers, annual population trends are most strongly influenced by prenesting temperatures between April 21 and May 11. Weather may operate directly on a population, or indirectly through an interacting, dependent variable.

between the extremes of each population shows a fair degree of constancy (Table 34), perhaps suggesting that there are maxima and minima to which density-dependent restraint will allow the populations to be carried by weather extremes. These maxima and minima appear to be of roughly similar magnitude in the different populations (Table 34).

The phase of oscillation also appears to vary within and between these populations (we discussed previously the differing lengths of time required by the Wisconsin population to reach the 1942 and 1955 peaks). And although the pheasant and ruffed grouse curves were parallel from 1932 to 1950 they went out of phase thereafter when grouse declined in the early 1950's (Dorney and Kabat, 1960) as pheasants were increasing, and then recovered some lost ground in the late 1950's when pheasants began to decline.

In view of this variability in phase and amplitude, we do not feel that the pheasant fulfills well enough the cyclic criteria. Pheasant fluctuations do go through a recurring sequence within a limited range, and we feel that the term "oscillation" is adequate.

Perhaps the most significant unanswered question in pheasant fluctuations—and probably in other "oscillating" or "cyclic" species as well—is the question of population momentum. It remains unexplained why populations, such as those in Figure 66 thrust beyond their means for two or more successive years. According to Figures 64 and 65, r values should approximate zero when a population reaches its mean. Occasional random increases or decreases are to be expected from extreme weather deviations, but these should occur in both directions and be quickly corrected by density-dependent adjustments in r.

At least the lower three populations in Figure 66 seem to increase steadily through a period of 5-8 years, and carry well past the mean in the process, increasing density pressure notwithstanding. They also decline steadily for 3-5 years, and carry past the mean despite the tendency for r to become positive once the density has fallen below the mean (Figs. 64 and 65).

The populations seem to gain some advantage during the increase period which enables them to offset the r-depressing effect of increasing density. They may likewise gain some disadvantage during the decline which prevents them from making use of the r-increasing effect of decreasing density. These tendencies seem to carry through several generations before they are finally overridden by density effect.

Errington (1945a, 1954) termed the decline period a "depression phase", and intimated that some meteorological or extramundane influence may be operative. These views were prompted by a degree of synchrony in fluctuations over large geographic areas which, he felt, must be due to some large-scale synchronizing influence such as weather.

There has been some synchrony in midwestern pheasant fluctuations and we observed the influence of spring temperature over large regions. But population changes have not been entirely uniform from the Great Plains to Ohio. Different aspects of weather probably are important in different areas, and the degree of synchrony is substantially less than complete.

TABLE 34

Ranges of Variation in the Fluctuations of South Dakota, Michigan, Wisconsin, and Indiana Populations Shown in Figure 66

State	Highest Density ÷ Lowest	Percentage Highest Density Exceeds Mean	Percentage Lowest Density is Below Mean
South Dakota	2.7	60	38
Michigan	3.1	40	55
Wisconsin	2.8	72	37
Indiana	2.3	59	31
Mean	2.7	58	40

However, population momentum seems to be characteristic of many areas and species, although they may not be in phase with each other. Hence, we are more inclined to look for something intrinsic within each population rather than a regionally operative, extrinsic influence.

Chitty (1957) observed what may have been a form of population momentum in European voles. Mortality in a declining population continued into the low period when voles were scarce. This mortality appeared to have been pathological, and Chitty suggested oscillatory shifts in the genetic make-up of the population which alternated between susceptible and resistant types.

One idea that bears investigation is possible nongenetic transmission of stress-induced physiological weakness from adults to young. This would reach its maximum as a population peaked, and carry through two or three generations with diminishing effect during the decline period. Chitty (1952) found a reduction in viability of young voles following density stresses in the adults. Christian and Lemunyan (1957) observed impairment of reproductive and growth rates through the F_2 generation of white mice from crowding the parental generation prior to breeding and production of the F_1. Jenkins (1961) found increased mortality of young European partridges in populations experiencing high prebreeding strife.

The transmission might occur during the embryonic life of mammals and birds. There are several published instances of young birds being adversely affected by factors influencing the parents, the effect apparently being transmitted through the egg. We previously discussed the probable effect of the hen's condition on the quality of the eggs and viability of pheasant chicks. Egg production, fertility, and hatchability in penned bobwhite are influenced by the amount of calcium and phosphorus in the breeding-season ration, one year previously, of the preceding generation (DeWitt, Nestler and Derby, 1949). The quality of eggs and viability of young European grouse appear to be affected by the spring diet of adult females (Siivonen, 1957). However, it has not been shown that such influences can be transmitted through 3-4 generations as may be required by population momentum in those species which require 3-5 years to increase or decrease.

Determination of Mean Density

The question of how and why a population balances itself at any given mean density within an area and why mean densities vary between areas is quite distinct from that of population balance, although the two are related. Failure to make this distinction has led to much of the current theoretical dispute in population ecology. In many cases, these arguments are basically semantic. The terms "control, regulate, and limit" connote flexible adjustment and fixing of limits which apply better to the phenomenon of balance. We have avoided their use in this chapter to enhance the distinction between balance and density determination.

The problem of explaining the mean density of pheasants within an area is complex and speculative because the available evidence is mostly circumstantial. At the same time, it is of greatest practical importance to management because our management objective is the maintenance and, if possible, increase of this level.

Mechanics of Density Variations Between Areas

Role of Density Dependence

We have seen that the mean of **r** approaches zero in all areas examined except Pelee Island. Attainment of this point occurs at different densities in different areas. We combined three of the regressions in Figures 64 and 65 into a single graph (Fig. 68) which places the lines for the different areas along the $\mathbf{r} = 0$ line, but spaced out at their respective densities.

We used the logarithm of kill to compare these densities because the numerical range between high and low points varies tremendously between the areas represented (48,000 in Indiana, 2,500,000 in South Dakota). However, the magnitude of difference between the highs and lows is quite similar (2.3 and 2.7, respectively, in Table 34). This semilogarithmic plot also permits a straight-line plot to a series of points varying exponentially as the curved lines in Figures 64 and 65 implied of these data.

While kill estimates or any other index of total numbers are not an entirely satisfactory basis for comparing densities between states, midwestern biologists generally agree that average pheasant densities in these states vary in the order shown. Minnesota and Michigan densities are intermediate between those of Wisconsin and South Dakota. They are not included in Figure 68, but their lines lay between those of Wisconsin and South Dakota and roughly parallel to them.

Extrapolation of the lines in Figure 68 suggests that the **r** values at low densities, such as those that existed when the populations were first getting started following introduction, are much higher than the contemporary values we observe during fluctuations within the range characteristic of each area.

As populations increase following introduction into favorable environments, their **r** values decrease progressively due to density-dependent action (Figs. 64, 65, 68), presumably the stress effects of intra-specific intolerance on reproductive rate and possibly mortality rate. This increase continues until **r** is reduced to zero, and populations are balanced.

Hence, the effect of density dependence is to bring **r** to zero from whatever value it may have had at introduction. This effect is a continuous one, present at all densities.

The degree of influence of the density-dependent action is expressed in the slope of the lines in Figure 68. Presumably this slope is a function of how strongly the population reacts to increases in its own density, and could be a species characteristic. That the slopes representing the three populations in Figure 68 are roughly similar suggests that their quantitative response is approximately the same to a given exponential increment to their numbers. If one of these populations were genetically different from the others in its behavior so that it were more intra-specifically intolerant, the slope would perhaps be steeper. It would then balance itself at a lower density than the other, more tolerant populations even though they all started at the same initial **r** value. But apparently these populations respond similarly to the same increments of growth, and hence their *differences* in mean density do not appear to be a function of their behavioral characteristics and consequent density-dependent action.

Role of Density Independence

The mean **r** values of the populations represented in Figure 68 are the same at their respective balancing densities: approximately zero. The significant way in which their characteristics differ is in the magnitude of **r** at very low densities such as those at the time of introduction. Areas which today have the highest mean densities have the highest low-density **r** values. Herein would seem to lie the key to explaining the differences in mean density between areas. We postulate the following interpretation.

Where pheasants are successfully introduced into an area, the environment obviously must be favorable enough to permit reproduction to exceed mortality (**r** must be positive). If this were not the case, the introductions obviously would fade away and never gain a foot-hold.

Where **r** is positive the population increases with a rate that is determined by the magnitude of **r**. Populations initially increased fastest in those areas which today have the highest densities (Fig. 68).

Although some authors have implied an increase rate following introduction that approached the biotic potential of the pheasant, there are few actual cases where this appears to have occurred. On Protection Island (Einarsen, 1945) fall-

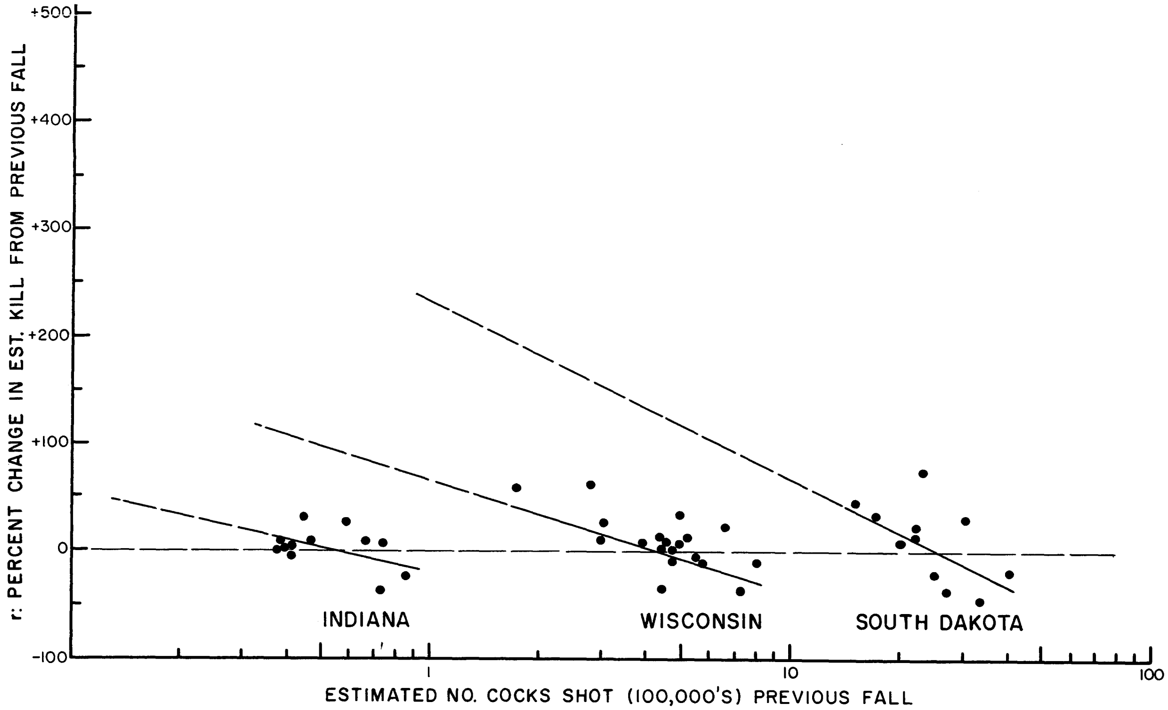


Figure 68. Correlation between the logarithm of breeding population density, as represented by population indices of previous autumns, and *r*, the percentage change between successive years, in Indiana, Wisconsin, and South Dakota. The data are the same as those used in Figures 64 and 65. The lines were fit by the method of least squares.

to-fall **r** values reached 326 percent in one year (1938-39), and were less than 200 in all other years reported. Pelee Island pheasants (Stokes, 1954:7) may have increased from 36 birds in 1927 to about 50,000 by 1934. This could have occurred with an annual increase rate of 150 percent. In some of the Plains States, notably South Dakota, populations increased very fast following introduction (Kimball *et al.,* 1956; Mohler, 1959). Extrapolation of the South Dakota line in Figure 68 suggests a very high low-density **r** value, but still somewhat short of the species potential. In other midwestern states, the evidence does not necessarily justify concluding that they increased at anywhere near the biotic potential.

Schorger (1947) summarized pheasant releases prior to 1900 in Wisconsin. If wild populations totaled 1,000 birds by 1900, then a mean increase rate of 15-20 percent per year could have built up populations equal to those of 1942 without further stocking. Since many thousands of birds were stocked during the period through state and private effort, the peak densities of 1942 could have occurred with a population in 1900 of 1,000 birds, and a mean annual increase rate of 15-16 percent.

Einarsen (1950) concluded: "Pheasant increases revealed in these studies do not indicate phenomenal hatches and large numbers of surviving young. The records from all island reproductive studies for a 13-year period show about 400 percent increase to be a high level of yield. In most states it is much lower. These records are supported by numerous examples in pheasant habitats throughout the United States. Hunters in California and South Dakota, both good pheasant states, waited from 20 to 40 years after stocking before their habitats could be hunted regularly for pheasants. Large increases may occur but they are not annual recurrences."

The basic point is that **r** values are high at low densities. But in almost any environment there are limiting factors which operate on a population at any density and make **r**, even though high, only a fraction of the biotic potential. These low-density **r** values vary between areas and determine the rate at which a newly introduced population increases.

Once it begins to increase, it immediately begins to incur density pressure. The **r**-depressing effect of population growth is continuous, and as observed in the last chapter, a given exponential increase in population reduces **r** by the same amount, regardless of the density. Consequently, the density at which balance occurs depends on the initial **r** value at introduction, and on the disparity between this value and zero which the density effect must close. Where a large disparity exists between initial **r** and zero (e.g. South Dakota), density must increase a great deal to apply enough pressure on **r** to reduce it to zero (Fig. 68). Where initial **r** is small (e.g. Indiana), a slight density increase will close the space to zero, and balance the population. Herein lies the basic population mechanism of density determination: an interaction between the influence of density-dependent factors and whatever influences determine the magnitude of **r** at the beginning of a population's growth.

Hence the major unanswered question remaining is what influences determine the magnitude of low-density **r**. The evidence on this is circumstantial but we postulate that it is density-independent factors. We have seen evidence in previous chapters that weather, haymowing, perhaps predation, and hen shooting may affect population density. Since some of these influences seem to operate largely independent of density—i.e. they operate as severely at very low densities as they do at high densities—they are probably responsible for the differences in low-density **r** values in the populations represented in Figure 68.

Unfortunately we do not know the ecology of these populations well enough to have measures of the influence of each factor with which we could test this hypothesis fully. But hay-mowing loss probably is more severe in Wisconsin's dairy farming pattern than in South Dakota's cash crop economy. We have seen that illegal hen loss may be twice as high in Wisconsin as in South Dakota. Wisconsin's greater woodland acreage could produce higher predator populations than South Dakota's. And with her higher human populations and attendant disturbances and accidents, Wisconsin may present a less hospitable environment to the pheasant in other respects than does South Dakota.

What is involved in the Indiana environment is less understood. With heavier hunting pressure, illegal hen kill may be more severe. Where predation, agriculture, and other factors not considered in this report, fit into the scheme are not known.

Nevertheless, the similarity of density responses between these areas make it seem unlikely that density dependence is the factor underlying the difference between their pheasant densities. Density independence is the only remaining possibility.

According to our hypothesis, if a density-independent limiting factor were removed from a balanced population in a given area, **r** would become positive and the population would increase much as now occurs in a year with above-average prenesting temperatures. As it increases, density dependence would progressively close the space between the new **r** and zero, and balance would once again be restored, but at a new, higher mean density. If a density-independent limiting factor were added, **r** would become negative and the population would decline, much as now occurs in those areas where more than 20 percent of the hens are shot in legalized hen seasons. As it declined, density pressure would ease, and **r** would gradually increase to zero and a new, lower balancing density. Thus, if density-independent factors are added or removed, the population decreases or increases, but it ultimately is leveled off by density dependence at some lower or higher mean density.

We sometimes assume that an area with high densities has a higher reproductive and/or survival rate than an area with low densities. Reproductive and survival rates could be identical in two areas of greatly different densities. These rates do appear to be higher in an area of typically high mean densities when their numbers are below balancing levels. But once they are balanced, density dependence makes up the difference. Furthermore, if the reproductive rate in one balanced area were higher than in another, then it would follow that the former area also had a lower survival rate.

In summary, we suggest the following generalizations about density determination in midwestern pheasant populations: (1) Balance is achieved by density dependence; (2) differences in mean density between areas may be a function of differences in density-independent factors; (3) the mean density achieved in any given area is a function of the combined action of both types of factors, both playing an essential part and neither being solely responsible. And herein, we once again emphasize the distinction between the achievement of balance and the determination of mean density.

These ideas suggest that pheasant populations are not wholly self-limiting, and that population balance can occur at any density, depending on the limiting factors present.

Related Concepts of Other Authors

Our views on the pheasant appear to be essentially similar to the generalizations of A. J. Nicholson. He has been most preoccupied with balance, which, he concluded results from density-dependent influence, primarily competition. His occasional use of "determination of density" appears to be synonymous with balance, and not similar to our use of the term. However, his recognition that density-independent factors play a part in the density at which balance occurs seems clear in the following quotations:

"Factors, such as climate and most kinds of animal behavior, whose actions are uninfluenced by the densities of animals, cannot themselves determine population densities, but they may have an important influence on the values at which competition maintains these densities . . ." (Nicholson, 1933).

"Compensatory reaction of the kind revealed by these experiments enables populations of the same species to maintain themselves under conditions which vary greatly in space and time, at densities determined by the prevailing conditions and the properties of the animals . . . Although factors which do not change in intensity with density may profoundly influence the densities at which the reactive factors adjust the populations . . ." (Nicholson, 1954).

"The quality of food or the temperature prevailing, however, may have an important effect upon the level at which a population is adjusted by governing factors . . ." (Nicholson, 1954a).

Similar Concepts in Other Species

Nice (1937:206-207) said of the song sparrow: "As I look at it, territory . . . ensures that there will be no crowding, and no over population . . . But climate and many other factors may keep the numbers of the species in a region so low, that territorial behavior has no chance to limit population . . . There are so many possibilities of unfavorable factors—major 'plagues' of droughts, floods, and severe winters, and local 'plagues' such as man on Interpont—that the birds are reduced at irregular intervals."

Solomon (1955) stated: "Some insects . . . seem to spend most of the time recovering, by annual increases, from occasional climatic setbacks; density-related influences may play an important part only in the event of very high density being reached before the next cataclysm . . . Such populations are at most time not being regulated, in the sense of being controlled by density-related processes; they are increasing, decreasing or fluctuating chiefly according to the physical conditions and sometimes the state of their food, within limits of density where (at least for the time) the density-related regulatory processes have little effect."

And according to Milne (1957): "A *perfectly* density-dependent factor or process will control increase of numbers endlessly. There is only one such in Nature for any species and that is competition between its own individuals . . . But in Nature, most species, in most places for most of the time, are held fluctuating at population levels where this kind of competition is relatively insignificant. That is, the ultimate controlling factor for increase is seldom evoked. The suggestion therefore must be that control of increase is, for most of the time if not almost endlessly, a matter of the combined action of factors which are density-independent and factors which are imperfectly density-dependent, *each supplying the lack of the other.*"

The basic similarity between these three views and our hypothesis lies in the recognition that density-independent factors play a part in density determination through much or most of the history of a species. The major differences appear to be two-fold. (1) These authors seem to imply that density dependence only operates at the upper extremes of density and alone determines the upper limit to which a population can increase. To us it appears to operate at all levels in the pheasant, and it determines the upper level of density only in combination with density-independent factors. (2) The implication seems to be present in these views that these species exist most of the time below their balancing densities (at least without any density-dependent regulation), and under the influence of density-independent factors. But if their long-term population trends are stable, they must be in balance which can only be effected by density dependence, as Cole (1948), Ricker (1954), and Lack (1954) have pointed out, and as we have seen for the pheasant. Were they not in balance, long-term population trend would be up or down.

We also strongly concur with Milne's (1957) incisive views which have dispelled certain assumptions that have long been accepted without critical scrutiny. The first is that some density-independent factors, particularly weather, while acting independent of density, have a *varying* rather than constant effect on a population. The second is that such factors as predation and parasitism, if density dependent at all, must be imperfectly so. They, and their effects on a population, are independently influenced by factors in their environment which prevent their continuous and sensitive density-dependent adjustment to their prey or host. Intra-specific competition remains the only factor that can adjust solely to population density. This is the only factor we have observed in mid-western pheasants which can definitely be shown to have density-dependent action.

We agree with Andrewartha and Birch (1954) that physical influences enter into density determination, and with their protest against the assumptions of some authors that density dependence alone determines density. However, we do not agree with their denial of the validity of the concept of balance, and of the reality of and distinction between density-dependent and density-independent factors.

Contrasting Views

Lack (1954) began his treatise with a discussion of population stability or, in essence, balance. He concluded that this can only occur through the action of density dependence, with which we concur for the pheasant. But he seems not to have made the distinction between balance and density determination. The implication seems to grow in his analysis that the two are synonymous, and the latter therefore is due to one or more of three presumably density-dependent factors: food shortage, predation, and disease. He seems to have conceded little possibility that intra-specific competition or strife, other than for food, could carry much weight. Hence our views differ in the distinction between the two phenomena in the possible importance of intra-specific strife, and in the role of density independence. Lack also asserted that any density-dependent action must operate on the mortality rate, and discounted any influence on the reproductive rate, something which does not appear to be true for the pheasant.

Errington's concept of density determination and carrying capacity, and similar views held by many American wildlife specialists, are similar to Lack's from the standpoint that both fail to distinguish between balance and density determination, and consequently imply that both are achieved by density dependence. Lack stressed the importance of food shortage, predation, and disease. Errington, as previously discussed, has stressed the interaction between social intolerance and the amount of cover available, or of territoriality, and concluded that populations are largely self limiting: "Self limitation is about what strong territoriality adds up to in population dynamics . . . Compared with the basic role of territoriality in the population of many higher vertebrates, predation enters as a secondary phenomenon and as one having, in more instances than are usually recognized slight if any real depressive influence on prey populations . . . Instead of every agency of mortality each depressing the end product in proportion to the number of animals it kills, we have a lot of nullification of what we conventionally regard as limiting factors. . . ." (Errington, 1956).

We agree there is compensation, or density dependence, in pheasants. In terms of the Errington concept, intercompensating limiting factors adjust to changes in mortality in order to remove, but not exceed, the annual surplus. The compensation we have found in pheasants does not adjust to variations in mortality, but to differences in population density (Figs. 64, 65, 67 and 68). Density must increase or decrease before the level of social strife is affected, and reproductive rate changed accordingly. The function of compensation is not to hold the mortality constant, but to rebalance a population at a higher or lower density following disturbance of the previous reproduction-mortality balance.

The annual surplus concept discussed earlier implies no correlation between fall densities, which vary according to the vicissitudes of the breeding season, and spring densities which are fairly constant because of the threshold of security or winter-bottleneck effect. However, we found that fall densities are correlated with densities of the following spring. Hence there is no clear-cut winter bottleneck, and no annual surplus. It is true that the pheasant has a high biotic potential, and only a small part of it is attained. If all of this disparity were density dependent—where what Milne (1957) termed perfectly density dependent—it would provide a tremendously flexible compensatory system with which populations could make up for all but the most catastrophic losses.

But pheasants do not come close to attaining their biotic potential. Regardless of density, eggs and young chicks are destroyed by mowers, weather, predators, accidents and perhaps by disease, lethal genes, and deficiencies in nutrition. They suffer what McAtee (1936) termed "... sweeping indiscriminate destruction of immature forms ...." Hens are killed by most of the above factors as well as by stress and hunters. Perhaps no more than one-half of the hens alive in spring succeed in rearing a brood by fall, and probably no more than 20 percent of the eggs laid in incubated nests end up as young birds in fall. Most of this loss occurs in summer when food and cover are at their annual high. Further density-independent losses of chicks and hens occur between fall and spring.

The space remaining for compensatory influence is not great. Where density-independent action is so great that it erases most of the biotic potential, only limited compensatory change is needed to bring **r** to zero. This can be brought about through limited alteration in **r** from intra-specific intolerance. We do not need to visualize density determination as occurring through the full utilization of some necessary resource such as food, cover, or space; or through filling up the available niches with annual production constituting a large surplus that inevitably disappears, almost irrespective of the variety and number of intercompensating factors. In short, pheasant populations do not appear to be wholly self-limiting. Their densities do seem to be influenced by what we conventionally regard as limiting factors.

If the concept of carrying capacity is to be used in pheasants, it must simply imply the mean level at which $\mathbf{r} = 0$. A given area apparently can sustain different densities of pheasants depending on the number and action of limiting factors whether they are hay mowers, predators, or hen shooters.

Summary

Population balance is variation within a limited range around a long-term mean. Neither range nor mean increases or decreases progressively. Long-term mean of $\mathbf{r} = 0$. The density-dependent correlation between **r** and density, presumably due to intra-specific intolerance, is responsible for balance. The value of **r** becomes negative and population decreases when density is above average; **r** becomes positive and population increases when density is below average, irrespective of the comparative density at which this occurs. Actually, balance is somewhat of a theoretical concept because it necessitates a constant environment. However, the tendency toward balance, and the approximate attainment of it, can be demonstrated in the pheasant.

Population fluctuations are induced by annual variations in the value of **r**. Weather, in terms of prenesting temperatures, is probably the most common causal agent in Wisconsin. The tendency for density dependence to restore a population to its mean prevents the full degree of randomness that would result from a population solely under the influence of weather, or any other density-independent factor, and induces a degree of oscillation into the population. Pheasant fluctuations are oscillatory with a limited degree of constancy in amplitude and irregularity of phase which, we feel, disqualifies them from the term "cycle".

When the **r**-density regressions for several midwestern states are evaluated, the lines suggest that the low-density **r** value for each area is correlated with its ultimate balancing density. The low-density **r** value may be a function of its density-independent pressure. As a population increases following introduction, **r** decreases progressively with increasing pressure from density. The level at which it eventually balances itself seems to depend on its initial **r** value, and the space between this value and zero which density dependence must close.

We postulate: (1) Balance is a function of density dependence; (2) differences in mean density between areas appear to result from differences in density-independent factors; and (3) mean density achieved in any given area is a function of the combined action of both types of factors.

Our views on pheasant population mechanics are most similar to those of A. J. Nicholson, somewhat similar to those of M. M. Nice, H. E. Solomon, A. Milne, and Andrewartha and Birch. They differ in some respects from those of David Lack, and the concepts which are basically derived from the views of Paul Errington.

PART IV—MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Our views on population balance and determination of mean density have practical implications for pheasant management. Leopold (1933:44) has called game management "... the purposeful manipulation of factors ...." If pheasant populations were largely self limiting, and annual surpluses disappeared almost irrespective of the presence or absence of what he has called "decimating factors", there would be little hope for this approach to pheasant management. However, this approach appears to be theoretically sound on the basis of evidence so far examined.

In Part IV we discuss utilization of the pheasant crop and management of the habitat. Consideration is given to long-range prospects for Wisconsin pheasant hunting.

CHAPTER XVII. HARVESTING THE COCKS

Biological Basis for Shooting Cocks

The principles involved in this subject have been discussed by other workers, particularly Allen (1942a, 1947), Bach (1948), and Dale (1951, 1952). We review them briefly to provide a perspective for developing a sound pheasant management program in Wisconsin.

At hatching, cocks and hens occur in about equal numbers. If cocks are not shot differentially, this balanced sex ratio persists in a pheasant population. In dense, unshot populations, cocks may outnumber hens suggesting that natural losses are more severe in hens than in cocks. This may possibly result from the greater stress loss of hens (Wagner, 1957).

The pheasant is polygamous. One cock will breed a dozen or more hens. Not only are extra cocks unnecessary for breeding, but in unshot or lightly shot areas where spring sex ratios are equal or only slightly distorted, some cocks do not succeed in establishing territories or in attracting hens, and show submissive, nonbreeding behavior.

Thus, a substantial percentage of the cocks can be taken annually through hunting without impairing the breeding productivity of the hens. Each year the hatch restores the population sex ratio to near equality because the population is predominantly young birds. If the surplus cocks which are not needed for breeding are not shot, they are lost to natural causes and hence are wasted.

It is this polygamous nature of the bird and the annual production of a new crop of young males that form the biological basis for shooting cocks. As Hickey (1955a) pointed out, this is quite different from the basis on which other small game species are harvested. In the latter where both sexes are taken, the basis for harvest must lie in the compensatory response of the populations. Such responses involve self-induced reduction in other sources of mortality and/or increased reproductive rates that compensate for the hunting kill and maintain the population.

With the cocks-only harvest of pheasants, there need be no compensation. The hens and a remnant portion of cocks are the breeders, and the harvest of most of the cocks has no effect on the productivity of the breeding population. As long as the hens are protected, the population can maintain itself and produce an annual crop of young, harvestable males.

In no other small game species do we utilize the annual crop more fully than with the pheasant where there is moderate to heavy hunting pressure and where the harvest may range from 60 to 90 percent of the cocks. The highly distorted cock age ratios, which in Wisconsin annually range between 90 and 95 percent young of the year, attest to the high utilization of each year's crop, and to the extremely transitory nature of most of the male segment of the population.

The majority of males are present in the population only about 4 months and never experience a breeding season. They hatch in June, barely have time to fully develop, and are removed from the population during the hunting season in October. During the remaining 8 months the population is composed largely of hens.

Desirable Degree of Harvest

Ideally, the desirable harvest should take just enough cocks so the remaining portion can stand any reduction through winter loss and still be adequate to breed the hens in spring. If the remaining cocks exceed this number, some that could have gone to the hunter will be lost through natural mortality. If any hens go unbred, the reproductive efficiency of the population has been impaired and the cock population overshot.

Theoretically cocks could be overshot in any area. It could probably occur in one or two somewhat related ways. The first way, perhaps a greater possibility in dense populations, is simply that the cocks might be shot down so low that the sheer number of remaining hens would be too great to be bred. As other authors have pointed out, there is no evidence that this has ever occurred. One cock can breed 50 hens in captivity without loss of fertility (Shick, 1947). A hen can continue to lay fertile eggs for 3 weeks after a single copulation (Twining, Hjersman, and MacGregor, 1948)—ample time for completion of a clutch.

Under natural conditions, sex ratios as high as 50 hens per cock over any sizeable area have never been observed. Buss (1946:54) recorded 22 hens per cock in Fond du Lac County in the winter of 1941-42; but in other first-rate pheasant counties, sex ratios in this and the previous winter more typically ranged between 6:1 and 13:1. During the period 1948-57, winter sex ratios in the best Wisconsin pheasant counties continued to fall in this general range (Table 7).

Reproductive rates in Wisconsin areas with the most distorted sex ratios appear to be as high as those in the less heavily shot areas. The percentages of hens with young in Green County, were as high as or higher than in three unshot areas (Table 13). The percentage of hens with young in the more heavily hunted areas in the state (better pheasant areas) compares favorably with those in the more lightly hunted areas (Table 14). Thus hens apparently are not going unbred in the most heavily shot areas in Wisconsin.

The highest winter sex ratios reported in other states are of the same general magnitude as the highest in Wisconsin. Pelee Island ratios typically range from 7:1 to 10:1 (Stokes, 1952). Ratios on Michigan's Prairie Farm were about 10:1 in the early 1940's (Shick, 1952:28). In California's Sacramento Valley, postseason sex ratios have occasionally reached 20:1, but more typically range from 6:1 to 10:1 (Harper, Hart and Shaffer, 1951). These states, too, report normal reproduction in areas with sex ratios of this magnitude.

Most other states and many counties in Wisconsin have substantially lower winter sex ratios. Hence, these areas could withstand a heavier kill and still have ratios no higher than the most distorted ones reported above.

A second way in which cocks conceivably could be overshot was suggested by Hickey (1955:349). His suggestion, proposed mainly for marginal pheasant range, breaks down into two possibilities. (1) Pheasants are sparsely distributed in disjointed pockets of habitat in marginal areas. Cocks could conceivably be shot out locally to the point where hens might not be able to find a mate in spring within the radius of their hearing and mobility. (2) Cocks could be so reduced locally that the remaining hens, in the course of grouping into harems around the few remaining cocks, might form densities "... in excess of the locally available and safe nesting niches ...."

The chance that these possibilities ever become realities in marginal range seems remote for several reasons. Marginal range gets less hunting pressure, and sustains a lower percentage kill than good range. Hence, the number of cocks per 100 hens is greater in marginal than good range. Furthermore, those areas in which the habitat exists in small disjointed pockets are so marginal, and carry so few birds that their numbers are inconsequential in the statewide picture; and pheasant hunting pressure is extremely light. Marginal range in Wisconsin has large acreages of woodland. Heavy kill in this type of cover seems unlikely, even if some degree of heavy hunting pressure were available.

However, the situations Hickey proposed might become a reality in good pheasant range. Although there is no indication that it is occurring under present hunting conditions, it is conceivable that at some future date cocks could either be shot out locally to the point where hens would not find them, or else the number of cocks remaining could be so low as to create unnatural crowding of large, residual hen populations.

Degree of Harvest in Wisconsin

Residual Cock Populations in Spring

We have not made actual determinations of spring cock densities over extensive areas of the state. However, results of the regular crowing-count transects (Fig. 13), along with actual determinations on a few limited areas, permit approximations of spring cock numbers.

Robertson (1958:39) described results of standardized crowing counts in Illinois on areas of known density. Two separate studies indicated that an average of 1 call per 2-minute count was equivalent to populations of 0.8 and 1.25 cocks per section. In the spring of 1959, John M. Gates (unpubl.) determined that a 7-section area in Fond du Lac County, Wisconsin, had a total of 36 cocks, or an average density of 5 cocks per section. Standardized crowing-count transects in the area produced counts of about 5 calls per 2-minute stop. These combined results suggest that 1 call per 2-minute stop is equivalent to approximately 1 cock per section.

The 5-year average number of calls per 2-minute stop for 33 transects run between 1953 and 1957 are shown in Figure 69 along with the major pheasant population density subdivisions. During these years when hunting seasons averaged about 4 weeks in length, spring cock densities varied from 5.8 to 9.3 per square mile in the best pheasant range and averaged 7.1. Spring densities varied from 2.7 to 5.4 cocks per section in the "Good" range and averaged 4.0. In the "Fair-Poor" range, spring cock densities varied from 0.2 to 3.2 per section, and averaged 1.6.

The remnant cock populations left in the better pheasant areas are larger than those left in the poorer areas even though the better areas have the heaviest hunting pressure and highest percentage of cock harvest. The very low values for the

"Fair-Poor" densities and those at the lower end of the "Good" scale probably do not reflect uniform, average densities over large blocks of range.

By comparison, other heavily hunted north central and eastern states show higher spring cock densities. Randall (1940) reported 10.3 cocks per section on his Pennsylvania area. Leedy and Hicks (1945) reported an average removal by hunting in Ohio of 74 percent of the cocks (p. 82) and a 1937 kill in Wood County of 89 cocks per square mile (p. 71). This suggests a posthunting remnant of about 30 per section. With about 8 percent further mortality during the 4 ensuing months (p. 82), the implied April cock density is roughly 27-28 cocks per section. Shick (1952:31) reported average spring cock densities for the Prairie Farm between 1940 and 1942 at about 11.5 cocks per section. Baskett (1947) observed spring densities ranging from 15 to 42 cocks per section in three seasons on the Winnebago County, Iowa study area.

Since World War II, increased hunting pressure has accounted for a higher cock harvest, but reported spring cock densities in other states still exceed those in Wisconsin. Stokes (1954:92) reported 370 cocks on Pelee Island in the spring of 1948, a density of about 23.5 per section. Spring cock densities for 13 Illinois areas from 1946 to 1951 varied from 3.4 to 28.4 cocks per section and averaged 10.6 (Robertson, 1958:38).

Factors Affecting Degree of Harvest

There appear to be several reasons for the thorough cock harvest in Wisconsin. First, Wisconsin pheasant range is limited and the number of pheasant hunters — 250,000 to 300,000 — is large in comparison with many states.

A second reason lies in the nature of the hunting regulations. The seasons are usually long, mostly ranging from 25 to 30 days, and the last 2 weeks of a 4-week season contribute materially to the kill. Sunday hunting is permitted and it provides a substantial kill. Hunting hours are long, usually coinciding with the early morning to evening schedule for waterfowl shooting. The season usually opens on a Saturday noon which permits concentration of maximum hunting pressure at the opening.

Other reasons are more speculative. One possibility is the date of season opening, consequent average age of the birds, and possible variations in vulnerability of birds to hunting. Wisconsin seasons open around mid-October. Because states farther south typically open 1-3 weeks later, and because nesting begins earlier in these states, the average age of their birds is greater than ours. Vulnerability of cocks to hunting seems to decrease with age and this may influence the differences in degree of harvest.

The nature of the habitat may also have a bearing on the ease with which cocks are taken. In most years, there is more dense cover provided by the Wisconsin farming pattern than by the cash-crop farming of other midwestern pheasant states. At first glance, it might seem that Wisconsin birds would be less vulnerable with their large acreage of protective cover. However, the reverse may be true. Where birds are given dense ground cover, they seem to be more prone to hide and hence can be approached by hunters and their dogs. Where ground cover is sparse, birds are more likely to run, and cannot be caught and flushed as easily. This may be especially true of prairie areas which have large corn or wheat fields where the birds can run unimpeded down rows up to a quarter or half mile in length.

From the magnitude of the residual spring populations, it appears that our pheasant resource is now being adequately utilized with seasons 4-5 weeks in length. Spring densities of 3-7 cocks per section must be approaching the lower limit desirable when the accompanying spring hen densities approximate 15-75 per section. These hens are already strongly grouped under the present situation, and if the cock densities were reduced to lower levels, it would mean even more extreme and artificial crowding. While there is no evidence to suggest that extreme grouping of large numbers of hens around a few cocks produces more density pressure than the same number of hens better distributed around more cocks, the possibility may exist. Even if it were possible to take 1-3 additional cocks per square mile in Wisconsin's primary pheasant range, the net gain would increase the statewide kill only 1-2 percent. This minor increase hardly seems worth the risks that could be involved in further reduction of the cock population.

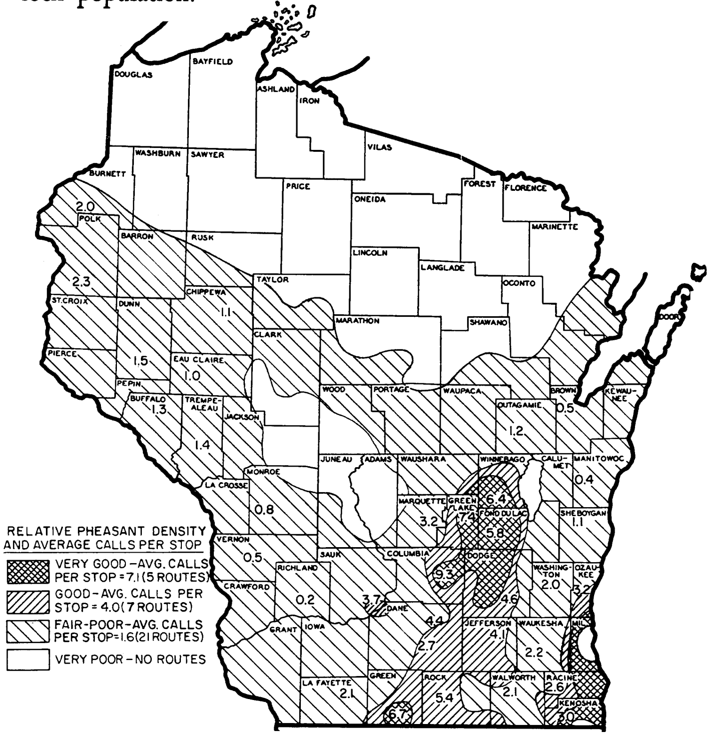


Figure 69. Five-year average number of calls per 2-minute transect stop, 1953-57 inclusive, and estimated pheasant population density (see Fig. 1, for derivation of pheasant-density classes). Each value is placed on the map in the location at which the transect is situated (see Fig. 13 for location of routes and details of technique), and represents the mean calls per 2-minute stop for the entire transect during the 1953-57 period.

Achieving Desirable Harvest Through Proper Regulations

Length of Hunting Season

We previously found a curvilinear relationship between season length and percentage of cocks shot (Fig. 18). The percentage of cocks shot increased rapidly to about 75-80 with season lengths of 30 days. The trend leveled off at this point, and extending seasons beyond 30 days increases the percentage of cocks harvested to a very limited degree. If we are to consistently harvest 75-80 percent of the cocks, as seems desirable when populations are near or above average, we should have seasons of 4-5 weeks in length.

A further consideration in length of season involves the use of hunting dogs. Few sportsmen would keep dogs for one or two weeks a year. The longer seasons would make it more worthwhile for dog owners and would result in better quality hunting.

The relationship between season length and percentage harvest may vary with pheasant population density (Fig. 19). A greater percentage of cocks can be harvested when populations are high than when low with the same length of season. Hence, a 30-day season during a population low presumably would permit a harvest lower than 75-80 percent.

Throughout our pheasant history seasons have been shortened during pheasant lows more as a precautionary measure than through knowledge of any population effect. Thus we cannot determine to what extent the self-limiting tendencies in pheasant hunting would reduce the take in seasons of 30 days; or whether the postseason residue of cocks would be comparable with those following the more intensive harvest of larger populations. If the residue were comparable, it would be possible to hold season length constant between years thereby simplifying regulations. There may be no biological reason for lengthening and shortening the season every time the population waxes and wanes.

The relationship between hen loss and season length must be considered in selecting optimum season length. Most of the loss occurs in the first 2 weeks of a 4-week season (Table 30). The loss occurring in the last 2 weeks represents somewhat less than 4 percent of the hens alive at the start of the season.

The question arises as to whether or not the season should be shortened when populations are low in order to ease pressure on the hens and allow them to recover more quickly. The fraction of hens saved — ca. 2-3 percent — by shortening from 4 to 2 weeks would make up such a small fraction of the total annual mortality rate that the effect probably would not be observable. At the same time a portion of the cock population would be wasted.

We concluded that the estimated annual shooting loss of 16 percent of our hens may effect some degree of limitation on the populations. Since one-half of this appears to occur in the first week of the hunting season, it does not seem possible to avoid it. Pressure from intra-specific intolerance relaxes when a population is low, **r** becomes positive, and the population recovers even though illegal hen loss continues to occur. Illegal hen loss is only one of the several factors that operate on a population, some of which (e.g. weather and intra-specific intolerance) evidently are more important and will override its effect. Closing the hunting season when the population is down would not ensure immediate recovery and would waste entire annual crops of cocks to natural mortality.

Timing of Hunting Season

Seasons should be set as early as possible to make use of a crop that shrinks daily because of natural mortality. Yet they should not be set until the majority of cocks are fully colored and developed, a condition not attained before they are about 16 weeks of age. The latter consideration precludes a season opening much earlier than mid-October.

An administrative consideration involves the relative timing of the pheasant and deer seasons. It seems desirable to have as little overlap as possible between these two seasons for several reasons. (1) By keeping them discreet we offer a maximum of recreation time. Overlap reduces the total hunting time available to the public. (2) Where the seasons are separate, a maximum amount of hunting pressure can be brought to bear on the pheasants, thereby abetting a thorough harvest. (3) Overlap of the seasons dilutes law enforcement effort which often must be concentrated on one or the other season.

The deer season usually opens around November 15-20. A 4-week pheasant season opening about October 15-20 will not overlap the deer season. One opening about October 20 to 25 will overlap it no more than about the final week when pressure and interest have largely waned.

A public relations consideration also involves timing of the crop harvests, mainly corn and soybeans. We tallied the number of picked and unpicked cornfields in southern Wisconsin each fall from 1950 to 1960. From 1950 to 1954 we recorded fields randomly observed. From 1955 to 1960, a 320-mile transect through Columbia, Dane, Dodge, Green, Jefferson, and Rock Counties was set up specifically for this purpose, and run biweekly between a day or two prior to the opening of pheasant season, and early to mid-December. Only picked and unpicked fields were tallied in order to visualize the timing of this process. Silage corn, cut in September, is not a hunting season consideration.

Corn picking in Wisconsin generally begins in early to mid-October and continues into early winter (Table 35). The timing in different years varies according to the weather during the growing season, and that of the ripening and picking season in the fall.

Preferably, the pheasant season should be set as late in the corn-picking season as possible for two reasons. (1) Many farmers are reluctant to permit hunting in standing corn because they may be picking the fields at this time and there

TABLE 35

Timing of Corn Picking in Southeastern Wisconsin as Shown by Percentage of Fields Picked on Varying Dates

	Percent of Fields More Than One-half Picked*				
YEAR	Mid-Oct.	Oct. 22-23	Nov. 1	Mid-Nov.	Dec. and Later
1950	—	—	—	—	56(41)**
1951	—	—	—	55(353)	89(421)
1952	—	—	90(540)	92(157)	94(100)
1953	31(71)	—	57(61)	92(219)	97(357)
1954	4(27)	—	32(225)	81(209)	—
1955	35(902)	—	78(800)	88(649)	96(531)
1956	17(975)	—	60(905)	93(792)	97(763)
1958	10(922)	—	44(851)	—	—
1959	—	36(974)	—	61(966)	—
1960	—	13(189)	—	—	—
Unweighted mean	19	25	60	80	88

*Cut fields were not included in the samples which are based only on picked and unpicked fields.

**Values in parenthesis are number of fields tallied in each sample.

is an element of danger to themselves; and they fear that hunters will knock down some corn which will be wasted because their mechanical pickers will not get it. (2) Standing corn may hinder a thorough pheasant harvest by providing more cover and dispersing birds, and certainly does so when farmers post unpicked fields to keep hunters out.

Whether or not the actual amount of corn lost through hunter damage is as high as sometimes alleged is questionable. In one small survey, Harold A. Steinke (unpubl.) counted the amount of corn in two randomly selected rows of a cornfield on the Mack Public Hunting Ground, Winnebago County. The field had been hunted very hard during the pheasant season. A number of stalks had been knocked down, but the mechanical picker was able to pick up most of these. After the harvest was complete, Steinke observed that the machine had failed to pick only about 0.2 percent of the corn in these rows.

It is not possible to open the season after most of the corn is picked, and still hold it reasonably early in the fall (Table 35). There will inevitably be some overlap between the hunting and picking seasons, but it seems desirable to delay the pheasant opening as long as possible in order to minimize the overlap. By opening the season between October 20 and 25, a sizeable amount of picking will have taken place. More than one-half of the picking will be completed by a November 1 opening, but this begins to crowd the pheasant season into the deer season.

Soybean harvesting also falls in this same general period. However, this crop in general is a minor one on the southeastern Wisconsin landscape, averaging only about 0.5 percent of all cropland, and exceeding 1 percent in only two counties (Table 36). Since cropland makes up 60-75 percent of the land area in these counties, the actual percentage of area in soybeans obviously is only a minute fraction of 1 percent. However, these problems may be very real in localized areas where soybeans are grown, and they do provide some further reason for delaying the pheasant season as much as is compatible with the other considerations involved.

An opening around October 20 appears to be the best compromise with all the considerations involved. As steps in this direction, the seasons of 1956-61 opened between October 19 and 24 in contrast to the October 13-18 openings of the early 1950's.

Weekend vs. Weekday Openings

Wisconsin pheasant seasons have traditionally opened on Saturdays. Such an opening, in contrast to a weekday opening, has both advantages and disadvantages. Among the advantages, it gives people who work inflexible, weekly schedules an equal chance with all other hunters to pursue from the start a limited and quickly reduced resource. Also, a thorough harvest is probably abetted by concentrating all available pressure at one time.

Another advantage is in the number of weekends of hunting which a season of given length, opening on Saturdays, provides. For example, a 23-day season opening on Saturday includes 4 weekends. A 23-day season opening on Wednesday includes only 3. The added weekend provides more recreation and enables a more thorough harvest through concentration of more total hunting pressure.

We sent postcard questionnaires before the 1954 season to a sample of 959 pheasant hunters who hunted in six southeastern counties (Wagner, 1955). About 87 percent of the hunters responded. Each hunter reported the number of hours hunted and pheasants shot on each day of the season. The 5 weekends constituted 33 percent of the total days in the

TABLE 36

Percentage of County Cropland in Southeastern Wisconsin in Soybeans, 1950-52

County	Percent in Soybeans
Columbia	0.2
Dane	0.3
Dodge	0.9
Fond du Lac	0.2
Green	0.1
Green Lake	0.3
Jefferson	0.4
Kenosha	0.8
Racine	1.3
Rock	1.0
Walworth	0.4
Waukesha	0.5
Winnebago	0.5
Mean	0.5

30-day season, but they sustained 68 percent of the total kill and 73 percent of the total hunting pressure. Except perhaps for a drop in kill on the second day, the total kill and pressure on Saturdays was about equal to those on Sundays (Fig. 70). A 1953 sample on the seasonal distribution of the kill in two southeastern counties revealed that 66 percent of the season kill took place on the 8 weekend days of the 26-day season. Totals for Saturdays and Sundays were again comparable.

The major disadvantage of a weekend opening is that the massing of the entire potential hunting pressure at one time creates the greatest difficulties for landowners, and degrades the sport. Hunting ethics and the quality of hunting decline as hunting pressure increases. With the competitive and confusing effect of large numbers of hunters, long-range shooting, crippling loss, and hen kill are probably magnified.

If hunter numbers continue to increase in the years ahead, and hunting opportunities and areas continue to decrease, these problems will be aggravated. In that event we might need to consider a change to weekday openings. For the present, it seems desirable to continue the Saturday openings.

Daily Shooting Hours

During the 1950's, daily shooting hours generally were from one-half hour before sunrise to one-half hour before sunset. In the interests of simplifying regulations and law enforcement, it seems desirable to make pheasant shooting hours concurrent with those for waterfowl as we have generally done in the past few years (sunrise to sunset).

Daily and Seasonal Bag Limits

The purpose of daily bag limits is to distribute the kill over a period of time and among a maximum number of hunters. The degree to which a daily limit curtails kill depends on the abundance of game and the ease with which hunters are able to fill that limit (Bellrose, 1944). The traditional two-cock daily limit in Wisconsin was settled on subjectively more than through any empirical evidence of the kill distribution effects of different bag limits.

Survey information of recent years sheds some light on the appropriateness of this regulation. Among hunters reporting in a 1958 survey (Besadny, unpubl.), the percentages of daily hunts by individuals that succeeded in bagging two birds were 38, 24, 27, and 24 in the four successive weeks of the season. Since the mean number of man-hours required to bag one bird was 3-5 hours during a typical season while the average hunting trip was less than 6 hours (Wagner, 1955), the probability of any hunter getting three birds in a day would be small.

A one-bird daily bag would seem to offer too little inducement to get hunters to travel 50-100 miles to areas of pheasant abundance. The two-bird daily limit seems well suited for Wisconsin hunting conditions.

Since 1959, the bag limit for the first two or three days of the season has been reduced to one. Population levels decreased in 1959 and the daily limit was reduced to better distribute the kill early in the season and prolong quality hunting. We have no direct way of evaluating the effectiveness of this reduced daily bag limit. Figures from earlier years are of limited value because the pheasant population was higher and undoubtedly a larger percentage of hunters bagged two birds in those years than would have done so during the population low. However, the 1958 survey showed that 43, 36, and 34 percent of the hunters contacted shot two birds on the first, second, and third days of the season, respectively. A one-bird bag on the first three days of the 1958 season would have reduced the kill.

Wisconsin has never had a seasonal bag limit but there are periodic suggestions for such a limit. Its objective would be more equitable distribution of birds among hunters. The limit most often suggested is 10 birds per season.

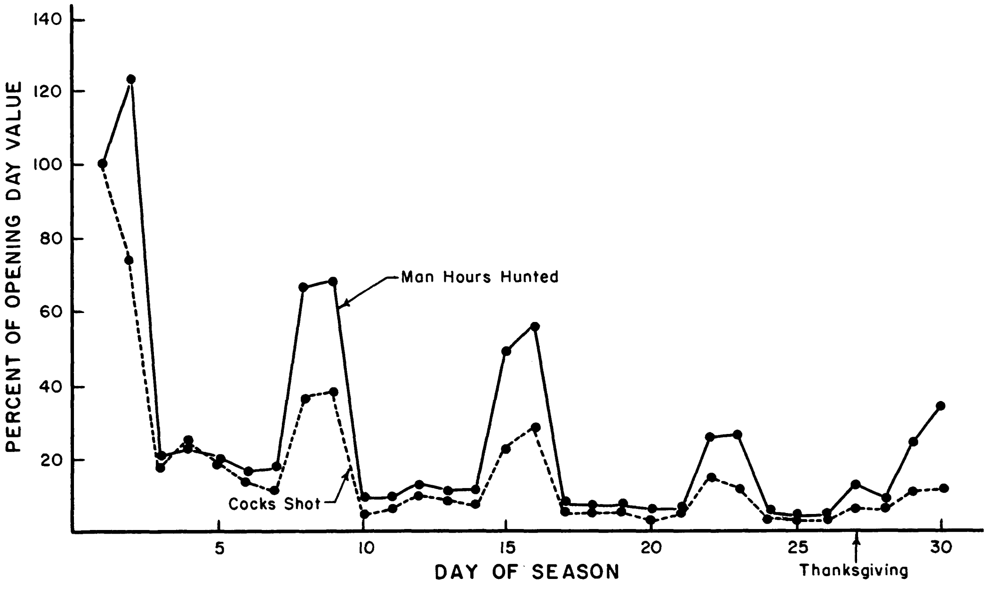


Figure 70. Daily hunting pressure and kill in six southeastern Wisconsin counties, 1954, expressed as percentages of opening day value.

Information from our surveys again sheds some light on the extent to which this objective might be realized. Based on a 10-percent sample of hunters in 1952, 5 percent of the birds shot were those taken by hunters who bagged more than 10 each (D. R. Thompson, unpubl.). Our 1958 survey showed 8 percent of the kill being bagged by hunters who shot in excess of 10 birds each. Hence, a minor percentage of the entire kill would be preserved for wider distribution among hunters. This percentage would decline further with an increase in hunters, and/or a decrease in pheasant populations.

It is doubtful whether or not a 10-bird seasonal limit would ever be realized. Most of the birds taken in excess of 10 per hunter are probably those shot in the latter part of the season by the limited number of more persistent and skilled hunters afield at that time. The small number of birds saved would not be made available to the large rush of hunters afield in the first week or two of the season. The net result might well be toward preventing these birds from being harvested rather than a better distribution of them among the mass of hunters.

Summary

The biological basis for shooting cocks is the polygamous behavior of the bird, which results in only a small percentage of cocks needed to breed the hens. Any excess above this percentage is subject to natural mortality and can be better utilized by hunters instead. Production of young, in which the sex ratio is roughly balanced, each year provides a crop of young males, most of which are harvestable. In no other small game species do we utilize the crop so fully. No population compensation is involved in this process.

The desirable harvest should leave just enough cocks to insure that what remains can stand the winter loss and still be adequate to breed all hens. Cocks conceivably could be overshot to the point where those remaining were not adequate to breed the hens. However, no sex ratios from Wisconsin or elsewhere suggest that this point has ever been reached. Following 25- to 30-day seasons in 1953-57 in Wisconsin, cocks in spring averaged 7.1 per square mile in "Very Good" pheasant range, 4.0 in "Good" range, and 1.6 in "Fair-Poor" range. This is a smaller remnant than reported for other heavily hunted areas, and along with the sex ratios and cock age ratios, further attests to the more thorough harvest in Wisconsin. This thorough harvest may result from: (1) the limited pheasant range and large number of Wisconsin hunters, (2) the nature of the hunting regulations, (3) the moderately early season, and (4) the nature of the habitat. It does not seem desirable to intensify the harvest any further.

Seasons of 4-5 weeks seem to be the most desirable in length from the standpoints of (1) thoroughness of the cock harvest, and (2) relationship to hen loss. An opening date around October 20 seems most desirable from the standpoints of: (1) the age of the birds, (2) minimizing or avoiding overlap with a mid-November deer season, and (3) minimizing overlap with corn and soybean harvest. Advantages of weekend openings outweigh disadvantages. Daily shooting hours that coincide with waterfowl shooting hours simplify regulations and law enforcement. A two-bird daily bag seems well suited to Wisconsin conditions, and a seasonal bag of somewhere near 10 would probably have little, if any, value in further distributing the kill.

CHAPTER XVIII. HARVESTING THE HENS

Hen Shooting to Effect Long-Term Increase in Total Bag

Utilization of Hens Now Shot and Wasted

Biological Basis

Approximately 16 percent of Wisconsin hens are illegally killed each year with shotgun and most of this occurs during the hunting season. Most of the birds are presumably left in the field, although there is no way of knowing what percentage is taken home. If regulations could be enacted that would allow hunters to utilize these hens without increasing the kill rate, it would increase the utilization of the resource by more than 20 percent of the present use. (Hens outnumber cocks, and 16 percent of the hens would approximate 20 percent of the cocks.)

Regulatory Problems

The problem of designing regulations that would permit hens now shot to be utilized without increasing the percentage killed is complicated by several factors. In principle, the mechanics of allowing a restricted percentage harvest of hens are not difficult. For example, a limited fraction of hunters could be allowed to shoot one hen through selection on a lottery basis or one hen could be permitted in the bag late in the season when only a fraction of the hunters is still afield.

If the loss that now occurs is largely willful, it could perhaps be absorbed by a limited, legal take. But if much of it is accidental, as seems likely, it is difficult to imagine how a limited, additional kill could supplant it. Some accidental and willful kill by persons not permitted a hen would probably occur in addition to the legal take, and there would be an added crippling loss. The net result would be an increase over the present level of kill.

During the three hen seasons in California, each hunter was permitted to take one hen per year. This is a less restrictive regulation than those we have suggested above. Roughly 200,000 California pheasant hunters took 500-600,000 cocks and 110-120,000 hens (Harper, 1960). Hence the average season bag was 2-3 cocks per hunter and 1 hen per 2 hunters. Presumably the California hunters could have taken a considerably larger fraction of the hen population. That they did not suggests that they were refraining from harvesting hens. This self restraint, rather than the restrictiveness of the regulations, probably explains why the hen kill was no higher than it was. We would hesitate to depend on such self restraint effectively restricting the hen kill over a period of years.

The ratio of pheasants to pheasant hunters is higher in California than in Wisconsin. If every pheasant hunter in California had taken a hen, the total kill might not have exceeded 20-25 percent of the statewide hen population. There are at least 50 percent more pheasant hunters in Wisconsin than in California and fewer pheasants. If every Wisconsin hunter took one hen per season, the total kill would constitute at least one-third of the hen population in an average year.

Augmenting the Bag with an Added Hen Kill

Effects on the Population

As previously discussed, legal kills exceeding 20-25 percent of the hens in Wisconsin, Minnesota, Indiana, and some areas in California appear to have reduced population levels. Legal kills below this level, mainly in California, had no perceptible effects implying that compensation was taking place or that legal kill was partially replacing illegal kill or that the effect was simply not measurable.

In states with good pheasant densities, and therefore high r values at below-average densities, populations apparently recover more quickly than in less optimum areas. The **r** values (Fig. 65) on Pelee Island allow the populations to recover very fast after periodic hen seasons; the Minnesota populations also seemed to have recovered lost ground quickly following hen seasons (Fig. 60).

Wisconsin pheasant populations recovered faster from the general decline of the 1940's in counties with higher marsh acreage and more favorable habitat. However, in the ten marginal counties which sustained hen seasons in the 1940's, it took at least 10 years for the "hen-season" counties to regain their dominance over the "control" counties (Fig. 59). At least two of these counties have never regained their former population levels. In 1943, St. Croix and Polk Counties had estimated harvests of 8,100 and 15,000 birds, respectively. In 1948, the first year after the hen seasons, the kill was only 18-19 percent of their 1943 high. Although they experienced the two- to three-fold increases between 1948 and 1955 as did the other counties, the 1948 level had been so reduced that these increases did not come close to restoring the kill to the 1943 level. The 1955 estimates for St. Croix and Polk Counties were approximately 4,300 birds in both counties.

In mediocre to poor pheasant areas, r values at below-average densities appear to be so low that populations recover very slowly from set-backs. Consequently, hen shooting not only has an immediate population effect, but the population reduction may persist for some years following hen protection. We surmise that a given level of hen harvest has a more profound original effect in areas like these, than in good pheasant areas, although we have no evidence to support this.

Administrative Considerations

The entire problem of hen shooting needs careful exploration from the standpoints of the effects of different levels of hen kill, the regulatory means for permitting a desired harvest level, and a decision as to what population effect we are to consider permissible.

Allen (1947) and Hickey (1955a) suggested that proper harvests should not affect the level of effective breeders the following year or reduce the capital stock to any degree. If we accept this view, then we must determine what, if any, is the maximum hen harvest possible without affecting the population level.

However, the desirable harvest level should perhaps be considered the one which permits the greatest bag on a sustained-yield basis even if from a slightly reduced mean population density. Conceivably a population could yield an annual combined bag from a slightly lower density that would exceed a cocks-only bag from a larger population. For example, a population might average 400,000 cocks and 600,000 hens each year, and yield an annual bag of 300,000 cocks. If an annual 20 percent hen kill lowered the population level 10 percent, the new population level would be 360,000 cocks and 540,000 hens. The same percentage cock harvest would yield an annual bag of 270,000 cocks, plus 108,000 hens (20 percent of 540,000) for a total bag of 378,000 birds. This is a 26-percent increase over the previous harvest from a 10 percent lower population. The one important requisite here would be that the population was balanced in the face of this kill, and not slipping away imperceptibly each year. This is a possibility for managers to consider but without more information on the control of hen kill and precise information on reproductive gains and mortality, we do not recommend it at this time.

Utilization of Stocked Hens

Hens Stocked in Marginal Range

There are periodic requests from sportsmen to legalize hen shooting in marginal range in Wisconsin. These requests are based on two assumptions: (1) that most or virtually all of the kill in marginal range is stocked birds, and (2) that few hens survive the winter in these areas, they do not contribute to any reproduction in the following year, and therefore should be utilized to prevent this waste. This reasoning was partially responsible for the 1946-47 hen seasons in the nine northwestern counties.

Neither assumption is correct. Besadny (1956) and Besadny and Wagner (1963) leg-branded all pheasant chicks stocked extensively in 29 counties through the day-old-chick program in various parts of the Wisconsin pheasant range for varying periods of years. Samples of pheasant legs were obtained from hunters in the counties and the percentages of stocked (branded) and wild-reared (unbranded) birds in the kill were determined. In most counties studied, including a number of very marginal ones, the number of wild-reared birds in the kill exceeded the number of stocked birds, indicating a substantial carry-over and reproductive effort of the hens. As previously mentioned, the kill in the marginal counties increased after the 1947 low just as did the kill in good pheasant range. Evidently the population dynamics in marginal range is at least somewhat similar to that in good range and the evidence shows a relatively good carry-over of hens each winter.

The long-term effects of unlimited hen shooting in marginal counties would depend on the percentage of stocked birds in the bag. Where stocked cocks equal or exceed wild-reared cocks in the kill, hen shooting would depress the wild-reared component. But cocks and hens are stocked in equal numbers. The annual addition of as many stocked hens to the bag as stocked cocks would double the contribution of stocked birds in the bag, and counterbalance the loss of wild-reared cocks. The long-term kill would probably equal or exceed the previous kill level, again depending on the number of birds stocked.

Where wild-reared cocks in the kill substantially exceed stocked cocks, hen shooting would depress the wild component. If its contribution were substantial (e.g. two-thirds or more), the annual addition of stocked hens to the bag and consequent doubling of the stocked component still would not offset the elimination of wild-reared birds. The long-term kill trend would be lower under hen shooting than with a cocks-only law.

These effects can be seen in the kill statistics for the 1946-47 hen season (Table 37). In four counties in which the estimated kill equalled or exceeded the number of birds stocked in 1945, the 1946 kill of both sexes increased two-fold as a result of the hen contribution to the bag. But in 1947, the kill of both sexes dropped more than half, and about equalled the 1945 cock kill. In 1948, with restoration of cocks-only shooting the kill declined to a point 42 percent below that for 1945.

In five counties in which the number of birds stocked substantially exceeded the estimated kill, the 1946 cock and hen kill again increased about two-fold over the 1945 cock kill. But in 1947, although the kill of both sexes dropped below that for 1946, it still exceeded the 1945 cock kill by 44 percent. With a resumption of cocks-only shooting in 1948, the estimated kill was only 20 percent below that for 1945.

This may be why the pheasant kill has not declined appreciably in southern California where cocks and hens have been shot in equal numbers since 1951. The number of birds stocked (23,198 in 1955) has approached the number of birds shot (27,000 in 1955) in nine southern counties (Ben Glading, in litt.). Quite possibly the stocked birds have braced the kill against substantial decline.

In conclusion, we cannot recommend hen shooting in marginal counties because wild-reared birds exceed stocked birds in the kill in the majority of cases. The few counties in which stocked birds predominate in the kill are scattered and do not lend themselves to blocking into a coherent harvest zone. Furthermore, if the stocking effort were terminated in these counties following several years of hen shooting, pheasant populations would be extremely low and perhaps not huntable. They probably would require a lengthy period of years to recover anywhere near substantial densities.

Hens Stocked on Public Hunting Grounds

Each year approximately 70,000 pheasants, half cocks and half hens, are reared at the state game farm. Most of the cocks are stocked in fall on state-operated public hunting grounds. About 10-12,000 hens are reserved for breeders the following spring; their eggs provide the new generation to be reared at the game farm and 150-200,000 chicks to be cooperatively reared by sportsmen's clubs throughout the state.

TABLE 37

Comparison of Kill Trend in Counties with Hen Seasons Before and During 1946-47 in Wisconsin Counties Where Estimated Pheasant Kill Initially Exceeded Number Stocked, and in Counties Where Number Stocked Exceeded Kill

	No. Shot Exceeded No. Stocked*		No. Stocked Exceeded No. Shot**	
Year	Est. Kill†	No. Stocked†	Est. Kill†	No. Stocked†
1945	10,308	5,630	12,433	16,961
1946	22,002	5,065	25,484	15,704
1947	10,828	5,615	17,907	14,304
1948	5,989	6,664	9,990	18,834

*Buffalo, Pepin, Polk, St. Croix Counties.

**Barron, Chippewa, Dunn, Eau Claire, Pierce Counties.

†Both sexes included.

This leaves an annual excess in summer of more than 20,000 hens at the game farm. These hens are released at the earliest possible age on a county allotment basis. They contribute very little to statewide pheasant populations and involve substantial rearing costs. Currently a day-old-chick sexing program at the game farm eliminates the necessity to rear many of these surplus hens.

It might be possible to release surplus hens on selected public hunting grounds and permit hen shooting. The situation here differs from that of county-wide stocking in that these are well-defined, limited areas with intensive stocking rates. However, some of the same reasoning applies here as in the case of hen shooting in marginal counties. On some public hunting grounds, mainly the ones in primary pheasant range, wild-reared birds exceed stocked birds despite intensive stocking (Kabat *et al.,* 1955). Hence, it would be necessary to ascertain the relative contributions of wild and stocked birds to the bag. Enough hens would need to be stocked so that their contribution to the bag more than made up for the near elimination of the wild-reared component. This might be most feasible on public hunting grounds in marginal pheasant range. In any event, the addition of these hens to the annual kill would contribute nearly as much as the present contribution of cocks stocked on public hunting grounds.

Archery Seasons in Populous Areas

The fringes of some cities frequently provide good pheasant habitat. Reduction in agriculture and expanding residential and commercial areas often create a patchwork of fallow fields, undeveloped lots, and small acreages of cropland still under cultivation. This provides excellent remnant habitat for transitory pheasant populations that often reach substantial densities.

The amount of human activity and development in this suburban zone makes shotgun hunting unsafe. Archery seasons in such areas permit relatively safe use of the recreational potential of the pheasant populations produced and help promote sport hunting. The annual archery season in Milwaukee County usually begins in October with the general pheasant season and continues well into the winter. It has been quite successful and yields an annual, either-sex kill of up to 2-3,000 birds. Coupled with a concurrent season on cottontail rabbits (*Sylvilagus floridanus*), it provides many thousands of outdoor recreation hours.

Such seasons might be feasible within the city limits of some of the other larger Wisconsin cities, when the need is more apparent and further knowledge available. They may provide an answer to the increasing number of local ordinances that prohibit hunting with guns in the areas immediately adjacent to city limits.

Summary

Regulations could be formulated which would permit the harvest of a restricted fraction of hens. However, any such harvest would probably increase the total hen kill above its present level.

In states with good pheasant densities, and therefore high rates of population increase (**r** values) at below-average densities, populations apparently recover more quickly than in less optimum areas. In mediocre to poor pheasant areas, **r** values at below-average densities appear to be so low that populations recover very slowly from set-backs. Consequently hen shooting not only has an immediate population effect, but the population reduction may persist for years following hen protection.

Wild populations maintain themselves in marginal range. Shooting hens in these counties would greatly reduce these populations. The long-term kill level would be reduced where wild-reared birds constitute a majority of the kill, and would be increased in counties where stocked birds exceed wild birds. Excess game farm hens might profitably be stocked and hunted on some marginal-range public hunting grounds. Either-sex archery seasons permit utilization of frequently good pheasant crops around the populous fringes of cities and provide many man-hours of outdoor recreation.

CHAPTER XIX.
MISCELLANEOUS MANAGEMENT PROBLEMS AND FUTURE RESEARCH

We have discussed most of the more strongly indicated management implications of our population data. However, several areas of pheasant management remain untouched including manipulation of the habitat and limiting factors. In this chapter, we mention briefly those management and research problems in Wisconsin to which our data are pertinent. We do not attempt to discuss the full gamut of problems, or all aspects of any one.

Habitat Management

Wetlands

Wetland drainage is one of the most significant changes occurring in the Wisconsin pheasant range. In some southeastern counties, between 30 and 50 percent of the wetlands have been drained within the past 25-30 years. In view of the importance of wetlands to pheasants, analysis of the drainage problem and its solution are among the most important and urgent pheasant management needs in the state.

There are approximately 2½ million acres of wetlands remaining in Wisconsin. Many of these are in private ownership, and if drained, are suitable for growing such high value crops as head lettuce, onions, carrots, sweet corn, and mint. While drainage will continue, it probably will be less rapid than in the past. Drainage of small tracts will be limited mostly by lack of cooperation among landowners to develop suitable drainage outlets or because of high costs of some drainage projects (Natural Resources Committee of State Agencies, 1964).

Information from studies on wetland-pheasant relationships summarized in this report is fairly general. We know that nesting occurs in wetlands and that they are used as winter cover. However, we do not have the quantitative evidence of their importance that would allow us to prescribe in detail a program of preservation and development. The entire scope of any wetland management program would depend on whether or not wetlands are primarily used for nesting or winter cover, and whether or not their total acreage is as important as their distribution. Another important facet is their role in interseasonal movement and the total area of spring and summer range ultimately utilized by birds dispersing from wetland wintering areas.

Information is needed not only on the optimum quantity of wetland cover, but also on quality of cover and the configuration of these areas. Certain sizes, shapes, composition of plant species, and proximity to food sources and other nesting cover types may be most important in attracting a maximum percentage of nesting hens. Intensive studies needed to provide this more thorough understanding of wetland-pheasant relationships in Wisconsin have been underway several years and are nearing completion. These should provide the information necessary to effectively manage pheasants in wetland cover.

If large wetland acreages are needed to maintain Wisconsin pheasant populations, our primary management goal is to prevent further loss. This could be accomplished through accelerated acquisition, easement or lease, and compensation to the landowner through tax base adjustment, or legislation preventing further drainage. Whether or not most of the remaining wetlands can be preserved and managed for wildlife involves a better understanding of the social and economic problems influencing drainage and close cooperation of all land-use agencies interested in promoting sound game management programs.

Croplands

Approximately 12 million acres of cropland on privately owned farms supply many of the basic habitat requirements for Wisconsin pheasants. Since dairying is the major agricultural enterprise on these farmlands there is a great demand for high quality forage crops and permanent pasture lands. Wisconsin ranks first in the nation in acreage of alfalfa cut for hay. Almost 4 million acres of cropland are devoted to hay production.

Our concern is the percentage of all potential nesting cover in tame hay and the relationship of other cover types, notably wetlands. We previously established a relationship between the hay:nonhay nesting-cover ratio and nesting success, and ultimate pheasant density. Any change in the Wisconsin farming pattern which materially reduced the hay:nonhay ratio or its frequency in the crop rotation would be an advantage to pheasant production. The hay:nonhay ratio can be influenced both by changes in the hay and nonhay cover. However, Wisconsin's agricultural economy is geared to dairy farming; therefore tame hay is expected to continue to occupy a large percentage of the landscape.

The 3-cutting system of hay management recommended for the southern two-thirds of the state will adversely affect pheasant production in hay cover. Changing the entire hay mowing system to favor pheasant production would be impractical and uneconomical. There currently are no recommended hay crop mixtures which would be sufficiently late in maturing to permit a first cutting late enough to avoid the peak pheasant hatch without damaging the crop. Thus, secure nesting cover will have to be provided by (1) establishing or maintaining desirable cover types other than hay, (2) making noncrop lands more attractive to nesting birds, or (3) providing incentives for farmers in selected areas to delay the first hay cutting (Natural Resources Committee of State Agencies, 1964).

The trend in Wisconsin and throughout the Midwest is toward larger acreages of row crops, mainly corn, and a reduction in small grains. The shift in the crop rotation system from corn-oats-hay to continuous growing of corn on highly fertile soils in some areas may decrease available nesting cover formerly provided by hay. However, this may be offset to some extent by the tendency of some farmers to keep some upland acreage in nearly permanent forage crop production. More corn acreage in southeastern Wisconsin pheasant range will help the winter food problem only if larger acreages are not harvested for silage and picked corn fields are not fall plowed.

Wisconsin's dairy herds also depend on large acreages of permanent pasture. While these are of little value to nesting pheasants, the intensity of their use may decrease as more cattle are confined to feed-lots. Perhaps some of these pasture lands could produce pheasants if grazing pressure were reduced. Studies are needed to determine what degree of grazing pressure pheasants can tolerate.

Special Land-Use Programs

In recent years, approximately 1 million acres have been diverted from agricultural crop production in Wisconsin under the Soil Bank and Feed Grain Programs of the U.S. Department of Agriculture. Increases in pheasant populations were associated with croplands converted to undisturbed, grassy cover (Besadny and Gates, unpubl.). Though feed grain lands left idle for only one year were of little value as nesting cover, they contributed significantly when left undisturbed for several years.

Many agricultural economists currently estimate that 50-70 million acres of good cropland should be converted to other uses to reduce crop surpluses. A well-designed and coordinated land conversion program could alleviate the surplus problem and create or maintain habitat essential for pheasant production. The converted land would not be drastically changed, soil fertility would be maintained, a recreational opportunity would be created, and if a national emergency should arise, these potentially productive lands could be immediately brought back into agricultural crop production. Thus, efforts should be made now by all land-use agencies to develop a new multiple-purpose land conversion program.

Experimental Habitat Management

A unique opportunity to effect substantial increases in pheasant populations through intensive habitat management on public lands exists in Wisconsin. The Game Management Division is rapidly acquiring considerable wetland and some upland acreages under the stimulus of the Outdoor Recreation Act Program. State-owned lands should provide the opportunity to apply practices for improving game habitat. Studies are being conducted to determine what habitat management practices and land-use manipulations could be most effectively and economically applied to make these areas more attractive for pheasants.

Habitat management efforts are being directed toward: (1) developing and maintaining well-spaced units of secure nesting cover on both wetlands and uplands; (2) developing a network of food patches near secure winter cover; (3) controlling brush invasion on selected sites; and (4) developing a plan to provide the best agricultural crop rotation compatible with optimum game production.

Habitat development and management confined to public lands, however, are not the ultimate answer to maintaining or increasing statewide pheasant populations. No one agency could afford to own all the land necessary to produce enough game to satisfy the needs of the public. Maintenance and development costs would be prohibitive on a large state-owned acreage and the tax base of local communities would be greatly altered. Since approximately 85 percent of the land in Wisconsin is expected to remain in private ownership, it is on these lands that game management efforts will have to be expended. Again, the landowner will need some economic consideration either through direct payment or through adjustment of the tax base before he will deliberately apply land management practices that will benefit pheasants (Natural Resources Committee of State Agencies, 1964).

Since the early 1940's, pheasant populations in Wisconsin have been adversely affected by urbanization and intensification of agricultural land-use practices which limit undisturbed nesting and winter cover. The future of pheasant populations and hunting in Wisconsin will depend upon recognition that this species is an integral part of a total land-use program.

Game management goals can be achieved through (1) continuation of the Department wetland acquisition program (upper) and acceleration of a habitat development program, (2) development of a federal cropland conversion program geared to benefit pheasants and other wildlife species (lower), and (3) development of programs which will provide economic incentives for game management on private lands.

Thus, an understanding of the broader aspects of pheasant productivity under current agricultural land-use practices is needed for evaluating the effects of changing land use on pheasant populations and making recommendations for habitat management on private lands.

Winter Feeding Programs

The Wisconsin Conservation Department maintains an annual winter feeding program for upland game. A number of species, including bobwhite quail (*Colinus virginianus*), sharp-tailed grouse (*Pedioecetes phasianellus*), prairie chicken (*Tympanuchus cupido*), and Hungarian partridge (*Perdix perdix*), are fed although most of the effort is directed toward the pheasant. Ear corn has largely been used, the amount varying from 91 to 242 tons and averaging 153 during the winters of 1954-59 (Bersing, 1959). Most of the corn is distributed in the east central and southern game management administrative areas.

Opinions vary as to the value of a winter feeding program. It is popular with the public, and in many areas is probably carried on as much for public relations purposes as for possible pheasant benefits. The utility of winter feeding as a general game management activity has been discussed by several authors (Gerstell, 1942; Allen, 1953, 1956:452). The question of its usefulness resolves into several component questions: (1) Does substantial pheasant loss occur in some or all winters? (2) If substantial loss occurs, does it result from starvation? (3) If there is starvation, is it mechanically and economically possible to distribute ear corn or other grain on a large enough scale to materially reduce this loss? (4) Might feeding have other desirable or undesirable effects?

We do not have direct measures of the extent of pheasant loss in winter. However, from indirect evidence it appears to be constant and/or light. We detected no correlation between winter weather and pheasant population change, except for the winter of 1958-59. Generally, loss from winter weather does not appear to us to be a problem of any significance in Wisconsin, a conclusion shared by Allen (1941a, 1946) for Michigan, and Robertson (1958) for Illinois.

When direct pheasant loss does occur in other states, it is most frequently due to the mechanical effects of snow drifting into birds' nares, mouths, and under feathers, and freezing. Death usually is due to suffocation and exposure, with body weights normal and showing no signs of malnutrition (Green and Beed, 1936; Kirsch, 1951; Throckmorton, 1952; Trautman, 1953). J. M. Gates (unpubl.) found some evidence of this type of loss following the 1958-59 Wisconsin winter.

The southeastern quarter of the state totals about 12,000 square miles. If the entire winter feeding effort (153 tons of corn) were directed to this area, the amount of corn fed per square mile would be about 26 pounds. The winter pheasant density in southeastern Wisconsin has averaged about 20-30 birds per section. Since rodents, rabbits, and other birds pilfer some corn, the ear corn fed has averaged only a fraction of 1 lb. per bird per winter. This obviously is only a very small fraction of what would be needed to sustain a bird through the winter, or even through an emergency period of a few weeks duration. An effective program capable of sustaining a majority of birds would need to be many dozen times the magnitude of the present one.

It is an old, familiar problem in game management. Animals cannot be fed, stocked, or otherwise catered to, or their predators trapped, one by one, with the resources available to a Conservation Department on a large enough scale to affect most of a population scattered over many thousand square miles. It is not feasible on a statewide basis, nor do the population data suggest a need for it.

However, a practice that is not feasible on a statewide scale may be feasible for an individual landowner or person interested in managing game on a limited area. One question that needs study is whether or not artificial feeding through a winter attracts, and/or holds for breeding on an area, more birds than would nest without such feeding. Birds may be forced to move about considerably during winter in search of food. A flock in an area at the beginning of winter may not be there by spring. This would entail no change in the township or county population. But it would mean significant change for the landowner on whose land the flock began the winter. Artificial feeding might have prevented the movement, held birds to spring, and resulted in a crop of young the following summer that would not have resulted without winter feeding.

The daily spreading of manure by Wisconsin dairy farmers provides a source of winter food for a large number of pheasants. This practice is carried on throughout the winter months in much of the state to comply with regulations in the production of Grade A milk. The spreading of manure with its associated waste grain, mainly corn, has carried many pheasants through rough winter periods.

Flushing Bars

Flushing bars on hay mowers have fairly consistently reduced hen mortality. The reduction ranges from virtually none (Nelson, 1955) to 87 percent (Swagler, 1951), with most values falling between 38 and 60 percent (Bue and Ledin, 1954; Nelson, 1956; Robertson, 1958; Klonglan *et al.*, 1959). As mowing speed increases, as it has over a period of years, flushing bars become less effective (Robertson, 1958).

The failure of most flushing-bar studies to show any population response (cf. Klonglan *et al.*, 1959) has been puzzling. Most of these studies have been conducted in the better pheasant areas where hayfield losses are numerically high and spectacular. But according to our findings in Chapter XI, the better pheasant areas seem to have a somewhat lower *percentage* of hens killed by mowers than in other areas. If this is 15-20 percent of the hens, and flushing bars reduced the mortality by 40 percent, the loss rates fall to 9-12 percent — rather minor reduction in what previously have been comparatively nominal rates. Furthermore, flushing bars do not prevent nest loss nor give any assurance that the hens saved will renest. If mowing is late, a good share of them may not. Hence, it becomes more understandable why marked population responses may not have been evident in these studies.

Flushing bars might be most effective in areas with large hayfield acreages and mediocre-to-poor pheasant densities. Here, few hens are killed by mowers, but these constitute a large percentage of the population. It has been difficult to persuade farmers to use flushing bars in areas of heavy pheasant losses because the instrument is a cumbersome nuisance. Where hens are infrequently encountered in hayfields, it would be even more difficult to persuade farmers to use them. However, the possibility that flushing bars would have more effect in range made marginal by large hay acreages should perhaps be explored.

Predator Control

Total or even partial predator control could conceivably result in some pheasant increase. However, predator control could not be recommended as a statewide management effort because (1) It would be prohibitively expensive to reduce substantially the densities of all pheasant predators over the entire pheasant range of a state. The New York studies (Robeson, 1950; N. Y. State Conservation Dept., 1951) showed very well the cost of fox control alone. The inefficiency of bounties in markedly controlling even a single species has been well analyzed. (2) We still do not understand fully the rodent and other pest-reducing value of predators, and it seems unwise to tamper with any ecological change so drastic as the total elimination of a major part of the biota. (3) The esthetic and educational values of raptors and carnivores give them human value as truly as that of game species. Persons who appreciate them for these reasons are just as much entitled to consideration as hunters.

Nevertheless, we should determine the relationships between pheasant density and predation to further our understanding of total pheasant ecology. An approach like that of Craighead and Craighead (1956), in which estimates were made of prey density (game and nongame), predatory density, and number of prey taken, would be most valuable. A second need is for more experimental reduction of predator densities, preferably in areas where prey and predator populations and predation loss are known. Studies of several years' duration would be desirable, and different treatments involving removal of different combinations of predators would yield knowledge of the effects of the different species. These would, of course, be exceedingly expensive studies.

Illegal Hen Kill

The effect of illegal hen shooting on a population needs further analysis. Our impression, on the basis of currently available evidence, is that it may effect some degree of population reduction. It will take experimental work to determine clearly the effect of different levels of hen kill on a population.

Meanwhile, our management policy should regard hen shooting as a limiting factor which should be reduced or eliminated. Intensification of public education might be worthwhile. If sportsmen were more fully conscious of the problem, some of the carelessness and snap shots could be prevented

Stocking Pen-Reared Birds

Analysis of the Wisconsin pheasant stocking program has occupied a major share of pheasant research effort in the state. Various phases of it have been reported on previously (Kabat *et al.,* 1955; Besadny, 1956; Besadny and Wagner, 1963). Two points merit brief consideration.

While the pheasant stocking program is considered large by the standards of many states, it only contributes 15-20 percent of the annual statewide pheasant kill (Besadny and Wagner, 1963). If Wisconsin pheasant populations decline progressively in the decades ahead, this stocked portion could rise to be a major fraction of the annual kill. However, by this time the total kill would be so meagre that pheasant hunting would be a submarginal venture, and probably not merit the stocking expense. Wisconsin pheasant stocking appears to pad the total kill to a limited extent, but it does not prevent, or noticeably damp, the population fluctuations that determine the quality of pheasant hunting in the state. It undoubtedly will not prevent long-term population declines resulting from habitat deterioration and increasing attrition from limiting factors.

We see no evidence, nor have we reason to suspect, that stocking young cocks in late summer or early fall creates a surplus effect with eviction and loss of native or stocked birds. The fall population can be markedly increased by intensive stocking. The percentage of stocked and wild-reared birds in a population appears to be largely a matter of simple arithmetic of the number of native birds present, and the number of pen-reared birds added (Besadny, 1956).

Hen stocking and reliance on reproduction is less effective as a means of adding cocks to the bag, although it contributes a few birds (Kabat *et al.,* 1955; Besadny and Wagner, 1963). The reasons for the poor performance of stocked hens seem to lie in the inherent characteristics of the pen-reared bird and its reaction to release rather than in any density-dependent constriction of the environment.

The Wisconsin State Game Farm efficiently raises birds of excellent quality from the standpoints of conformity, plumage, and vigor. But despite their quality, the contrast between the behavior of these birds and that of wild-reared birds is obvious. Hatched in incubators, raised in pens on artificial feed and without the educational benefits of wary brood hens, these birds evidently experience considerable loss immediately following release.

Buss (1946:89) observed postrelease weight loss which we also found on several study areas and which attests to the postrelease shock these birds experience. This alone may account for substantial loss. In addition, the birds often congregate on roadsides in unwary flocks for days after release making them vulnerable to predation and accident. Between August release and the October hunting season, we normally expect a loss of 40-50 percent of released cocks (Kabat *et al.*, 1955), and this probably applies equally to hens. Add to this a 16-percent hunting season loss of the hen survivors, further loss to various factors during winter, and the percentage surviving to the nesting season is probably well below the percentage of native hens surviving through the same period. Hence, the stocked component of a population cannot maintain itself and slips away quickly.

The second point about stocking is the possible genetic consequences of annually releasing some 200,000 pen-reared birds into the wild populations. Some of these birds survive, reproduce, and eventually merge genetically with the wild stock. Perhaps on the beneficial side, the birds increase the genetic variability of the wild stock. Game farm Chinese ring-necks have been cross-bred with Mongolian, Formosan, versicolor, and black-neck subspecies. Periodically the game farm obtains breeders from other states, in some cases wild-trapped birds, to mix into its stock. Within recent years, wild birds from South Dakota, Hawaii, and other states as well as trapped birds from unstocked Wisconsin areas have been added. Consequently the game farm pheasant displays variability as do the wild-reared birds about the state.

However, some selection toward domesticity may occur in pen-reared birds. Presumably this involves physiological and behavioral characteristics which are the converse of those associated with wildness or the ability to survive in a wild environment. Leopold (1944) discussed similar selective tendencies in game farm wild turkeys. They are apparently genetically inferior from the standpoint of their ability to survive in the wild. Merging of such birds with the wild stock could conceivably be detrimental, perhaps being the opposite of continued pruning by natural selection.

We have no evidence that this is occurring, but since pheasant stocking is expected to continue as a game management tool in Wisconsin, it merits further study from a basic, population genetics approach.

Long-Range Prospects for Wisconsin Pheasant Hunting

One of the most influential factors affecting Wisconsin pheasant hunting conditions is human population growth. Population projections by the Department of Resource Development place the 1980 Wisconsin population at approximately 5 million and the population in the year 2000 at 6.4 million. Most of this increase is expected in urban areas especially in the southeastern quarter of the state.

Whether the number of pheasant hunters will increase proportionately is less certain. A decade ago we were concerned over indefinite increases in hunting pressure. However, the sharp postwar increase in hunting license sales leveled off during the 1950's, then dropped quickly to respond to the 1958-59 decline in pheasants and other small game. With small game populations again on the increase, there has been a corresponding increase in license sales.

We are not certain whether the number of hunters will reach a saturation or "carrying capacity" level as determined by the quality of hunting, by hunter density and intolerance, and by the area available for hunting. Hunters today make up less than 10 percent of the Wisconsin population. If their ranks fail to keep pace with the population growth, they will become a declining minority of the population as is occurring in California (Ben O. Glading in discussion following Berryman, 1961). If hunter numbers should increase rapidly, and if pheasant populations remain at their present level or decline, the pheasant:hunter ratio will decline. That ratio is now about one cock per hunter.

Since the early 1940's pheasant populations in Wisconsin have been adversely affected by urbanization and intensification of agricultural land-use programs which limit undisturbed nesting and winter cover. The decline of pheasants is not recognized in its true proportions. Despite publicity, there is still a feeling that stop-gap measures such as stocking and paying of fox bounties will return pheasants to former high levels. The future of pheasant populations and hunting in Wisconsin will depend upon recognition that this species is an integral part of a total land-use program and must be considered as such (Natural Resources Committee of State Agencies, 1964).

As one of its major objectives the Game Management Division has established a base-line annual harvest goal of 500,000 pheasant cocks and is directing management efforts to this level. This goal can be achieved through (1) continuation of the Department land acquisition program and acceleration of a habitat development program, (2) development of a federal land conversion program geared to benefit pheasants and other wildlife species, and (3) development of inter-agency programs which will provide economic incentives for game management on private lands.

Summary

Since wetland drainage is one of the most significant changes occurring in Wisconsin's pheasant range, analysis of the drainage problem and its solution are among the most important and urgent pheasant management needs in the state. We need to determine the optimum quantity, quality and distribution of wetland cover in the pheasant range. The solution of the drainage problem must involve a better understanding of the socio-economic problems influencing drainage.

Wisconsin pheasants would benefit not only from an increase in secure nesting cover, but also from a reduction in the acreage of hay in the farming pattern. Since Wisconsin's dairy economy is geared to large hay acreages, secure nesting cover will have to be provided by (1) establishing or maintaining desirable cover types other than hay, (2) making noncrop lands more attractive to nesting birds, or (3) providing incentives for farmers in selected areas to delay the first hay cutting.

An understanding of the broader aspects of pheasant productivity under current agricultural land-use programs is needed for evaluating the effects of changing land use on pheasant populations. This information would be useful in making recommendations for habitat management on both public and private lands by all land-use agencies.

A statewide winter feeding program would be generally ineffective because (1) winter losses do not appear to be of much consequence, and (2) what losses occur may more often be due to mechanical icing than starvation. However, winter feeding by an individual landowner could be beneficial.

Flushing bars have generally reduced hayfield hen mortality, but are not followed by population responses. They might be most effective in marginal range where pheasants are sparce and where hayfield losses are numerically small but perhaps extensive percentage-wise.

Pen-reared birds contribute about 15-20 percent to the annual fall kill. The quality of Wisconsin pheasant hunting is largely a function of the wild-reared population and the factors affecting it. Failure of hen stocking could be due to the genetic and learned deficiencies of the game farm hens rather than environmental constriction. The possibility of this genetic weakness affecting wild populations detrimentally should be explored.

Hunters today make up less than 10 percent of the Wisconsin population. If their ranks fail to keep pace with the population growth, they will become a declining minority of the population. However, if their numbers increase rapidly, and pheasant populations remain at their present level or decline, the pheasant:hunter ratio will decline.

One of the major objectives of the Game Management Division has been to establish a base-line annual harvest goal of 500,000 cocks and direct management efforts to achieve this. The future of pheasant populations and hunting in Wisconsin will depend upon recognition that this species is an integral part of a total land-use program.

APPENDIX A

Age Characteristics of Juvenile Pheasants Used for Determining Age of Broods*

Age	Sex	Height	Tail Length	Silhouette Area**	Plumage and Remarks
1 week	Both	3 inch	Feathers just started		Natal down except for primaries and secondaries (flight feathers) which are conspicuous.
2 weeks	Both	4 inch	½ inch		Natal down still predominates, but feathers starting on breast, back and rump. Birds capable of short flights.
3 weeks	Both	5 inch	1½ inch		Contour body feathers developed, but natal down still on head, neck and belly.
4 weeks	Both	7 inch	2 inch	¼	Down only on head, fuzzy appearance.
5 weeks	Both	7½ inch	2½ inch		Uniformly feathered except for down and black markings on side of head.
6 weeks	Both	8 inch	2¾ inch		Uniformly feathered, black marking on side of head gone.
7 weeks	Cocks only	9 inch	3 inch		Red beginning to show on breast, top of head dark.
8 weeks	Cocks only	10 inch	3½ inch	½	Dark red extending down sides of breast, red wattles just starting to show through feathers around eyes.
9 weeks	Cocks only	11 inch	4 inch		Red wattles prominent around eye, breast feathers showing some purple, scapular feathers showing golden and purple.
10 weeks	Cocks only	12 inch	4 inch (postjuvenile molt)		Greenish black spots just starting to show on head and neck. Dark red on sides of breast joined on lower breast to form a U shape of color. Bluish-green conspicuous on rump; coppery feathers prominent on back.
11 weeks	Cocks only	13 inch	5½ inch	¾	Head and neck spotted with greenish black. Black line conspicuous under eye.
12 weeks	Cocks only	14-14½ inch	6½ inch		Greenish black spots on head becoming solid on top and back. Black markings over ear.
13 weeks	Cocks only	15 inch	8 inch		Colorful postjuvenal plumage now more prominent than remaining juvenal plumage, mottled appearance. Head and neck covered by green feathering.
14 weeks	Cocks only	15½ inch	9½ inch		White ring around neck just starting to show, throat still buff colored.
15 weeks	Cocks only	16-16½ inch	11 inch		White ring conspicuous, appearance of adult cock but thinner and unkempt looking.

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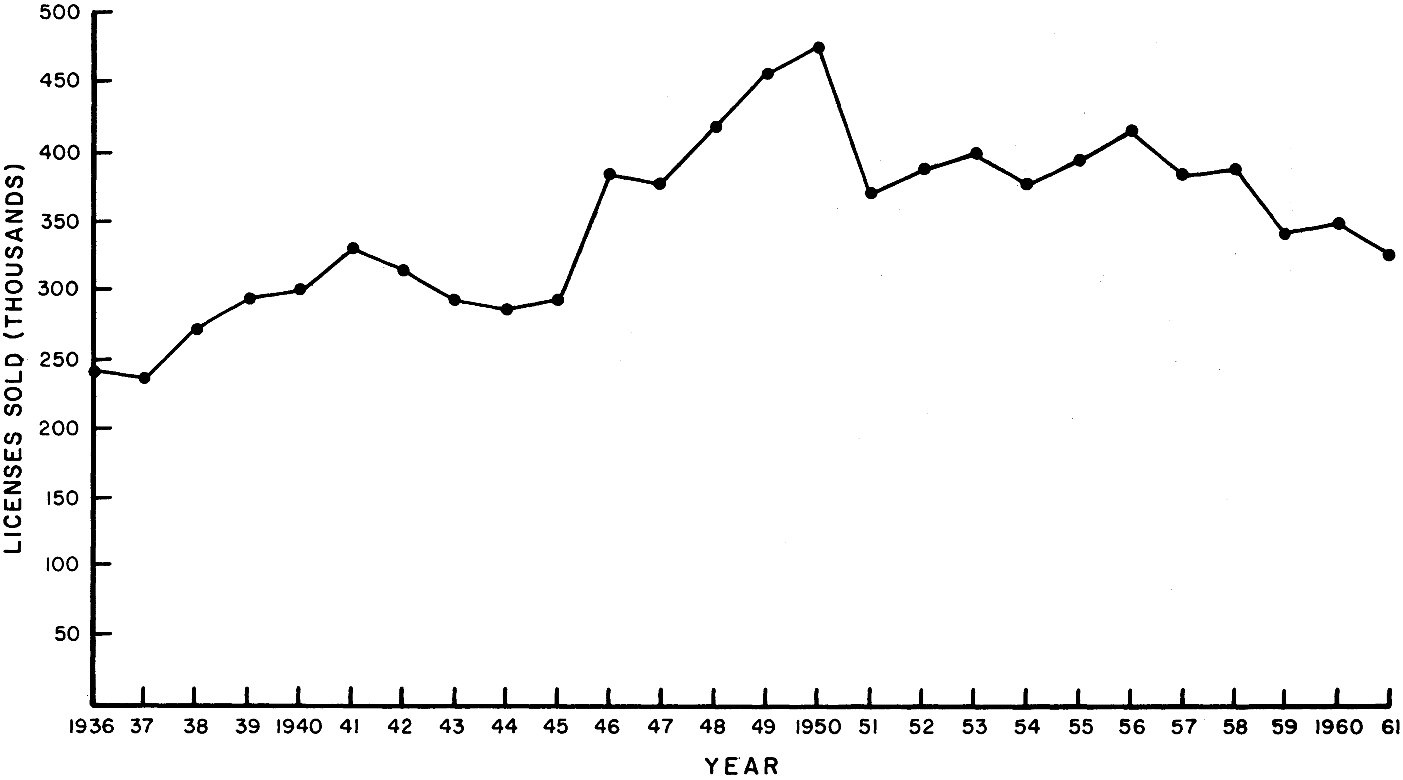
*These criteria are based on characteristics of known-age game-farm birds.

**In proportion to adult hen pheasant.

APPENDIX B

Resident Small Game and Sportsmen Hunting License Sales, 1936-61



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