

# **REPRODUCTION of an EAST CENTRAL WISCONSIN PHEASANT POPULATION**



**Technical Bulletin No. 85  
DEPARTMENT OF NATURAL RESOURCES  
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## ABSTRACT

Pheasant reproduction was studied from 1958 to 1966 in southwestern Fond du Lac County and adjacent parts of Green Lake and Dodge Counties, Wisconsin. This area traditionally supported some of Wisconsin's highest pheasant population.

Egg laying in first clutches began in mid-April in an average year, peaked in early May, and terminated in mid-May. Clutches established after mid-May in a normal year consisted mostly of renesting efforts. No evidence was found of an extended period of random egg laying and nest abandonment preceding actual nesting; these phenomena appeared to be density dependent actions that do not characterize all levels of pheasant density as previously supposed. Annual variation in nesting phenology depended on the physiological condition of the hen in late winter and early spring.

Preferred nesting cover was residual vegetation in wetlands in early spring and new growth in hayfields as the season progressed. Nest placement in both wetlands and hay was random with respect to edge. Nest densities in hay were highest in unharvested stands. It is a basic principle of Wisconsin pheasant ecology that pheasants are largely dependent on wetland cover for successful reproduction. Nest mortality in hay is too high for populations to maintain themselves unless alternative cover is present to counterbalance heavy production losses in hayfields.

Nest success was highest in unharvested hay, followed in order by wetland cover, strip cover, small grains, harvested hay, and peas. Success of all nests varied from 24 to 46 percent per year and averaged 30 percent for all years studied. Farming operations and predation were leading causes of nest failure. However, predation was viewed as the major limitation of nest success because much of the mortality from farm machinery ultimately stemmed from need to renest after nest destruction by predators.

A significant relationship between the average size of incubated clutches and the mean weight of hens in late winter led to the conclusion that physical condition of the nesting hen was the chief variable affecting egg production. Yearly variation in chick production stemmed from annual differences in nest success and the rate of hen survival during nesting. Under Wisconsin conditions, renesting apparently contributes less to annual production than is true in many other areas. Wetland cover types contributed 63 percent of successful production in an average year, higher than all other types.

Sharpness of hatching curves in Wisconsin may depend on the extent to which hayfields attract initial nesting attempts, an attraction which is stronger when nesting is delayed. Average hatching dates showed no relationship to the onset of clutch production or the average date of nest establishment. Delayed onset of nesting was not offset by compensatory extension of clutch production later into summer. Only about 3 percent of the spring hen population succeeded in brood production by virtue of successful renesting after hay cutting.

Farming operations, principally hay mowing, were responsible for poor survival of mid-season broods. Chicks from earlier in the season were older and less vulnerable to mowing; late-hatched chicks appeared after mowing was completed. Rates of juvenile mortality between hatching and October 1 varied from 28 to 51 percent and averaged 42 percent.

Productivity (number of juvenile hens recruited to the fall population per breeding hen) was used as the measure of reproductive success. Productivity varied from a low of 1.1 chicks in 1959 to a high of 1.9 in 1964. Reproductive success depended chiefly on hen survival during nesting, and was principally controlled by winter weather through dynamics of hen condition at the start of nesting and hen survival during reproduction.

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**By  
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# NATURE OF THE INVESTIGATION

## BACKGROUND

Information on the ecology of Wisconsin pheasants began with the research of Aldo Leopold and his students in the 1930's. Their projects resulted in publications with major emphasis on nesting (Buss 1946), related aspects of breeding behavior (Taber 1949, Buss et al. 1951), and measurement of annual mortality (McCabe 1949). In the late 1940's, studies of broader scope were begun by the Department of Natural Resources to determine population mechanisms on a regional or statewide basis. These were summarized and collated with findings in other states by Wagner et al. (1965).

Among their important conclusions was that the distribution and abundance of Wisconsin pheasants was strongly associated with the amount of wetland cover present. This relationship had long been suspected on less formal grounds, but whether it depended on the importance of wetlands as nesting or winter cover had never been fully evaluated. The present study was begun in 1958 to obtain an up-to-date picture of year-round pheasant habitat requirements. Such information was urgently needed to appraise the effects of wetland drainage on pheasants and to develop guidelines for wetland preservation and management.

As our study progressed, several companion objectives received emphasis: (1) determine the magnitude and causation of yearly variation in reproduction and mortality; (2) identify processes contributing to yearly changes in populations; and ultimately, (3) construct a life equation for Wisconsin pheasants providing additional insight into factors limiting pheasant abundance.

Our study was an intensive, comparatively short-term investigation of a local population. By contrast, the study of Wagner et al. (1965) was based on a much longer series of statewide population data. It seems reasonable that extensive in-

vestigations of the latter type would be most sensitive to environmental influences operating with wide geographic uniformity, whereas, investigations such as ours would be more closely attuned to localized factors and short-term influences tending to become obscured when statewide data were examined over a period of years.

Neither the extensive nor intensive type of investigation is categorically preferable. In our opinion, they complement each other, since mechanisms which operate at one level of population integration must certainly exist at the other. Where in our judgment results of the present study seemed to contribute to a more clear understanding of mechanisms affecting statewide populations, we have attempted to revise previous hypotheses or formulate new ones consistent with both lines of evidence.

Field work on this project began in August of 1958 and was pursued as a full-time endeavor between January of 1959 and May of 1965. Certain phases of data collection were continued on a part-time schedule through May of 1966. Although 1959-1965 represented the main period of study, data collected outside this period have been used whenever available.

The total results of our study were used by the senior author as his Doctoral Dissertation at the University of Wisconsin (Gates 1971). Readers wishing to see more on analytical details and expanded data summaries are referred to this thesis.

## OBJECTIVES

Nesting and production studies had two principal objectives: (1) determine cover preferences for nesting, including identification of those cover types in which hatching success was highest and therefore most essential to pheasant production; and (2) obtain yearly estimates of chick production as a measure of annual variation in

breeding success.

Other studies of pheasant nesting in (Leopold 1937; Buss 1946; Bell 1954; and McCabe 1955), did not have objectives as comprehensive as these. Results of the present study provide initial insight into many ecological aspects of pheasant nesting heretofore unevaluated by actual field investigation in this state.

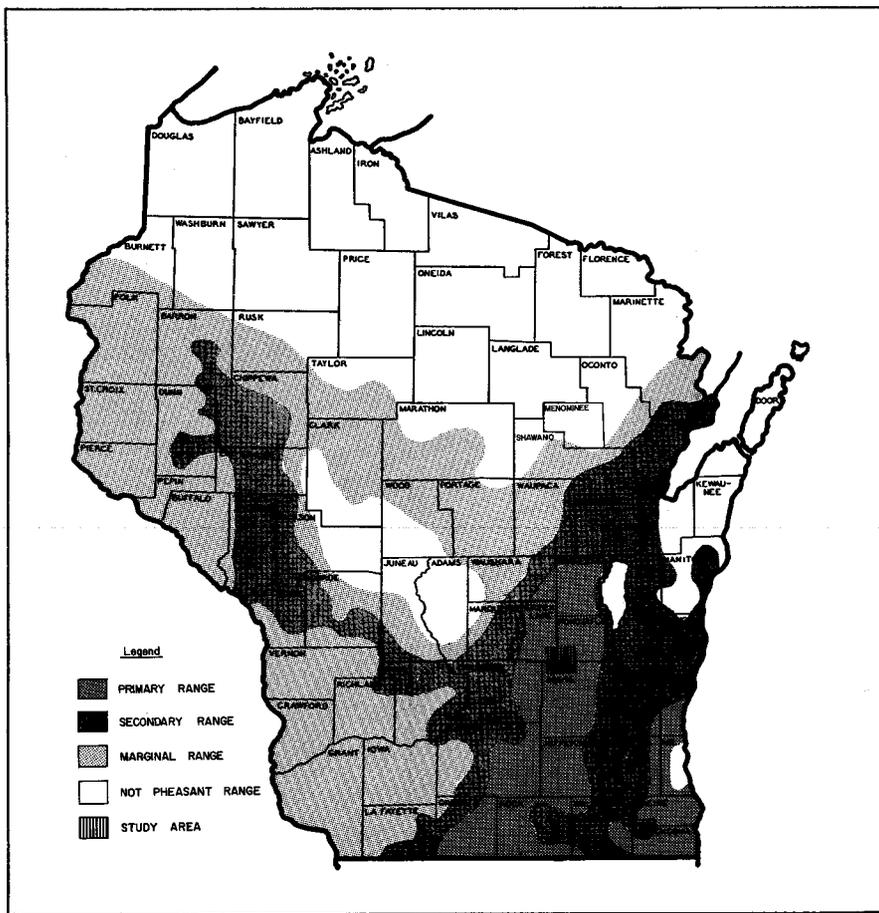
## STUDY AREAS

Our study was conducted in southwestern Fond du Lac County and adjacent parts of Green Lake and Dodge Counties. This general area has traditionally supported some of Wisconsin's highest pheasant populations (Fig. 1).

The Waupun Study Area, 42 square miles in size, served as the principal study area (Fig. 2). Trapping and marking of pheasants was confined chiefly to this area, but because of extensive mobility of marked birds, movement studies were conducted over the entire area shown in Figure 2. Several other phases of the investigation also extended into this larger area, including brood observations, evaluation of wintercover preferences, and determination of sex and age ratios. The Alto and Mackford areas were selected for more detailed investigation of nesting and wintering populations than could be accomplished on the Waupun Study Area at large.

Data in this report are identified with the study area on which they were obtained. Unless otherwise labeled, generalized discussions apply to the Waupun Study Area. Results incorporating information from outside this area are designated "Waupun Study Area and vicinity".

Topography of the Waupun Study Area is level to slightly rolling, with elevations varying from 920 to 1,020 feet above sea level. Soils are mainly silt loams that rank among the best agricultural soils in the state. Organic soils characteris-



**FIGURE 1.** Location of Waupun Study Area and vicinity in relation to generalized distribution of Wisconsin pheasants. Distribution map modified from Wagner and Besadny (1958) based on surveys described by Wagner (1952, 1953).

tically fill the deeper glacial depressions.

Curtis' (1959) map of the original vegetation of Wisconsin shows the Waupun Study Area astride an ecotone between prairie and oak savanna. Extensive areas of treeless wetlands were present. Today, except for scattered remnants of dry prairie and a few small woodlots, all upland soils have been converted to cropland. Wetlands have been less intensively exploited for agriculture, but those that remain exhibit varying degrees of disturbance due to grazing, mowing, peat fires, and partial drainage.

During our study, agriculture consisted mainly of dairy farming. Cash crops for canning, chiefly peas and sweet corn, provided secondary farm income. Roughly 78 percent of the land area was cultivated (Table 1). During the years 1961-65, land diverted from crop production under Federal land retirement programs amounted to 4 percent of the area.

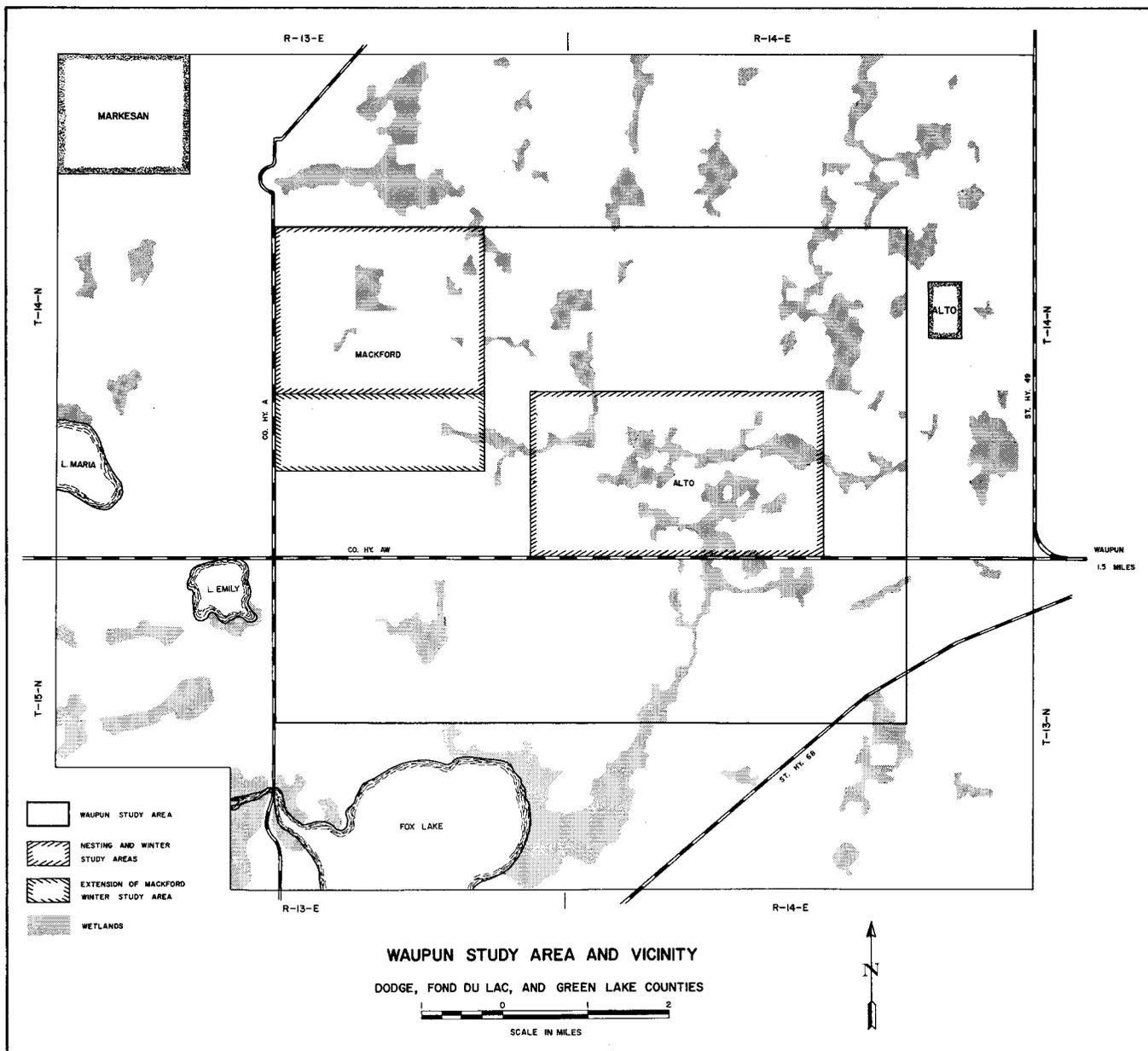
Climate of the region is continental. Winters are relatively cold and snowy, and summers short but warm. Annual precipitation averages 29 inches, 55 percent of which falls between May and September. Snowfall averages 41 inches per winter, and growing seasons average 151 days (Wisconsin Crop Reporting Service and U.S. Weather Bureau 1961).

Nesting studies began in 1959 on the 7-square-mile Alto Study Area (Fig. 2). This area had more extensive wetland acreages and higher pheasant densities than did the Waupun Study Area at large. At the conclusion of the 1959 field season, it became apparent that comparative nesting studies were also needed on an area with fewer wetlands and a lower pheasant population level. Concurrent studies were thus begun on the 5-square-mile Mackford Study Area in 1960. This area contained about one-fourth as much wetland cover and

supported a breeding population one-third as dense as the Alto Study Area. Full-scale nesting studies were conducted on both areas during 1960-64, followed by limited nest searching in certain cover types in 1965.

Because area-to-area differences in breeding population density in this study appeared to be closely tied to the amount of wetland cover present (Gates and Hale 1974:34), which in turn accounted for the large majority of successful nesting, reproductive success within the Waupun Study Area probably was subject to a slight degree of area-to-area variability. Hence we believe that productivity rates observed on nesting-study areas could be projected to the larger population with comparatively little risk of error. At the very least, there was no reason to believe that yearly trends in productivity on the two smaller areas would have fluctuated independently of the larger.

**FIGURE 2.** Map of Waupun Study Area and vicinity, showing location of areas used for intensive nesting studies.



# METHODS OF STUDYING NESTS AND NESTING COVER

Nine cover types were considered primary sources of nesting cover. These were classified as follows:

## Nonagricultural

(1) Permanent wetlands—All vegetation on muck or peat soils too poorly drained for cultivation and according to local residents not having been used as cropland for at least 3 years preceding original cover mapping of study areas (1959).

(2) Temporary wetlands—Early stages of secondary succession on muck or peat soils temporarily retired from cultivation. Most of the acreage was diverted from crop production under terms of the U.S. Department of Agriculture Feed Grain Program beginning in 1961.

(3) Roadsides—All vegetation between the road surface and the adjacent cover type, including both sides of the exterior fence line when present.

(4) Fencelines—All interior fencelines, excluding those bordering on wetlands which were typed with adjacent cover.

(5) Ditch banks—All vegetation between bottom of drainage ditch and adjacent cover type, excluding those with wetland cover on one or both sides which were typed as wetlands.

## Agricultural

(6) Harvested hayfields—Grass and/or legume mixtures mowed for hay, chopped for feedlots, or utilized as rotational pasture.

(7) Unharvested hayfields—Grass and/or legume mixtures maintained as cover crops on land diverted from crop production under the U.S. Department of Agriculture Soil Bank and Feed Grain Programs.

(8) Small grains—Principally oats, with small acreages of barley, grown for harvest or planted as annual cover crops on retired cropland.

(9) Peas—Cash crop grown for canning.

In addition to these nine, nest searching was also carried out in four miscellaneous types which were excluded after 1961. These were woodlots, gravel pits, uncultivated rocky outcrops, and unoccupied farmsteads. Only 60 acres of these cover types were present on both study areas combined, and the average density of nests was only 1 per 12 acres in 1959-61. Eventually exclusion of the four did not therefore represent an appreciable source of error.

Heavily pastured wetlands and permanent upland pastures were not examined for nests at any stage of the study. All cover so classified consisted of close-cropped redtop grass or bluegrass judged to be insufficient for nest concealment. Nor did we make any attempt to measure nest densities in row crops, even though pheasant nests in other

areas are occasionally found in such cover, particularly soybeans (Stokes 1954:49; Warnock and Joselyn 1964a). Row crops in this study consisted almost exclusively of corn (Table 1). If it is assumed that nesting in row crops is dependent on shortage of alternative cover, the probable number of nests we overlooked must have been very small. Well over half the landscape provided obviously better cover for nesting than the bare-soil conditions at ground level in most row crops.

In certain years, nesting occurred in cover types that were destroyed before searching of sample plots began. In 1960 and 1961, substantial acreages of corn stubble and old legume seedings were plowed down after nesting was already underway. In 1961 and 1963, some wetland cover was also burned late enough in spring to disrupt early nesting attempts.

We concluded that virtually 100

TABLE 1. Average land use statistics, Waupun Study Area, 1959-65

Cover Type	Percent of Total Area
Permanent Cover	12 <sup>2</sup>
Wetlands	10
Woodlots	< 1
Strip Cover*	2
Cropland	78
Corn	31
Small Grains	20
Hay	18
Peas	5
Other Crops**	2
Idle	2
Other	10
Permanent Pasture <sup>1</sup>	7
Roads, Feedlots, Farmsteads, etc.	3

\*Roadsides, fencelines, and ditchbanks.

\*\*Lima beans, soybeans, buckwheat, and sugar beets.

<sup>1</sup>Includes upland permanent pasture, exclusive of grazed woodlots, and all wetland acreages typed as heavily pastured.

<sup>2</sup>The following policy is adopted in reporting decimal percentages in this report. In instances where percentages appearing in a given table are to be used in later calculations, they are carried out one place beyond the first significant digit and the final calculation has been rounded off. In instances where percentages are not so utilized, they have been rounded off to the nearest significant digit when first presented.

percent of all cover in which pheasants nested was represented in the nesting study. Errors of omission could not therefore have created significant bias in estimates of total nest production or in the number of successful clutches produced.

In principle, the sampling procedure used was a stratified random design with optimum allocation based on variable costs of sampling individual strata. (Cochran 1953:75-76). Each of the nine cover types listed above was considered a sampling stratum. This design should have allowed us to estimate total nest production with minimum degree of sampling error from a fixed amount of sampling input. Use of such a design ordinarily required preliminary estimates of the variability and unit cost of sampling each stratum, from which the most efficient allocation of sampling effort between individual strata can be calculated. In general, higher sampling rates are planned for those strata which are larger in size, more variable from sample to sample, and less costly to examine.

Information on the number of man-hours per acre required to search individual types of nesting cover was obtained by personal communication with other field workers, but variance estimates for individual cover types under Wisconsin conditions were unavailable. Stokes (1954:16), however, showed that variances between cover types tended to be proportional to the average density of nests. From review of literature, we made a tentative ranking of cover types by anticipated order of nest density to determine sampling rates that would be used during the initial year of field study (1959). Minor adjustments were made in 1960 based on 1959 results, but we were deterred from subsequent revision in sampling rates because by 1960 it became clear that nest densities between cover types were subject to considerable yearly fluctuation. Variances between strata probably were also subject to change, hence there was no assurance that a design used in one year would be equally efficient the next. Roughly comparable rates of sampling were used in each of the largest strata after 1960. In general, we searched 15 to 20 percent of the permanent wetlands, 25 to 33 percent of the

strip cover (roadsides, fencelines ditch banks), 30 percent of the harvested hay, 20 percent of the peas, and 10 percent of the small grains.

Study areas were mapped in mid-May and cover type acreages were totaled by square-mile sections. Sampling effort in a given cover type was proportionally allocated between sections and between cover units within each section. In wetlands, for example, 1 acre out of 6 was ordinarily sampled. A section with 60 acres of wetlands was therefore assigned 10, 1-acre plots. A 25-acre unit would have been assigned 4 plots, a 20-acre unit 3 plots, and a 15-acre unit 2 plots, the remaining plot being assigned at random to one of the three units. Similar procedures were used to sample agricultural cover. One-acre plots were used in wetlands and 5-acre plots in cropland.

Plots were drawn to scale on 8-inch-to-the-mile cover maps by positioning a millimeter rule parallel to the long or short axis of a particular unit of cover to which a sample plot had been assigned. In agricultural cover the short axis of the field was used and in wetlands the long axis. From a table of random numbers, a point on the rule was selected through which a line was drawn the entire width or length of the cover unit. This represented one of the plot boundaries. The length of the plot was measured and its width adjusted to obtain the desired sample acreage. All 5-acre plots in agricultural cover thus paralleled the long axis of the field, and all 1-acre plots in wetlands paralleled the short axis. In large wetland tracts, where plot widths would have been less than 20 yards, a base line was established bisecting the unit from which plots extended outward on either side.

Separate sampling procedures were necessary in strip cover. Roadsides and ditch banks were divided into 1-acre segments from which a random selection was made as study plots. Each roadside plot was 0.4 mile long. Ditch bank plots were highly variable in length because of variable cover widths. Seldom were fencerows long or wide enough to furnish acre samples, hence a random sample was made of individual fencerow segments, typically 1/4 mile in length, until the cumu-

lative sample acreage was equal to the desired sample size.

Modification of this basic design became necessary in 1964 because of reduction in manpower. Instead of reducing the sampling rate in all strata, small grains and peas were not examined, since both had turned out to be relatively unimportant for nesting in previous years. New plots were selected at the start of each field season.

As time permitted, supplemental searching was also conducted outside study plots. Nests found in this manner provided additional information on hatching success and phenology of nest establishment, but were not used in comparing nest densities between cover types. This activity was uniformly spaced throughout the nesting season with exception of harvested hayfields in which searches were restricted to first hay cuttings only.

Sample plots were laid out by pacing from cover type boundaries or other convenient landmarks. All plots scheduled for a second search were marked to facilitate relocation.

Nest searching ordinarily began about May 20 and terminated at the end of August or early September. Study plots were examined by 5 or 6 men, but occasionally as many as 8 men assisted when field work ran behind schedule. In an average year, approximately 3,500 man-hours were devoted to nest searching.

Sample plots in nonagricultural cover were searched twice each year. Plots in strip cover were examined in late May and again in mid-July. Wetlands were searched for the first time in June and July and for the second time in July and August. Second searches were conducted in the same sequence as the first. In 1959 and 1962, the second search of wetland cover was not completed, but all plots were re-examined that had been initially covered up to June 30 and July 15, respectively. In both years, these plots comprised better than two-thirds of the total sample and all the best nesting cover. Failure to complete the second search in these years was not regarded a serious error, since few nests were established in wetlands after June 30.

In agricultural cover, small grains and peas were searched once, immediately after harvest. Plots in unharvested hay were also searched

once. Those clipped for weed control in mid-summer were examined as soon as possible after clipping had been completed. Those left undisturbed were examined in early to mid-August, late enough that additional nesting attempts would not have been started after nest searching was finished. Plots in mowed hayfields were searched after the first hay cutting, usually in windrowed condition but occasionally after baling. Repeat searches were routinely conducted after the second hay harvest. Hayfields used as pasture throughout the nesting season were given a single search in mid-June.

Except in harvested cropland, each crew member carried a heavy stick to part the vegetation and secure an unobstructed view of the ground surface. Strip cover was usually examined by men working in pairs. Other cover was searched with the full crew lined up abreast, the spacing between individuals depending on cover density. One man on the end of the line was responsible for maintaining a constant compass bearing and periodically marked the crew's progress by setting stakes. Stakes were retrieved on the return trip and reset at the opposite end of the line, indicating the amount of ground covered on the second sweep. This procedure was repeated until the entire plot width had been covered.

Each nest bowl or depression with which two or more eggs were associated was considered a nesting attempt. Care was taken to avoid accidental flushing of hens. To estimate the stage of incubation, one egg was removed from each nest that appeared to represent a complete clutch, though hens were not deliberately flushed for this purpose. Probable hatching dates were estimated and nests were not revisited until after the anticipated date of hatching. Clutches for which estimated hatching dates were unknown were checked at approximately weekly intervals. Active clutches were marked as inconspicuously as possible, or more often left unmarked in which case the nest site was described in relation to natural landmarks. All clutches of one or more hatched eggs were considered successful. Records were maintained of occurrence of single eggs on study plots, and all evidence of



*Searching for pheasant nests on a sample plot in wetland cover*

pheasant mortality was also noted.

In 1961, 85 artificial clutches of 5 pheasant eggs apiece were concealed on study plots in nonagricultural cover. Sixty-six of them were subsequently found. The location of each dummy clutch was carefully recorded beforehand, and whenever one was missed an attempt was made to determine the cause of its having been bypassed. Of the 19 clutches apparently overlooked, no trace of 9 were found. The other 10 were still intact or with broken eggshells present, indicating that efficiency of search was approximately 87 percent.

Whether this was a fair appraisal of first-search coverage of study plots was problematic. Natural nests usually contained more than 5 eggs per clutch and were much more conspicuous. More reliable information on the frequency of missed nests was available by comparing results of first- versus second-plot searches. Out of 277 nests known to be present on study plots at time of second searching, 86 percent were relocated. Although crew members doubtless remembered certain nest locations between visits, we believe this was a fairly reliable statistic. Almost all plots in nonwetland cover were examined by different personnel the first and second time. If second searches were 86 percent efficient, then first searches must have been virtually 100 percent, since cover was less dense and nest

sign fresher during initial coverage.

In agricultural cover, nest finding efficiency was evaluated only in mowed hay. In 1961, 16 out of 19 artificial clutches concealed on study plots several days in advance of hay cutting were found when plots were searched after baling had been completed. Doubtless this represented a minimal figure for natural nests, since most hay plots were searched before baling in order to avoid as much as possible the obliteration of nest sign by farm machinery.

We believe that coverage of study plots in major cover types was accurate to within 5 or 10 percent of the nests actually present. Corrections were not applied for missed nests because most plots were long and narrow, hence the ratio of edge to area was rather high. With this configuration, a tendency probably existed to include some nests in plot totals that actually fell just outside plot boundaries, thus tending to compensate for the few nests overlooked inside. Though reasonable care was exercised to avoid this bias, nest discovery was a rare enough event that the natural enthusiasm of most crew members to report positive results may have led to slight bias along this line.

Throughout the study, we occasionally encountered empty nest bowls, obviously belonging to pheasants, from which it appeared that entire clutches of eggs had

been removed. In nonagricultural cover, all eggs from approximately 5 percent of the active clutches under observation disappeared without trace before hatching. Fates of both artificial and natural clutches suggested that egg removal was most prevalent in strip cover (Table 2). Cause of clutch disappearance was not identified, but probably depended on certain egg predators which selectively hunted these cover types. Crows and 13-lined ground squirrels were believed to be most important in this regard. Neither fox snakes nor bullsnakes, both with egg eating habits that might have explained the disappearance of eggs (Stokes 1954:39; Sharp and McClure 1945:231), were observed on the area. All other nest predators known to us typically devoured the eggs at the nest site and left ample evidence of egg remains behind.

To minimize this error, we eventually regarded as unsuccessful nesting attempts all well-constructed nest bowls large enough to contain a complete clutch of pheasant eggs and which also contained pheasant feathers. Seventeen of these nest structures occurred on sample plots in 1959-64, but bias could not be completely avoided because not all such nest bowls would have been discovered.

A related bias of perhaps greater importance resulted from gradual wastage of nest sign as the season progressed. By the time of second plot searching, all evidence had disappeared from roughly 9 percent of the nests initially located (Table 2). Among 29 recorded instances of nest-sign disappearance, none represented a successful clutch. Field sign of successful nests apparently persisted longer than preyed upon or abandoned clutches due to larger clutch sizes, more substantially built nest structures, and presence of both eggshells and egg membranes to increase the total amount of sign present.

The nest effect of these biases was to reduce the density of unsuccessful nests on sample plots with little if any effect on the density of successful nests. Estimates of total nest production and rates of nest success were therefore regarded as minimum values, but estimates of the number of successful clutches produced were believed to be essentially unbiased statistics. Because

nest disappearance was most prevalent in strip cover (Table 2), both nest density and nest mortality in these cover types were somewhat underrated in relation to other nesting cover.

Of 115 hens present at the nest site at time of nest discovery, 47 were inadvertently flushed but only 9 failed to return. Observer contact as a cause of clutch desertion thus appeared to be negligible. Desertion was most prevalent among hens still in process of egg laying. Seven out of 17 hens flushed from apparently incomplete clutches did not return, compared with 2 out of 30 flushed from clutches in various stages of incubation.

The possible influence of nest searching on rates of nest predation was evaluated from the fate of incubated clutches in wetlands and strip cover where predation was the predominant cause of nest failure. Among 198 clutches that had reached incubation but had terminated before discovery, 60 percent were successful. By comparison, 112 clutches in which incubation was still in progress at discovery showed 72 percent hatching success. At first, it appeared that human activity at the nest site was somehow associated with reduced likelihood of predation, but on closer inspection it became clear that length of exposure to nest mortality was not comparable between groups. The mean stage of incubation at time of nest discovery among active clutches was approximately 12 days, and from a 23-day incubation period it follows that hatching success was observed over an average interval of 11 days. The inactive group, however, included all clutches that had reached the earliest detectable stages of incubation, which doubtless occurred well before the 12th day. If it is assumed that we could identify incubation after the 5th day among unsuccessful clutches in this group, then nest mortality would have an 18-day period, on the average, in which to operate. The instantaneous rate of clutch survival over the above-mentioned intervals was calculated at 97 percent per day among both active and inactive groups, from which it did not appear that nest searching had any measurable influence on nest predation.

In agricultural cover, virtually all

nests were previously destroyed by farm machinery, and nest searching would have had no bearing on their outcome. Unharvested hayfields were an exception, but this cover type was examined at a time when active nests were seldom encountered. From these results, we conclude that observer contact had essentially no influence on success or failure of nests. In Nebraska, more detailed analysis of this subject by Evans and Wolfe (1967) also indicated that nest searching had a negligible influence on hatching success.

Nesting phenology can be most reliably inferred from a representative sample of clutches backdated to the date of first egg laying. In this study, 751 nest histories were considered complete enough for this purpose. In backdating we assumed a laying rate of 1.3 days per egg (Buss et al. 1951:35), an incubation period of 23 days, and age criteria for pheasant embryos described by Labisky and Opsahl (1958). One egg from each active clutch was routinely sacrificed for aging when obtainable without disturbance to the nesting hen. In instances where accurate information on clutch size was lacking, but stage of incubation could be determined, backdating was based on an assumed average clutch size appropriate for the season in question. Among clutches that had already terminated by time of discovery, the date of hatching or failure was estimated from field sign. Admittedly these estimates were subject to error, but probably were compensatory when each year's data were combined for eventual comparison.

The percentage of clutches that could be reliably backdated was not constant between cover types, nor were cover types searched for nests at comparable sampling rates. A weighting procedure was therefore necessary to establish the phenology of nesting in all cover types combined. Nest starting dates were segregated by cover type, grouped by 10-day intervals, and the resultant frequency distributions applied to estimates of total nest production for each cover type. The number of first-egg dates in each period was then cross-totaled between cover types to obtain the overall frequency distribution of

clutch establishment. Separate calculations were also made representing successful clutches only, from which were ultimately derived: (1) the distribution of first-egg dates in successful nesting attempts only; and (2) rates of hatching success by period of clutch establishment.

Alternative information on nest-

ing phenology was also available from posthatching methods of age determination, viz., from summer brood aging and from the postjuvinal primary molts of young cocks shot in fall. Backdating by these methods, however, represented successful clutches only, the validity of which depended on a constant rate of hatching success throughout

the nesting season. Clearly this was an assumption that could not be met. Under average conditions of study, 32 percent of the clutches begun in April succeeded, compared with 34 percent of the clutches begun in May, 20 percent of those started in June, and only 18 percent of those established in July and August.

TABLE 2. Summary of available information on rates of nest disappearance by cover type

Cover Type	Dummy Nests*		Active Natural Nests**		All Natural Nests on Study Plots <sup>1</sup>	
	Number Set Out	Percent from Which All Eggs Disappeared	Number Under Observation	Percent from Which All Eggs Disappeared Before Hatching	Number Found on Initial Plot Searches	Pct. from Which All Nest Sign Disappeared by Second Search
Roadsides	66	20	47	4	49	12
Fencelines	65	32	27	15	49	18
Ditch banks	44	21	20	5	40	5
Wetlands	100	4	57	2	174	7
Harvested Hay	35	6	--	--	--	--
Totals and means	310	16	151	5	312	9

\*Data obtained in 1961 and 1962. Rate of egg disappearance calculated over 4-week interval in nonagricultural cover and over 3-week interval in harvested hay.

\*\*Data obtained in 1960-63.

<sup>1</sup>Data from 1960-63. Interval between plot searches variable, generally between 7 and 10 weeks.

# NESTING PHENOLOGY AND NESTING BEHAVIOR

## TIMING OF NEST ESTABLISHMENT

Egg laying in clutches generally began in mid-April, peaked during the month of May, and terminated in late July (Fig. 3). In an average year, 15 percent of all clutches were started in April, 61 percent in May, 19 percent in June, and 5 percent subsequent to July 1. The earliest nesting attempt of the study was backdated to an April 5 starting date (1963) and the latest to August 5 (1961). Although the maximum span of nest establishment was roughly 4 months, most nesting activity fell between April 20 and June 20. Roughly 86 percent of all clutches were established during this period.

The cumulative frequency distribution of nest starting dates, related to the spring population estimate of hens, revealed that only 25 percent of the hen population began clutch production before May 1. The remainder began clutch production between May 1 and May 15, so that virtually all clutches started after May 15 in an average year represented re-nesting efforts. Results of this analysis showed a wide range of yearly variability, however. Dates by which the cumulative number of clutches equalled the spring population estimate of hens were May 20 (1959), May 12 (1960), May 9 (1961), May 24 (1962), May 7 (1963), and May 16 (1964). On the whole, phenology of clutch production in this study appeared to be comparable to that previously reported for Wisconsin by Buss (1946:42) and Wagner et al. (1965:43).

## RANDOM EGG LAYING AND CLUTCH ABANDONMENT

Random egg laying, laying in dump nests or nests of other species, and voluntary abandonment\* of clutches have been widely observed in pheasants, especially during the early stages of nesting (Hamer-

strom 1936; Baskett 1947; Dustman 1949; Stokes 1954:36; Linder et al. 1960; and many others). Buss et al. (1951) observed that captive hens in Wisconsin laid an average of 13 eggs apiece at random and another 12 in clutches that were subsequently abandoned before they finally produced a clutch that was incubated. Essentially similar behavior was reported among captive pheasants in Ohio by Seubert (1952).

Buss et al. (1951) also examined the ovaries of wild Wisconsin hens and obtained ovulated follicle counts which generally exceeded the average size of incubated clutches in the wild. Four hens collected in June of 1944 were still in laying condition and had already produced an average of 37 eggs apiece, indicating almost continuous egg production from the start of egg laying to the date of collection. Based on such evidence, Buss et al. (1951) suggested that random laying of single eggs and abandonment of one or more clutches also typified the reproductive behavior of wild pheasants.

Throughout this study, we were constantly impressed by the low rates of clutch abandonment observed and by the scarcity of single eggs. Less than 1 percent of all eggs found on study plots occurred as singles, and the estimated total production of eggs laid outside clutches averaged only 12 per 100 nesting hens (Table 3). On the whole, egg laying on our study area appeared to be a much more orderly process than that pictured by Buss and his co-workers.

Observed rates of clutch abandonment, 12 per 100 nesting hens (Table 3), were also lower than reported in captive birds by Buss et al. (1951) and by Seubert (1952). In reality, some of the clutches

whose failure we attributed to predation or other mortality may have been previously abandoned. This was most likely in harvested cropland where disturbance of nest sites by farm machinery often made interpretation of nest fates difficult. On the other hand, clutches left unattended after death of the nesting hen would have been wrongfully interpreted as abandonment. The second source of error probably did not compensate for the first, and calculated rates of clutch abandonment may also have been minimum values.

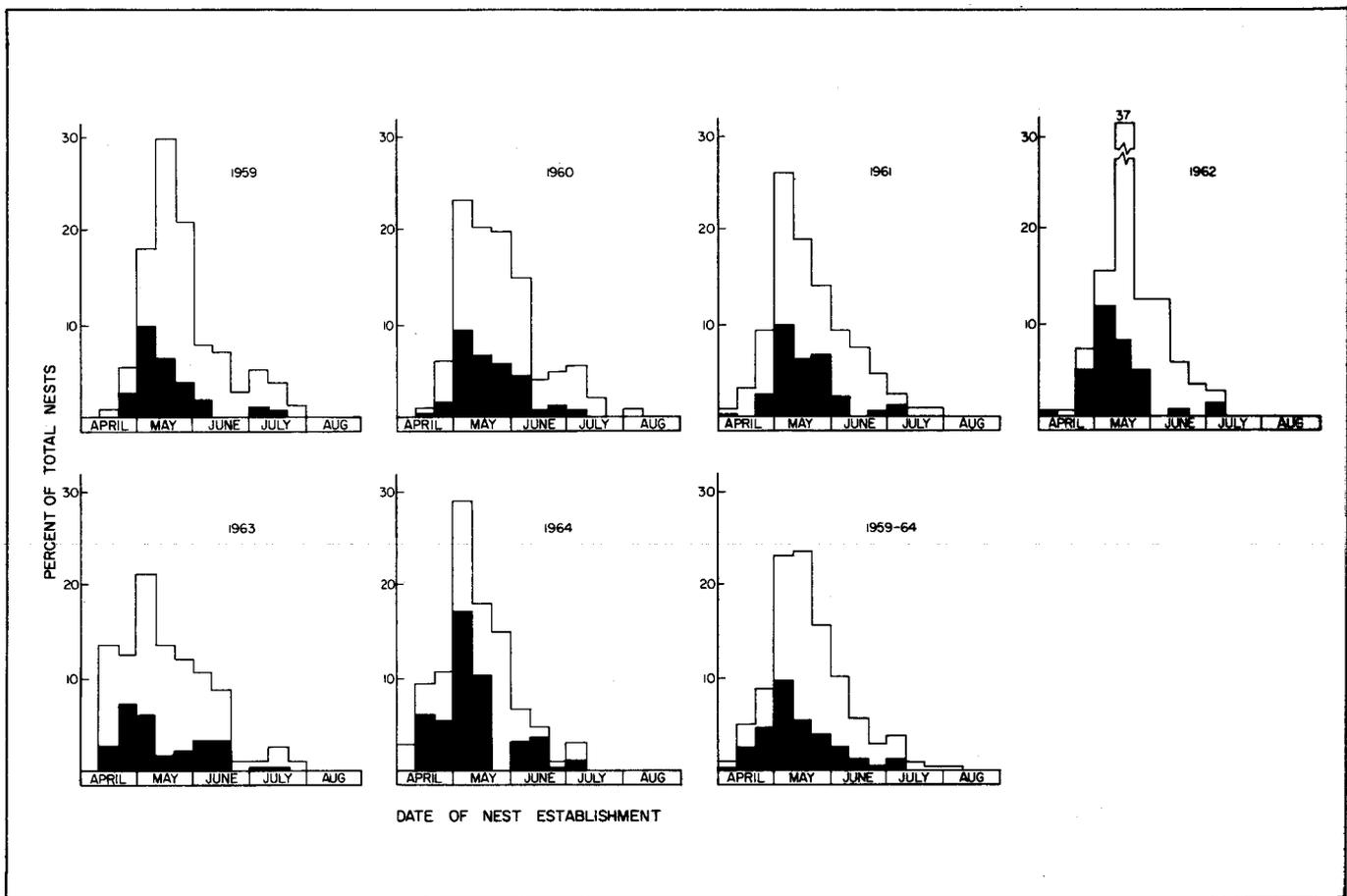
Estimates of total clutch production for 1959-64 (Gates 1971:840-850) averaged 1.76 per hen. Of these, approximately 70 percent, or 1.23 per hen, consisted of unsuccessful nesting attempts. If it is assumed that no causes of nest mortality other than abandonment operated in this population, then the maximum possible rate of abandonment would have been scarcely half the rate of two clutches apiece reported in captive birds by Buss et al. This too was an unreasonable assumption, from which it was clear that nest abandonment at Waupun was less prevalent than Buss et al. concluded was typical of wild populations.

Egg laying in dump nests was also infrequent. Only 20 clutches of 18 eggs or more were discovered during the study. Of these, only 3 were known to have been unincubated and therefore qualified as dump nests. Other evidence of the unimportance of dump nesting was available from dummy nest observations. Out of 275 artificial clutches placed in nonagricultural cover during May of 1961 and 1962, only 5 eggs were added by wild hens.

All evidence, then, indicated that wild pheasants in this study exhibited nowhere near the level of random egg laying and clutch abandonment that characterizes captive birds. Subjectively, we doubt that such behavior accounted for 15 percent of total egg production.

The relationship between population density and rates of abandonment was pointed out by Stokes

\*We will follow Stokes' (1954:35) distinction between the terms abandonment and desertion, reserving the former for instances in which failure of a hen to return to a clutch was believed to be a voluntary act and the latter for instances in which it was believed to be the result of disturbance



**FIGURE 3.** Calculated distribution of nest-establishment dates by 10-day periods representing total clutch production (open bars) versus successful clutches only (solid bars). The height of the former relative to the latter is proportional to nest success between periods. Sample sizes indicated in Table 52.

**TABLE 3.** Occurrence of single eggs and abandoned clutches on study plots projected to total cover-type acreages and related to the spring population of nesting hens\*

Year	May 1 Hen Population	Single Eggs			Abandoned Clutches		
		No. Found on Study Plots**	Projected Total	Total Per 100 Hens	No. Found on Study Plots <sup>1</sup>	Projected Total	Total Per 100 Hens
1959	348	12	59	17	11	50	14
1960	427	4	23	5	17	66	15
1961	524	10	48	9	10	46	9
1962	353	14	57	16	12	40	11
1963	333	10	49	15	14	49	15
1964	353	10	52	15	9	39	11
Totals and weighted means	2,338	60	288	12	73	290	12

\*Based on results from Alto Study Area in 1959 and combined results from the Alto and Mackford Study Areas in 1960-64.

\*\*Difference between years in occurrence of single eggs on study plots nonsignificant (chi-square with 5 df = 9.31; reference value at 0.05 = 11.1).

<sup>1</sup>Difference between years in occurrence of abandoned clutches on study plots nonsignificant (chi-square with 5 df = 5.99; reference value at 0.05 = 11.1).

(1954:36). His review of earlier field studies showed an abandonment rate of 3 to 5 percent of total clutch production at spring densities lower than 15 hens per 100 acres, increasing to almost 40 percent abandonment at densities greater than 60 per 100 acres. Hen densities in the present study averaged less than 6 per 100 acres, and the observed percentage of nests abandoned was 7.

On Protection Island, Einarsen (1945) reported increased prevalence of random egg laying, laying in dump nests, and abandonment of clutches associated with population irruption. In north central Iowa, the largest percentage of abandoned nests observed by Baskett (1947:17, 25) was during a population high. Linder et al. (1960) reported that as hen populations increased on a Nebraska study area, rates of nest abandonment did likewise. On two study areas in Iowa, Klonglan (1962:192) demonstrated a significant correlation between the density of nesting hens in spring and the subsequent percentage of clutches abandoned. In Illinois, Labisky (1968:281) similarly concluded that the prevalence of clutch abandonment was related to the degree of crowding. Rates of abandonment changed from 23 percent in 1957 to 49 percent in 1961, associated with joint increase in population density and with reduction in amount of nesting cover available to nesting hens.

In captive pheasants, Kabat and Thompson (1963:119-121) observed that the percentage of eggs laid singly was directly related to the degree of crowding. Seubert's (1952) study of pen-reared birds also indicated that proportionally more eggs were laid singly and that fewer clutches were incubated at higher population densities.

That random egg laying and clutch abandonment in pheasants are density-dependent variables seems well established among both captive and wild-reared population. Conceivably one of the outcomes of population pressure in this species is a behavioral derangement which leads to reduced nest attentiveness and/or delay in physiological processes regulating clutch production. Possibly the situation is analogous to that in experimental mouse popu-

lations where declining litter survival, one of the chief restraints on population growth, results in part from inhibition of lactation (Christian 1956) and/or deprived maternal behavior (Southwick 1955).

## ANNUAL VARIATIONS

Yearly trends in phenology of nesting were based on the calculated percentage of the May 1 hen population that began clutch production by May 10 (Table 4). For two reasons these results were best viewed as index values: (1) Some hens were almost certainly reneesting by May 10. (2) Nest establishment began in mid-April, some 2 weeks ahead of the spring census date, at which time hen populations would have been somewhat higher than on May 1. Both biases would have led to an over-estimate of the proportion of the hens beginning clutch production by May 10.

Possibly these biases were not constant between years. Yearly differences in early nest mortality probably led to varying degrees of reneesting activity by May 10. Hen survival also differed from one breeding season to the next, but probably had little effect on the calculations. In any event, the range of index values in Table 4 was too great to be explained by these influences alone, and results therefore represented real differences in phenology of clutch production from year to year. Because random egg laying was of minor importance in our population, these trends could be regarded as representative of all types of egg laying. No distinction, therefore, was made between onset of clutch production and the beginning of egg laying per se.

Three annually varying influences were examined as possible determinants of nesting phenology: (1) differences in the age composition of the breeding hen population; (2) variation in spring weather; and (3) variation in the physical condition of nesting hens.

Studies on captive pheasants by Westerskov (1956:55-56) and by Kabat and Thompson (1963:120-122) revealed earlier egg laying among adult than juvenile hens. Earlier reproduction in adults has also been reported in bobwhite quail (Parmalee 1955), California quail

(Lewin 1963), and chukar partridge (Mackie and Buechner 1963).

Wide fluctuation in the winter hen age ratio characterized our study (Gates and Hale 1974:7-9), and it was reasonable to suppose that similar differences in age structure prevailed at the start of reproduction. If adults were first to begin egg laying, time of nesting may have depended in part on the age composition of the breeding hen population. The late winter age ratio included the highest proportion of adult hens in 1959 and 1962 and the lowest proportion in 1963. Egg laying, however, was earliest in 1963 and considerably delayed in 1959 and 1962, exactly counter to expectation. Other factors were clearly more important than age composition in regulating the onset of clutch production.

Trends in spring temperature were first related to nesting phenology by comparing values in Table 4 with mean daily temperatures for the period April 20 to May 10. This was the interval suggested by Wagner et al. (1965:75) as having maximum influence on phenology of nesting under Wisconsin conditions. Temperature data were from the city of Fond du Lac, the long-term mean at this station for the period in question being approximately 55 degrees F.

Essentially no relationship existed between onset of nesting and prenesting temperatures. The two warmest springs of study, 1959 and 1964, showed nearly 2-fold variation in the percentage of hens beginning clutches by May 10. The two seasons of earliest nesting, 1961 and 1963, were much cooler than normal or about average in temperature, respectively. Trends in mean temperature were also examined for the periods April 1 to May 10 and April 10 to May 10. Neither demonstrated a suggestive relationship.

Precipitation records for the period April 1 to May 10 were also examined. Rainfall during this interval was above normal in 1960 (8.7 inches), below normal in 1959 (2.8 inches) and 1961 (2.3 inches), and near average in 1962 (3.3 inches), 1963 (3.6 inches), and 1964 (4.6 inches), demonstrating no association between precipitation amounts and time of egg laying. On

**TABLE 4.** Annual variation in nesting phenology based on the calculated percentage of the spring hen population beginning clutch production by May 10\*

Year	Percent of Total Clutches Started by May 10**	Projected Total Clutch Production <sup>1</sup>	Calculated Number of Clutches Started by May 10	May 1 Hen Population	Calculated Percent of Hens Starting Clutches by May 10
1959	25	554	138	348	40
1960	32	881	280	427	66
1961	42	1,065	442	524	84
1962	26	484	128	353	36
1963	49	638	310	333	93
1964	51	495	254	353	72
Totals and weighted means	38	4,117	1,552	2,338	66

\*Based on results from Alto Study Area in 1959 and combined results from Alto and Mackford Study Areas in 1960-64.

\*\*From Figure 3.

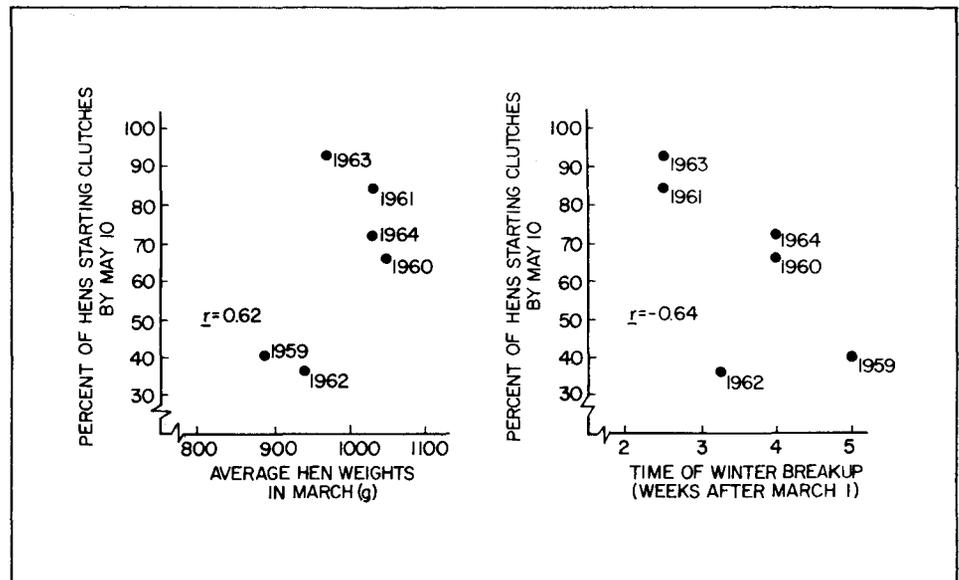
<sup>1</sup>Data from Appendix V in Gates (1971:840-850).

such grounds, we concluded that spring weather after April 1 had negligible influence on phenology of nesting under conditions of the present study.

Figure 4 indicates a nonsignificant, though highly suggestive relationship between differences in late winter hen weights and onset of nesting. In 1959 and 1962, March hen weights averaged 915 grams (Gates 1971), and the estimated percentage of the hens that began clutch production by May 10 was only 38. Corresponding means during other years of study were 1,014 grams and 79 percent.

Figure 4 also suggests a possible connection between time of winter breakup and earliness of nesting. Apart from 1962, earlier disappearance of snow cover tended to be followed by earlier egg laying. From events in 1963, late winter hen condition and time of winter breakup probably exerted joint influence on nesting phenology. In 1963, March hen weights averaged 969 grams, only 6 percent above the mean for 1959 and 1962. Winter breakup, however, occurred shortly after mid-March in 1963, one of the two earliest years in this regard, which was followed by the earliest nesting season on record.

These results seem to imply that differences in nesting phenology were chiefly related to the physical condition of the hen in late winter and early spring. Reproduction tended to be earlier in springs when



**FIGURE 4.** Relationship of late winter hen weights and time of winter breakup to onset of clutch production. Correlations nonsignificant at the 5 percent level (reference value at 0.05 with 4  $df = 0.81$ ).

hens had not undergone winter depletion in body reserves or in springs when snow disappeared early enough to facilitate early recovery of weight loss. Unfortunately, we did not have an adequate sample of hen weights between winter's end and the start of reproduction each year to document actual weight trends during the prenesting period. Experiments with captive pheasants, however, lend considerable support to this hypothesis. Gates and Woehler (1968) showed

that onset of egg production varied directly with degree of late winter weight reduction. Delayed egg laying associated with late winter under-nutrition in captive pheasants has also been reported by Gerstell (1942:68) and Kozlik (1949:62) and in captive wild turkeys by Hayden and Nelson (1963). In pen-reared pheasants maintained year-round on subsistence diets, late egg laying was also reported by Breitenbach et al. (1963). A similar inference has also been drawn in at

**TABLE 5.** Annual variation in phenology of egg laying among captive pheasants at the Wisconsin State Game Farm, Poynette\*

Year	Date at Which Daily Rate of Egg Laying Reached 25 Percent of Maximum Production
1953	April 7
1954	April 9
1955	April 8
1956	April 10
1957	April 7
1958	April 6
1959	April 13
1960	April 6
1961	April 4
1962	April 13
1963	April 8
1964	April 3
1965	April 6
1966	April 1

\*Based on egg production records averaging approximately 8000 eggs per day at maximum production. (Furnished by N. E. Damaske)

least one other wild pheasant population (Edwards et al. 1964).

## MECHANISMS OF VARIATION

Previous Wisconsin Hypotheses. From research conducted largely in Wisconsin there has developed a comprehensive hypothesis explaining yearly differences in nesting phenology, various elements of which may be found in papers by Buss et al. (1951, 1952), Lauckhart and McKean (1956:43-89), and Wagner et al. (1965). The hypothesis may be summarized as follows: (1) Egg laying begins approximately the same time each year regardless of variation in winter and spring weather. (2) But time of nest establishment does vary, with an annually varying period of promiscuous egg laying, laying in dump nests, and clutch abandonment preceding egg laying in clutches that are eventually incubated. (3) Stimuli that trigger egg laying cannot therefore be the same as those which regulate incubation, the former apparently

being governed by daylength, the latter by spring temperature.

The conclusion of Buss et al. (1951) that egg laying began at practically the same time each year was based in large part on the reproductive behavior of captive pheasants. In each of the 5 years they studied, most hens were laying eggs by mid-April, although there was considerable variation in first-egg dates.

Wagner et al. (1965:44) offered egg production records from the Wisconsin State Game Farm in support of the conclusion of Buss et al. In 1953-56, these data showed less than 3-day variation in the dates at which daily egg production attained 25 percent of the maximum daily rate. These same records extended by us through 1966, however, showed a larger range of annual variation (Table 5). As a 14-year mean, the 25 percent point was reached on April 7, but with yearly extremes falling 6 days on either side of this average date. In our judgement, the evidence does not firmly establish that egg laying begins at comparable dates from year to year.

If a variable period of random egg laying and nest abandonment accounted for yearly differences in nesting phenology, field studies should reveal quantitative increase in such behavior during years of delayed nesting. This did not occur under conditions of the present study (Table 3). On Pelee Island, nesting was 2 1/2 weeks later in 1950 than 1949, but neither the rate of nest abandonment nor the incidence of single eggs was appreciably higher in 1950 (Stokes 1954:23-24, 41, 44). In northwest Ohio, nesting was nearly a month later in 1947 than 1946, yet the percentage of abandoned clutches increased from only 3 to 8 (Dustman 1949:138). To our knowledge, only Klonglan (1955:631) in north central Iowa reported actually finding increased numbers of dump nests and single eggs during a delayed nesting season. Robertson (1958:70) suggested that random egg laying may have been prolonged during the delayed nesting season of 1950 in Illinois, but this was not supported by actual field observations demonstrating higher incidence of such behavior. In Illinois during the years 1957-61, clutch production was earliest in 1959 and latest in 1958; however, the number of single eggs encountered, adjusted for differences in the size of the spring hen population, was actually higher in 1959 (Labisky 1968:53, 167, 307). From such evidence, we concluded that onset of clutch production was generally no more variable than onset of egg laying per se.

That prenesting temperatures are somehow related to nesting phenology was demonstrated in Wisconsin and for several other midwestern states as well by Wagner et al. (1965:74-80). They also postulated that the start of egg laying was regulated principally by gonadotrophin production through photostimulation of the anterior pituitary, a mechanism demonstrated in pheasants by Bissonette and Csech (1936, 1941). Since day length does not vary between years, time of egg laying was believed to be more or less constant each spring. Actual onset of nesting, however, was said to be governed by prolactin. The postulated connection between prenesting temperatures and clutch production involved a stress re-

sponse. Subnormal spring temperatures were viewed as an environmental stress stimulating ACTH output and increased adrenocortical activity for maintenance of body temperature. Since ACTH apparently takes precedence over biosynthesis of other pituitary hormones, below-normal spring temperatures tended to delay the physiological processes culminating in clutch production and broodiness. Implicit to this hypothesis is the necessity for ACTH interference with biosynthesis of prolactin without corresponding influence on gonadotrophins.

The more-or-less separate influences attributed to photoperiod and temperature in the hypothesis of Wagner et al. were basically an outgrowth of their contention that phenology of egg laying and clutch production were unrelated. On the basis of our studies, however, this hypothesis does not always hold true, at least as a generalized phenomenon operating in all areas and at all levels of pheasant density.

If our opinion that one need not dissociate those influences governing time of egg laying from those governing actual nesting is correct, then it follows that spring temperature must be involved in regulating the onset of egg laying. Marshall (1961:321-323) has reviewed evidence in a number of temperate-zone species indicating that temperature and day length jointly interact to regulate gametogenesis and ovulation. Clear relationships between temperature and time of oviposition have been established in passerine species such as the song sparrow (Nice 1937:97-104), the great tit (Kluijver 1951:47-57), and the house wren (Kendeigh 1963).

An alternate hypothesis explaining yearly variation in nesting phenology under Wisconsin conditions must be consistent with the following observations: (1) The relationship established by Wagner et al. between prenesting temperatures and time of nesting; and (2) The relationship suggested by our study in which time of nesting was related to the physical condition of the hen in late winter and early spring.

Within broad limits set by day length, we suggest that onset of egg laying depends on how early a hen is able to mobilize sufficient energy reserves to meet the high energy

requirements for egg production. Under normal conditions, hens gain weight rapidly in late winter and early spring and attain peak physical condition just prior to reproduction (Kirkpatrick 1944 and Kabat et al. 1950). It seems reasonable that a minimum weight exists below which egg laying is impossible or at least long delayed. In captive pheasants, Gates and Woehler (1968) found that egg laying was delayed among hens that suffered late winter weight loss until near-normal weights were regained in spring. Such a weight threshold would be more rapidly attained after winters in which hens did not undergo progressive depletion in body reserves and during springs in which early disappearance of snow cover resulted in improved feeding conditions well before normal onset of reproduction. The influence of spring temperature in this framework would be to alter the rate at which energy reserves are accumulated by varying the percentage of daily energy intake that can be spared from the more immediate necessity of maintaining body temperature.

This interpretation may be somewhat oversimplified. Spring temperature may act directly on the neuroendocrine centers of the body which govern time of reproduction. Along with nutritional and psychological factors, the rate at which hens are able to build up their energy reserves in spring, as well as the weight level from which they begin, probably all interact to regulate onset of egg laying. In broad outline, however, our hypothesis is consistent with the total body of field evidence presently available from Wisconsin pheasants.

In Illinois, Labisky (1968:152) postulated that spring temperature exerted a dual influence on time of nesting, through direct effect on the physiology of the hen and through indirect effect on vegetation growth, a certain threshold of cover development being essential as a psychological stimulus to clutch production and incubation. In Wisconsin, it seems improbable to us that cover conditions would be a very critical influence. In view of the large amount of cover available to early nesting hens, particularly in wetlands, pheasants would seldom be obliged to wait for new growth as

nest concealment. On the other hand, the mechanism we have postulated between hen condition and time of nesting may not apply outside Wisconsin. In areas where winter weather is not as severe, condition of nesting hens may be less variable from year to year and the influence on nesting phenology less profound.

## SUMMARY

Egg laying in clutches representing initial nesting attempts began in mid-April in an average year, peaked in early May, and terminated in mid-May. Clutches established after the middle of May in a normal year consisted predominantly of renesting efforts. Reproduction in Wisconsin appears to begin somewhat later, but ends about the same time as egg laying farther south, leading to somewhat shorter nesting seasons and perhaps less time for renesting to compensate for high rates of nest mortality that characterize most pheasant populations.

No evidence was found of an extended period of random egg laying and nest abandonment preceding actual nesting. Review of previous studies led to the conclusion that random egg laying and clutch abandonment are density-dependent phenomena that do not characterize all levels of pheasant density as previously supposed.

Year-to-year variation in nesting phenology appeared to depend on the physiological condition of the hen in late winter and early spring. Onset of egg laying was earliest in years when hens did not experience appreciable weight loss over winter and in springs when snow cover disappeared early enough to facilitate early weight recovery. No influence of spring temperature on time of nesting was detected, although this factor obviously plays a critical role in nesting phenology as demonstrated by previous Wisconsin research. The hypothesis was suggested that phenology of egg laying in Wisconsin, within limits set by photoperiod, is related to the condition of the nesting hen at winter's end and how fast she is able to accumulate sufficient energy reserves to meet the high energy requirements for egg production.

# NEST DISTRIBUTION BY COVER TYPES

## GENERAL DISTRIBUTION

Significant differences in pheasant nest density prevailed between most cover types (Fig. 5). Lowest nest densities occurred in small grains and peas, intermediate densities in wetlands and hayfields, and highest densities in strip cover (roadsides, fencelines, and ditch banks). The generalized pattern of cover selection was not basically different from that reported elsewhere, most previous studies also reporting preferential use of nonagricultural cover over cropland (Hamerstrom 1936; Baskett 1947; Stokes 1954:140-141; Trautman 1960; Linder et al. 1960; and others).

Results in Figure 5 were only part-way meaningful in demonstrating actual cover preferences, since the average density of nests observed in a given cover type also depended on how long this cover was available to nesting birds. Nonagricultural cover was present throughout the nesting season, whereas most cropland cover was not. Hayfields did not become suitable for nesting until mid-May in an average year, were harvested in mid- to late June, and thus were unavailable to nesting hens for more than a 6-week span. The fact that nest densities in hay left unharvested were nearly as high as in wetlands seemed to imply that hay and wetlands were about equally preferred for nesting. Small grains at the other extreme were clearly avoided by nesting hens. Nest densities in strip cover could not be compared with other cover, since the linear configuration of the former made nest-per-acre figures a rather meaningless statistic for this purpose.

Nesting in individual cover types exhibited a high degree of seasonal variability (Fig. 6). Wetlands and strip cover were most important for early nesting, with cropland cover most important for late nesting. Calculations described in the previous section suggested that clutches

begun after May 15 in an average year consisted predominantly of renesting efforts. Accordingly, 28 percent of the nests in strip cover and 35 percent of those in wetlands represented renesting attempts, compared with 76 percent in hayfields and 100 percent in small grains and peas.

In 1963 and 1964, information was recorded on whether nests in strip cover and wetlands were established in residual plant material or in new growth vegetation of the current year. Of 148 nests so classified, 82 percent originally depended on residual cover for concealment, 10 percent on new growth, and 8 percent on combination of the two.

Heavy use of strip cover early in the season doubtless depended on absence of alternative cover on the uplands before there was adequate growth of hay and other crops. Progressively greater use of cropland as the season advanced seemed to imply an avoidance of strip cover when greater variety of upland nest sites became available. In most wetland types, new growth was long enough delayed that residual cover predominated until early June. Decline in nesting use thereafter may have been a function of the excessively dense vegetation which developed in most ungrazed stands as summer wore on. Highly preferred cover for early nesting (e.g., canary grass) typically attained such height and density by early July that most stands appeared virtually impassable to nesting hens.

In summary, the observed distribution of nests between cover types represented the outcome of complex interplay between cover preferences, cover availability, and changing cover conditions as the nesting season progressed. In general, preferred cover seemed to consist of blocks of vegetation rather than strip cover; and of comparatively low, dense ground cover available chiefly as residual plant material in wetlands in early spring or as new

growth cover in hayfields after a certain threshold of cover had been reached.

## WETLAND VEGETATION TYPES

Wetland cover was first divided into temporary and permanent stands. Temporary wetlands consisted of all lowland sites recently retired from crop production and arbitrarily included all former cropland on muck or peat soils abandoned less than 3 years prior to original cover-mapping of study areas. Vegetational composition of these stands was highly variable, but typically consisted of lesser ragweed, smartweeds, thistles, goldenrods, asters, and sedges. None of the acreage was subject to grazing or flooding.

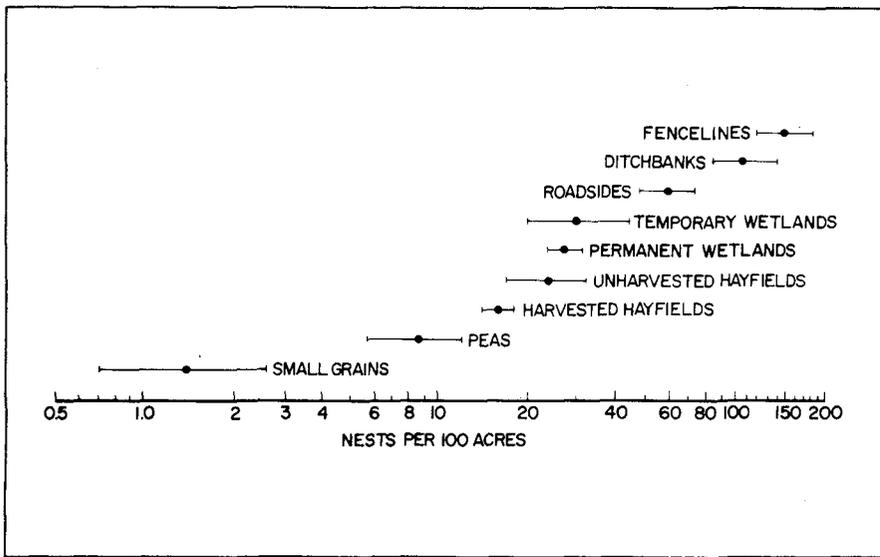
Permanent wetland cover was classified in five subtypes: (1) sedge meadows; (2) canary grass; (3) herbaceous; (4) cattail; and (5) shrub-carr.

### Sedge meadows

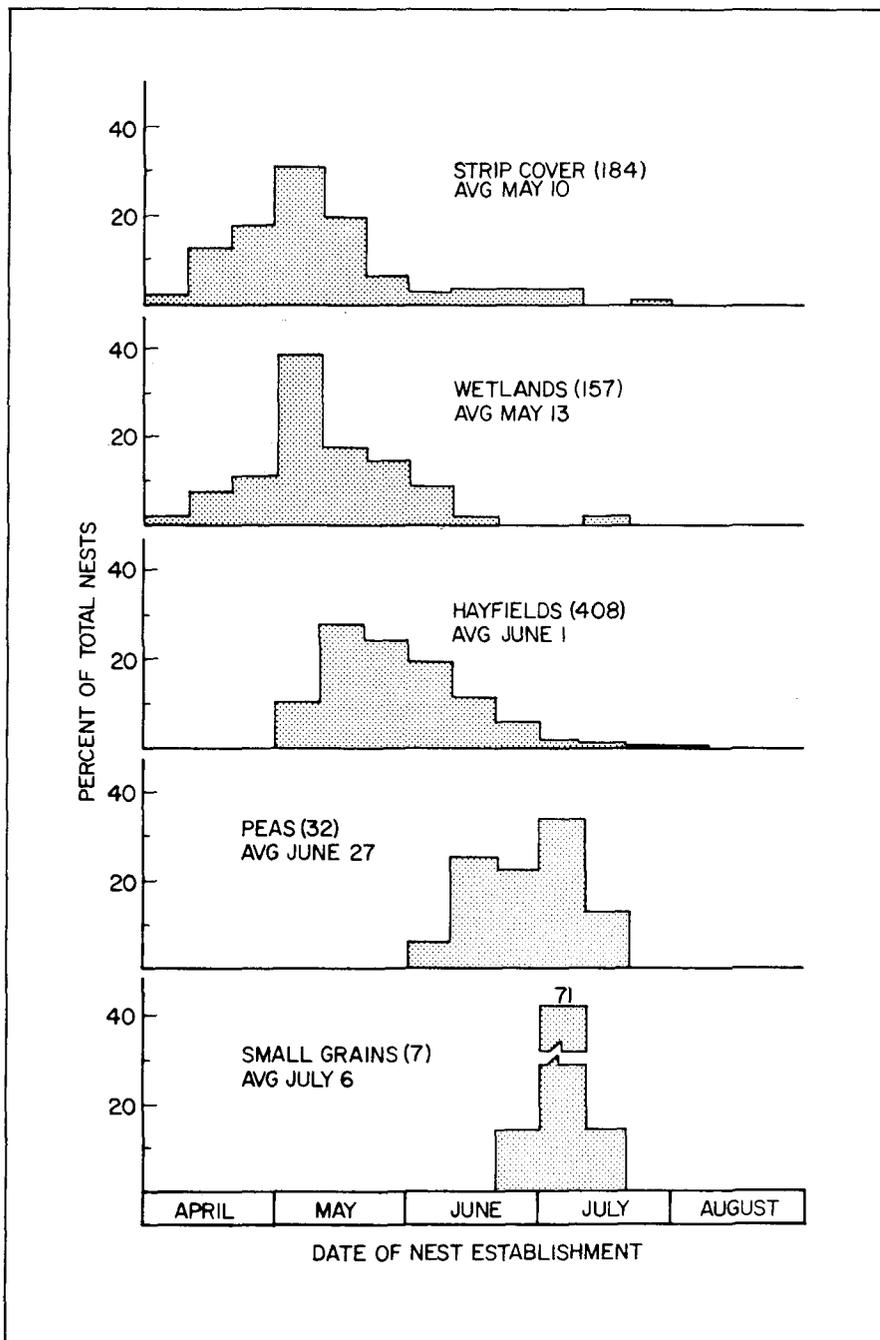
Sedge meadows were the commonest wetland type on the area (Table 6). Curtis (1959:365) characterized the sedge meadow as "...an open community of wet soils, where more than half the dominance is contributed by sedges rather than grasses." In the wetland classification of Shaw and Fredine (1956), these correspond to Type 2 wetlands—inland fresh meadows.

Sedge meadows typically occupied glacial depressions where the water table was at or just below the soil surface. Flooding was common during spring runoff, but in most years water levels dropped rapidly unless precipitation was above normal. In an average year, less than 20 percent of the sedge meadow acreage still retained surface water at the peak of nest establishment by pheasants in early May (Table 6).

Sedge meadows were almost invariably hummocky. Presence of this irregular ground surface was



**FIGURE 5.** Average nest densities and 95 percent confidence limits for individual cover types, 1959-64. Confidence limits based on Poisson distribution. Based on sampling results from the Alto Study Area in 1959 and combined results from the Alto and Mackford areas in 1960-64. Information from Gates (1971:834-850).



**FIGURE 6.** Frequency distribution of nest establishment dates between cover types by 10-day periods, 1959-65. Sample sizes shown in parentheses. Strip cover includes roadsides, fencelines, and ditch banks. Wetlands include both temporary and permanent cover. Hayfields include both harvested and unharvested stands. Differences in mean dates of nest establishment between cover types highly significant by analysis of variance ( $F$  with 4 and 733  $df = 8.50$ ; reference value at 0.01 = 3.39).

WETLAND COVER TYPES USED FOR PHEASANT NESTING



*Herbaceous*



*Sedge meadow*



*Canary grass*



*Cattail*



*Shrub-carr*

**TABLE 6.** Classification of permanent wetland cover by vegetation type, degree of grazing pressure, and spring water levels

Vegetation Type	Acreage*	Percent Affected by Grazing			Percent Flooded in Early May**					
		Ungrazed	Lightly Grazed	Moderately Grazed	1959	1960	1961	1962	1963	1964
Sedge meadow	621	48	40	12	15	41	28	23	11	0
Canary grass	179	63	19	18	11	53	15	20	8	0
Herbaceous	78	100	0	0	0	19	0	2	0	0
Cattail	43	100	0	0	100	100	100	100	90	53
Shrub-carr	96	100	0	0	88	93	84	80	52	17
Totals and means	1,017	61	28	11	24	48	28	27	12	5

\*Acreages of individual types subject to little change during the study apart from areas drained and broken for cultivation. Figures in this table represent combined results from the Alto and Mackford study areas using 1960 as a representative year.

\*\*Based on water level surveys conducted during the first half of May.

ultimately dependent on the tussock-forming growth habit of *Carex stricta*, the dominant sedge species in most meadows, but grazing had apparently accentuated the clumps through compaction of the intervening soil (Curtis 1959:372). From the ubiquity of hummocks 18 to 24 inches tall in many of the ungrazed stands, much of the sedge-meadow acreage appeared to have been subject to more intensive grazing in the past. Also testifying to this conclusion were numerous fences in various stages of disrepair that formerly subdivided many of the larger stands into smaller grazing units. Nearly half the sedge meadow acreage was ungrazed during the study. Another 40 percent was only lightly grazed (Table 6).

Sedge meadow vegetation was highly variable and could be characterized as a continuum in which sedge, principally *Carex stricta*, shared dominance with wet prairie plant species on the driest sites and with emergent aquatic plants on the wettest. A typical, more or less undisturbed stand at the midpoint of the moisture gradient consisted of sedge and bluejoint grass as the major dominants, with bluegrass, cordgrass, canary grass, and several species of asters, goldenrods, and mints among

the more prevalent subdominants.

### Canary Grass

These were essentially monotypic stands of reed canary grass, all of which apparently had been artificially established in the past for utilization as marsh hay or lowland pasture. According to Fassett (1951:69-70), there are two races of this grass in Wisconsin, the American which is native and the European which in earlier years was widely planted on low ground and which often crowds out native vegetation. Presumably the latter constituted most of the solid stands of this type present on the study area.

Canary grass was also prevalent in many sedge meadow stands, apparently having invaded these sites as a result of overgrazing and other types of disturbance. Many ditch banks were also vegetated by canary grass, and isolated clones of this grass also were common along fencelines and roadsides.

Most of the canary grass type occurred on sites where drainage had been artificially improved. Flooding was accordingly little threat to pheasant nesting (Table 6). Roughly 40 percent of the acreage was pastured, and another 10 percent was annually harvested

for marsh hay.

### Herbaceous and Cattail

The herbaceous type consisted of weedy vegetation in which various forbs instead of grasses and/or sedges were dominant. Solid stands of nettle comprised 15 percent of the total, generally occurring at sites where water tables had been lowered and followed by peat fires. The remainder consisted of dense stands of aster and goldenrod, occasionally with sunflower and giant ragweed, restricted to sites drained and formerly used as cropland. Such vegetation represented a more advanced stage of secondary succession than the temporary wetland type described earlier. None of the herbaceous type was subject to grazing or flooding.

Cattail achieved dominance in only a single stand. From 1959 to 1962, persistently high water levels in this tract precluded any possibility of its being used for pheasant nesting.

### Shrub-carr

Shrub swamps, or shrub-carr, were described by Curtis (1959:353) as "...a wet-ground plant community dominated by tall shrubs other than alder with an

understory intermediate between meadow and forest in composition." Ordinarily the shrubs are 4 to 12 feet tall. Successionally, shrub-carr follows the sedge meadow type and is replaced in turn by lowland forest in absence of disturbance (White 1965).

Shrub-carrs occurred at four sites, all on the Alto Study Area. The largest, 78 acres in size, exhibited a nearly closed canopy and in most years was too wet for pheasant nesting. Three smaller stands averaged 30 to 60 percent canopy closure and rarely contained standing water. Commonest shrub species were willows (*Salix petiolaris*, *S. bebbiana*, *S. discolor*, and *S. interior*), red-osier dogwood, silky dogwood, and spiraea. Sedges and bluejoint grass were most prominent in the understory. None of the shrub swamp acreage in this study was subject to grazing.

### COMPARATIVE NESTING USE

Of the six wetland types, herbaceous cover contained the highest average density of pheasant nests—68 per 100 acres (Table 7). Although this type comprised only 7 percent of the total wetland acreage, nearly 18 percent of all wetland nests were located therein.

Temporary wetland cover contained 29 nests per 100 acres, which was roughly comparable to the overall mean for all wetland types combined (Table 7). Both herbaceous and temporary wetlands represented secondary succession on drained lowlands after abandonment as cropland, which provided better nesting cover than sites closer to undisturbed condition. As succession on these drained sites proceeded toward dominance by asters and goldenrod, nesting use increased proportionately.

Canary grass contained the second highest density of nests—33 per 100 acres (Table 7). Individual stands that were consistently dry and ungrazed throughout the study averaged as high as 80 nests per 100 acres. Attractiveness of canary grass was further demonstrated by the disproportionately large number of roadside and fenceline nests concealed in off-site canary grass. Only scattered clumps of the species were

**TABLE 7.** Comparison of pheasant nest densities between wetland vegetation types, 1959-65

Vegetation Type	Acres Searched	Nests Found	Nests Per 100 Acres
Permanent wetlands			
Herbaceous	72	49	68
Canary grass	187	62	33
Sedge meadow	626	145	23
Shrub swamp	89	9	10
Cattail	40	2	5
Temporary wetlands	83	24	29
Totals and weighted means	1,097	291	27

present, but furnished concealment for 17 percent of the nests located in roadsides and fencelines. Selective use of canary grass also appeared to explain frequent nesting on ditch banks (Fig. 5), where over half the total plant cover consisted of this species.

Nesting in cattail was expectedly low. Forty acres of sample plots fell in this cover type, but only 11 were dry enough to require actual nest searching. Only two nests were found in this 11-acre subsample, both positioned on stand edges where mixed cattail and bluejoint grass furnished actual nest concealment.

Information on nesting in shrub swamps was unfortunately dominated by a single closed-canopy stand which comprised over 80 percent of the total acreage available for study. The low density of nests in this type as a whole (Table 7) was largely a consequence of the consistently high water levels in this tract. In 1959, 1963, and 1964, parts of this swamp did not flood or dry out early enough for potential use as nesting cover. Twenty-six acres of sample plots in these three years contained only 2 nests, however. The remaining 7 nests in shrub cover were located in an 11-acre tract on a comparatively dry site with dense understory of sedge meadow vegetation. Shrub cover in this stand was estimated at 40 percent, and nest densities averaged 47 per 100 acres.

Based on these relatively meager data, shrub swamps did not appear to be avoided for nesting provided the ground surface was dry and the shrub canopy was sufficiently open

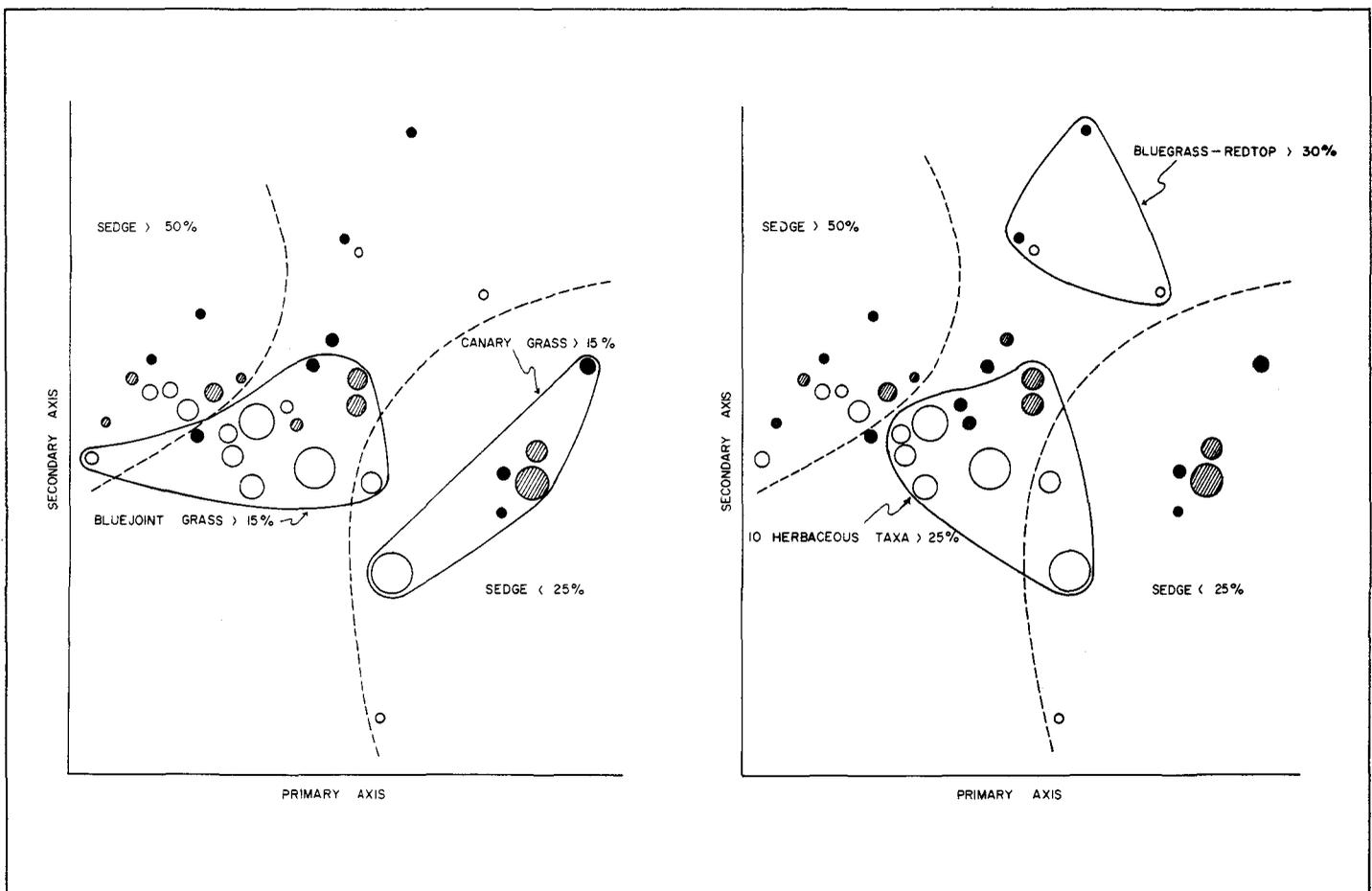
to maintain a reasonably dense understory. At least provisionally, we believe that 50 percent shrub cover is not excessively dense for pheasant nesting, but that more shaded stands are progressively less attractive as nest sites. Additional study is needed to clarify the relationship between shrub density and nesting use. Such information would be of considerable management significance in view of the regular successional conversion of sedge meadow vegetation to shrub cover on wetland areas purchased for wildlife management and subsequently protected from disturbance.

### INFLUENCE OF GRAZING, WATER LEVELS AND EDGE

Sedge meadows and canary grass were the only wetland types subject to grazing. Heavier grazing pressure in each of the two was associated with lower nest density (Fig. 7). In view of the importance of residual cover for nest concealment, the difference probably resulted from less carry-over of residual plant material from one growing season to the next.

Nests in pastured sedge meadows were commonly situated on tops of hummocks. Out of 44 nests in grazed stands, 73 percent were so elevated, compared with 26 percent of 68 nests in ungrazed cover. Clutches elevated in this manner tended to be safe from trampling by cattle.

As a result, no difference in nest success was observed between grazed and ungrazed stands.



**FIGURE 7.** Behavior of certain plant taxa plotted on 2-dimensional ordination of 34 sedge meadow stands. Percentages refer to relative importance indices described in text. Diameter of point representing each stand proportional to the sample density of pheasant nests observed in

1959-64. Open points represent ungrazed stands, cross-hatched points lightly grazed stands, and solid points moderately grazed stands. Heavily grazed stands not searched for nests and not included in the ordination.

Wetland water levels were normally highest at spring runoff and progressively declined thereafter. Drying was sufficiently rapid so that in most years less than 30 percent of the overall wetland acreage was considered too wet for pheasant nesting by early May (Table 6).

Water level trends in 1960 were the only exception to this generalization. Abnormally heavy spring rainfall prevented significant drying, and nearly half the wetland acreage remained flooded throughout the nesting season. Nevertheless, the percentage of nests in wetland cover in 1960 was higher than in either 1959 or 1962, which were much drier by comparison. Sufficient dry cover apparently was available in 1960 so that high water levels did not exert controlling influence on the distribution of nests between upland and lowland cover.

Less than 15 percent of the

wetland acreage in this study occupied flood plains subject to overflow. Furthermore, we knew of no stand on either study area in which water levels had not been affected to some extent by ditching or other forms of drainage. Whether these hydrologic characteristics were typical of wetlands in Wisconsin pheasant range, we are unprepared to say. If anything, our impression was that wetland cover in our area tended to be drier than normal and hence especially well suited for pheasant nesting. This may be an important consideration in applying results of this study to other areas of the state. Many wetland acquisition projects of the Wisconsin Department of Natural Resources in southeastern Wisconsin are situated on flood plains and consist of generally lower lying cover than the type of habitat we observed. Wetlands which remain consistently wet after the middle of May are of

comparatively little value as nesting cover and cannot be counted upon as significant assets to pheasant production (Fig. 6).

Nelson et al. (1960) pointed out that the only objective test of the relationship between nest placement and edge is to compare the percentage of nests occurring within a specified distance of an edge with the percentage of the total cover type acreage included within the distance.

Entire wetland tracts were rarely examined for nests. Sample plots, however, were distributed at random in wetland cover, and nest occurrence could be regarded as a representative sample of nest location. Analysis was based on 276 nest sites in 34 stands. The size of individual stands varied from 9 to 96 acres and averaged 26. Maps of each tract were drawn to scale and ruled into concentric zones 25 yards in width. The percentage of the

total wetland acreage that each zone comprised was then related to the percentage of the total nests it contained.

Slightly heavier density of nests occurred within 50 yards of a wetland edge; however, the disproportion was slight and the overall distribution of nests did not depart significantly from random expectation (goodness-of-fit chi-square with 6 df = 6.24; reference value at 0.05 = 12.59). Nesting hens apparently exhibited neither an avoidance nor a preference for peripheral sites.

Over 80 percent of all nesting in wetland cover began before June 1 in an average year (Fig. 6). By this date, new growth vegetation typically provided less cover than residual plant material from the previous growing season. Absence of edge effect thus applied mainly to the location of nests dependent on residual cover at time of clutch establishment. Under the denser cover conditions of early to mid-summer, nesting hens more often selected peripheral nest sites. Among 25 wetland clutches in which egg laying began after June 1, 16 (64%) were located within 25 yards of an edge.

## AVAILABILITY AND USE

Whether there is an optimum percentage of the landscape beyond which additional wetland acreages tend to receive proportionally less use for nesting may be of considerable importance in evaluating the impact of wetland drainage on pheasants. This was examined by projecting sample nest densities to total cover type acreages for each of the individual sections making up the two nesting study areas. The percentage of total nest production that occurred in wetlands, averaged over the entire period of study, was then related to the percentage of the land area occupied by wetland cover. Only high quality nesting cover was considered in this analysis, viz., ungrazed and lightly grazed sedge meadows, herbaceous cover, and canary grass stands.

Nesting in wetlands tended to be directly proportional to the overall amount of such cover available (Fig. 8). If indeed there was a breaking point, after which nest density began to fall off, presum-

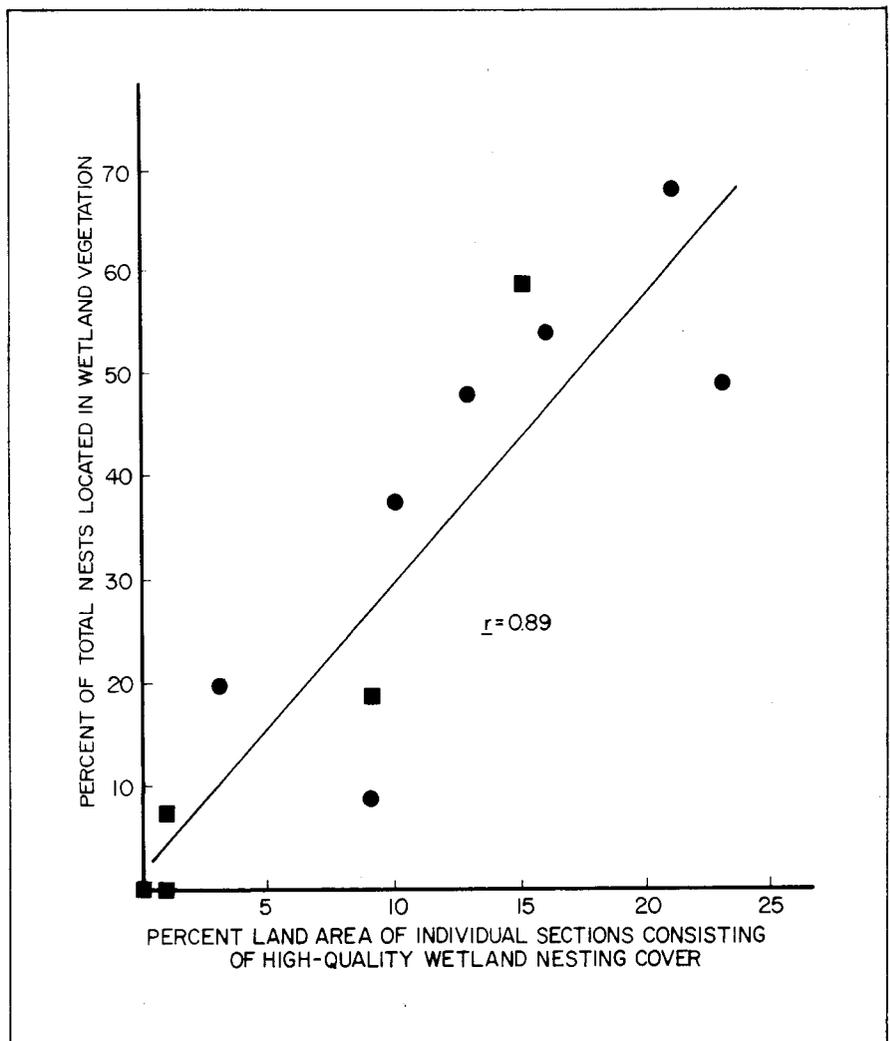


FIGURE 8. Relationship between availability of wetland cover and nesting use by pheasants. Circles represent the Alto Study Area (1959-64) and squares the Mackford Study Area (1960-64). Excludes cattail and shrub swamps and all moderate and heavily grazed wetland cover. Correlation significant at 1 percent level (reference value with 10 df at 0.01 = 0.71). Information from Gates (1971:834- 850).

ably it occurred somewhere beyond the 20 percent point. Under conditions of the present study, up to 20 percent of the land area in high quality wetland vegetation did not appear to be an excessive amount of nesting cover.

## NESTING IN SEDGE MEADOWS

Sedge meadows contained an average density of 23 nests per 100 acres (Table 7). In spite of this comparatively low density, sedge meadows were the most important wetland type for nesting. Sedge meadows constituted 61 percent of

the permanent wetland acreage (Table 6) and contained 54 percent of all wetland nests (Table 7).

Plant composition and nest density showed wide variability from stand to stand. An important aim of this investigation was to identify plant indicators of vegetation combinations which were most attractive for nesting, so that fieldmen could evaluate sedge meadow vegetation as potential nesting cover.

We analyzed sedge meadow vegetation as a continuous variable by employing the ordination techniques of Curtis (1959). The first step was to obtain a quantitative

**TABLE 8.** List of 21 most prevalent plant taxa in order of decreasing importance indices based on compositional studies of sedge meadow vegetation

Scientific Name	Common Name	Importance Index*
<u>Carex</u> spp.	Sedge	1,431
<u>Calamagrostis canadensis</u>	Bluejoint grass	423
<u>Solidago</u> spp.**	Goldenrod	412
<u>Phalaris arundinacea</u>	Reed canary grass	410
<u>Poa pratensis</u> ; <u>P. palustris</u>	Bluegrass	283
<u>Agrostis gigantea</u>	Redtop grass	150
<u>Helianthus grosseserratus</u> **	Sunflower	115
<u>Glyceria striata</u>	Manna grass	91
<u>Eupatorium maculatum</u> **	Joe-pye weed	81
<u>Spartina pectinata</u>	Cordgrass	81
<u>Thalictrum dasycarpum</u> **	Meadow rue	77
<u>Salix</u> spp.	Willow	75
<u>Urtica dioica</u> **	Nettle	70
<u>Verbena hastata</u> **	Vervain	65
<u>Cirsium arvense</u> **	Canada thistle	61
<u>Typha latifolia</u>	Common cattail	52
<u>Asclepias incarnata</u> **	Marsh milkweed	46
<u>Mentha arvensis</u>	Mint	45
<u>Polygonum</u> spp.	Smartweed	41
<u>Ambrosia trifida</u> **	Giant ragweed	39
<u>Aster</u> spp.**	Aster	30

\*Combined index values based on vegetational ratings made on 408, 1-acre plots distributed at random in 34 sedge meadow stands, 1959-64.

\*\*Herbaceous plant taxa whose combined relative importance values are plotted on the sedge meadow ordination in Figure 7.

description of the vegetation of each sedge meadow stand. Each wetland tract typed as sedge meadow was considered an individual stand. At time of nest searching, the vegetation of each 1-acre plot assigned to each stand was individually described. Because plot locations were randomized, a composite of these records obtained over the period of study provided a reasonable basis for characterizing the composition of each stand. Certain stands were excluded from analysis; (1) those which showed evident changes in plant composition owing to succession or change in water levels during the study; (2) those which

contained fewer than 5 sample plots in total; and (3) those in which wetland vegetation other than the sedge meadow type was conspicuously present. In spite of this final precaution, many of the stands showed a considerable degree of vegetational heterogeneity, particularly in relation to grazing which was characteristically heavier on the edges than toward the center. In total, 34 stands were selected for analysis. These varied from 9 to 53 acres in size. Information on stand composition was available from 5 to 44 plot descriptions per stand.

A 10-point scale was assumed for each plot. Six points were arbitrarily

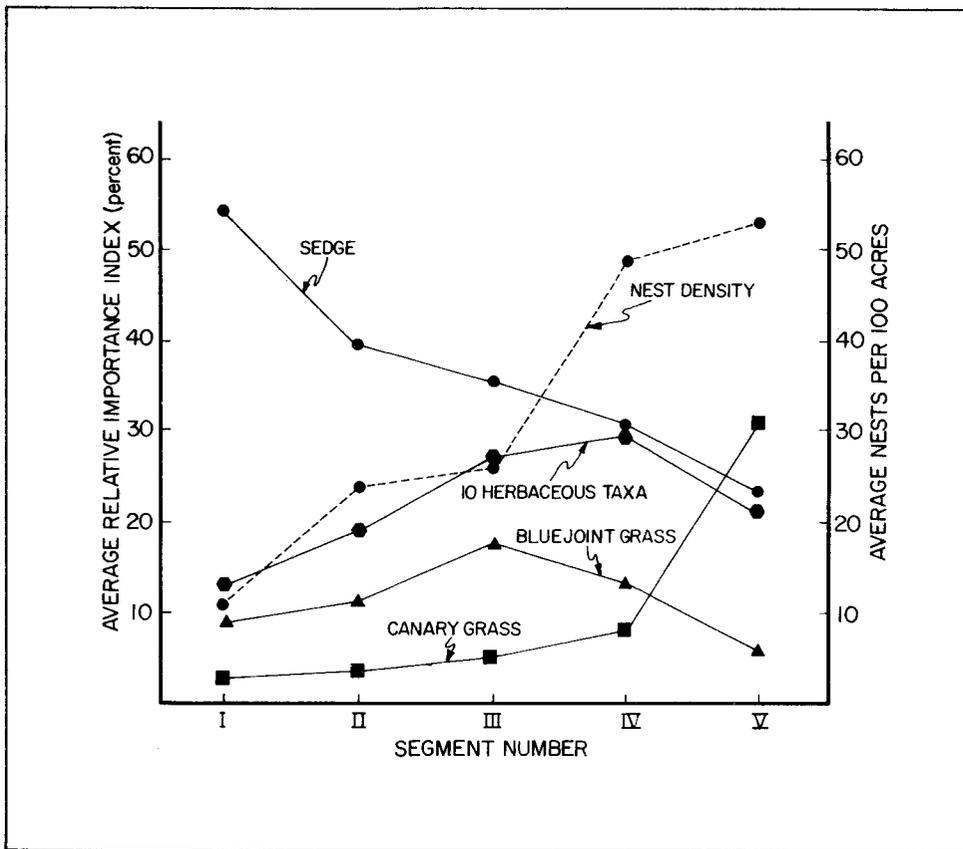
assigned to the dominant or codominant species and four to the subdominants. If more than four subdominants were listed, each of the top four received one point apiece and the others were ignored. If fewer than four subdominants were listed, each received a single point and the unused points were transferred to the dominant group. Codominant plants shared equal ratings. Ratings for each plot in a given stand were then added to give an *importance index* for each taxon in that stand.

The number of plant taxa listed per stand varied from 14 to 44 and averaged 21. Individual taxa were then ranked according to their combined importance index in all 34 stands as a group, and the 21 leading taxa were counted off (Table 8). Subsequent handling of the data was restricted to these 21 most prevalent taxa. The *relative importance index* of each of the 21 was then calculated for each stand. These totaled 100 for each stand and made it possible to compare directly the relative importance of each taxon from stand to stand.

Each stand was next compared with each other using the *index of similarity* (Curtis 1959:601). Finally, a 2-dimensional ordination of the 34 stands was constructed from a matrix of these values according to methods described by Bray and Curtis (1957). The purpose of this ordination was to show graphically the relationship of each stand to all others (Fig. 7), and the distance between any two stands being inversely proportional to their vegetational similarity. On such an ordination, it was possible to plot nest densities from stand to stand against the behavior of selected plant taxa and to examine the results for possible correlations.

Information on grazing intensity was also incorporated into the analysis. At time of nest searching, each stand was subjectively rated as ungrazed, lightly grazed, or moderately grazed. Heavily grazed stands were typed as lowland pasture and were not sampled for pheasant nests.

Figure 7 demonstrates a gradient in nest density running from upper left of the ordination to lower right, higher nesting use being generally associated with decreasing im-



**FIGURE 9.** Relationship between vegetational composition of sedge meadows and density of pheasant nests in each of five segments along 45-degree diagonal drawn from upper left to lower right of ordination in Figure 7. Based on 22 individual stands, excluding all moderately grazed stands and all stands in which relative importance indices for bluegrass and redtop grass exceeded 30 percent. Herbaceous plant taxa identified in Table 8.

portance of sedge. The relationship between vegetational composition and nest density, however, was somewhat obscured by stand-to-stand differences in grazing pressure. At all locations on the ordination, it was clear that heavier grazing pressure was associated with less intensive use for nesting.

All moderately grazed stands were removed from consideration to clarify the relationship between stand composition and nest density. Stands which showed high importance values for bluegrass and redtop grass, also were excluded since these stands were seldom used for nesting whether in grazed or undisturbed condition.

To carry the analysis further, a line was drawn at a 45-degree angle through the ordination. Perpendiculars to this line were dropped from each of the 22 points which excluded all moderately grazed stands as well as all stands in which

bluegrass and redtop grass achieved a combined relative importance index greater than 30 percent. This gave a linear arrangement of stands along a gradient of increasing nest density. The sequence was then divided into five segments, from upper left to lower right, and the average relative importance of the various plant taxa in each segment was plotted against the average density of nests.\*

With effects of grazing minimized, it became clear that nest density was inversely related to the relative importance of sedge, and that nesting use progressively increased where sedge shared dominance with either canary grass or a mixture of lowland forbs (Fig. 9). Highest nest densities were in

\*We are indebted to Dr. O. L. Loucks, University of Wisconsin Department of Botany, for suggesting this method of arranging stands along a diagonal.

stands which showed maximum representation of canary grass, herbaceous species, and to a lesser extent bluejoint grass.

Nest densities averaged 53 per 100 acres in sedge meadows where canary grass importance was highest (Segment V), compared with 43 per 100 acres in ungrazed monotypes of this species. In sedge meadows where herbaceous taxa attained the highest relative importance (Segment IV), nest densities averaged 49 per 100 acres, versus 68 per 100 acres in stands typed as predominantly herbaceous (Table 7). Nesting in sedge-canary grass or sedge-herbaceous cover was therefore about comparable to essentially pure stands of canary grass or herbaceous vegetation. Sedge meadows in which these taxa achieved codominance thus were rated as highly as the herbaceous and canary grass types as pheasant nesting cover.

In general, we believe that the greater attractiveness of sedge-canary grass and sedge-herbaceous cover could be attributed to the quantity and quality of residual cover present in spring. Stands of essentially pure sedge, sedge-bluegrass, or sedge-redtop tended to become severely flattened over winter; whereas the coarser stems of canary grass and lowland forbs were more resistant to compaction and provided more favorable ground cover for nest concealment. Heavier stems of these species also tended to support vegetation which was more susceptible to lodging, producing more abundant clumps of cover in which nests could be concealed before new growth of vegetation began in spring.

Of 145 nests located on sample plots in sedge meadows, plant cover providing actual nest concealment in 56 percent of the cases did not include sedge, and sedge was listed as the primary source of concealing vegetation at only 21 percent. This comparison further demonstrated the importance of nonsedge cover to pheasant nesting in the sedge meadow type.

It was clear that sedge meadow stands in this study which contained the highest density of nests had undergone major disturbance in the past. Frolik (1941) and Curtis (1959:426) collectively listed canary grass and 7 out of the 10

herbaceous taxa represented in Figure 7 (Table 8) as increasers or invaders of the original sedge meadow community following disturbance by overgrazing, partial drainage, or peat burning. In our area, effects of overgrazing and artificial lowering of water tables were especially evident. Our impression was that those stands which consistently held the highest density of nests had undergone the same general sequence of disturbance in the past—beginning with complete or partial drainage, followed by heavy grazing pressure, and subsequent abandonment as lowland pasture. Present-day vegetation of these stands was doubtless drier and characterized by greater prevalence of canary grass and/or lowland forbs than the original sedge meadow community. Sedge-redtop and sedge-bluegrass stands probably originated in a similar manner, but generally occupied drier sites which may have accounted for absence of canary grass and lowland forbs in the vegetational make-up.

#### NESTING IN HAYFIELDS

For both study areas combined, approximately 79 percent of the hay acreage in an average year consisted of alfalfa or grass-legume mixtures in which alfalfa predominated; the remainder was composed of red clover or red clover mixtures. Seventeen percent of the harvested hay acreage was utilized as pasture, 11 percent was chopped for feedlot use, and 72 percent was cut and baled.

Unharvested hayfields consisted largely of grass-legume mixtures maintained as cover crops on land temporarily diverted from cultivation. About 41 percent was clipped for weed control each year, the remainder being left undisturbed. Roughly half of each year's acreage consisted of stands that had been out of production one or more previous years.

Phenology of hay growth was based on a sample of 30 to 40 fields in which cover height was measured at weekly intervals between mid-April and completion of the second hay harvest. Phenology of hay cutting was based on mowing dates recorded for all fields in which nest study plots were located.

Earliness of hay growth differed importantly from year to year (Table 9). Cover development was unusually early in 1964 and much retarded in 1961. The average date at which the 10-inch growth stage was reached was significantly correlated with average daily temperature between April 10 and May 15 ( $r$  with 5 df = -0.87; reference value at 0.05 = -0.75), but there was no correlation with total rainfall during the period. Soil moisture was apparently adequate each spring, and temperature was the major variable affecting hay growth.

Cover development also varied with stand composition and age. In an average year, 50 percent of the first-year alfalfa seedings reached the 10-inch growth stage by May 9, compared with the May 6 among older alfalfa seedings. Clover fields did not attain similar height until

May 22.

First-crop hay harvests ordinarily began in early June and extended to early July (Table 9). Average mowing dates were significantly correlated with the number of days in June with measurable precipitation ( $r$  with 5 df = 0.92; reference value at 0.01 = 0.87). The correlation between hay growth and mowing phenologies, however, was non-significant ( $r$  with 5 df = 0.61), suggesting little tendency for delayed harvest in years when hay growth was retarded. This was significant because it set the stage for annually varying rates of nest success owing to differences in how long hay was safe for nesting. The interval between the mean date at which the 10-inch growth stage was reached and the mean date of mowing served as an index to the length of this period and showed up to 11-day variation between years (Table 9).

Dates of nest establishment were known for 54 clutches located in fields in which hay growth had been periodically measured. Of the 54, first egg dates of only 8 preceded the 10-inch growth stage and only 3, the 6-inch stage. Because height measurements in individual fields were taken at only a single station, whereas nesting hens may have sought taller-than-average cover when hay was just becoming suitable for nesting, 10 inches appeared to be a reasonably close approximation of the height at which hay began to be used by nesting birds.

Nest densities averaged 5 per 100

TABLE 9. Annual variation in phenology of hay growth and time of first hay harvest

Year	Mean Date of 10-inch Growth Stage	First Hay Cutting			Interval in Days Between 10-inch Growth Stage and Mean Date of First Cut
		Start	Finish	Mean	
1959	May 14	June 6	July 5	June 13	30
1960	May 16	June 4	July 16	June 24	39
1961	May 25	June 2	July 6	June 22	28
1962	May 10	May 29	July 3	June 15	36
1963	May 11	June 3	June 26	June 19	39
1964	May 9	June 1	June 30	June 12	34
1965	May 16	June 3	July 5	June 15	30
Means	May 14	June 2	July 4	June 17	34

**TABLE 10.** Comparison of pheasant nesting use of hayfields by cover composition, treatment, and age of stand, 1959-64\*

Cover Composition Age, and Treatment**	Acres Searched	Nests Found	Nests Per 100 Acres <sup>1</sup>
Pastured hayfields			
Subtotal	533	27	5
Mowed hayfields			
Red clover	370	69	19
Alfalfa	1,048	212	20
First year seedings	540	94	17
Older seedings	508	118	23
Subtotal	1,418	281	20
Unharvested hayfields			
First year unharvested	88	18	21
Subsequent years	91	37	41
Subtotal	179	55	31

\*Based on sampling results from Alto Study Area in 1959 and combined results from Alto and Mackford areas in 1960-64.

\*\*Pastured and mowed hayfields segregated for this comparison, but combined for sampling purposes as harvested hayfields.

<sup>1</sup>Difference in nest density between treatment subtotals highly significant (chi-square with 2 df = 69.88; reference value at 0.005 = 10.60). Difference in nest density between first-year and older alfalfa seedings significant (chi-square with 1 df = 4.03; reference value at 0.05 = 3.84). Difference in nest density between first-year and subsequent years of nonharvest highly significant (chi-square with 1 df = 20.31; reference value at 0.005 = 7.88).

acres in pastured stands, 20 per 100 acres in mowed stands, and 31 per 100 acres in unharvested stands (Table 10). Light use of pastured hay was doubtless related to the short period of time this cover was available for nesting. In most years, grazing began shortly after cover growth was sufficient for nest concealment. Most fields were subdivided and grazed in rotation. For example, a 20-acre field might be fenced into halves and alternately grazed by 15 to 30 cattle. Cover deterioration was rapid under these circumstances, and pastured stands soon lost all potential value as nesting cover.

Nest density in mowed fields did not differ between red clover and alfalfa stands, but did show a significant difference between first-year and older alfalfa seedings (Table 10). Buss (1946:32-34) also reported an apparent preference for older seedings and attributed the difference to greater carryover of residual plant material from one growing season to the next. This interpretation may well have been true under the less intensive agriculture of Buss' time, but under the 3-cut system of alfalfa management followed by most farmers in the

present study, old seedings contained no more residual plant material in spring than new seedings. Alternatively, we believe the difference could be attributed to earlier growth of old seedings and accordingly to the longer period of time these stands were available for nesting. No difference in average mowing dates prevailed between old and newly established stands.

Only 7 percent of all hayfield nests occurred in second-growth hay. Ordinarily about 2 weeks were required for second-growth hay to grow to 10 inches in height. The mean date of the first hay cutting for all years combined was June 17, hence little of the hay acreage was again available for nesting until early July, by which time nest establishment was virtually finished for the year (Fig. 3). Infrequent nesting in second-crop hay was also reported by Baskett (1947), Dustman (1949), and Klonglan (1955).

Unharvested hayfields contained the highest average density of nests. Nesting in such cover during the initial year of retirement was not appreciably heavier than that which occurred in mowed stands, but nearly doubled during subsequent

years of nondisturbance. The large volume of residual plant cover provided by second-year and older retired stands appeared to be not only highly attractive for nesting, but also extended the period of time these stands were available to nesting birds.

Contrasting views have long been held on the relationship of nest placement to hayfield edges. Hamerstrom (1936) and Wight (1950) concluded that pheasants tended to select peripheral sites, whereas Leopold (1937), Baskett (1947), Klonglan (1955), and Nelson et al. (1960) reported no such tendency.

Methods previously described as a test of edge effect in wetlands were repeated for hayfields. Analysis was based on all treatment and cover types combined; however, the sample was heavily weighted to mowed stands. Results based on all years of study combined failed to reveal a significant departure from a random distribution of nests (goodness-of-fit bi-square with 5 df = 10.50; reference value at 0.05 = 11.07).

From alleged concentration of pheasant nests near edges, delayed mowing of field exteriors has occasionally been recommended as a means of improving pheasant production (Erickson et al. 1951:42 and Thompson 1964). Absence of an overall edge effect in the present study suggested little potential gain from such a practice.

The relationship of field size to nest density was evaluated by comparing nest densities on sample plots according to field size in which plots were located. In fields smaller than 10 acres, nest density averaged 16 per 100 acres (59 nests), compared with 22 per 100 acres (143 nests) in fields 10 to 20 acres in size, 23 per 100 acres (63 nests) in fields 21 to 30 acres in size, and 27 per 100 acres (12 nests) in fields 31 to 40 acres in size. While the difference fell short of statistical significance (chi-square with 3 df = 7.04; reference value at 0.05 = 7.81), a probable preference for larger blocks of nesting cover seemed indicated. At least provisionally, fields larger than 10 acres are recommended over smaller acreages where hay is to be set aside and left unharvested to encourage pheasant production.



*Strip cover on a roadside*



*Hayfield cover - - a first cutting in alfalfa*

### NESTING IN STRIP COVER

Roadside cover was subdivided into four categories: (1) grassy; (2) herbaceous (3) sedge-canary grass; and (4) woody. Grassy roadsides made up 80 percent of the total, consisting largely of bluegrass, quackgrass, and occasionally bromegrass. Herbaceous roadsides typically included wild parsnip, goldenrods, burdock, common milkweed, and assorted other forbs. Sedge-canary grass cover occurred where roadsides bordered wetland areas and consisted mainly of sedge, canary grass, and bluejoint grass. Commonest woody species were black cherry, plum, locust, boxelder, American hazel, gray dogwood, and blackberry. Cover types were based principally on vegetation occupying that half of the roadside opposite the road surface. Over 90 percent of all roadside nests were located in this strip.

Three categories of fencerow vegetation were recognized: (1) grassy; (2) herbaceous; and (3) woody. Cover composition was similar to corresponding types described above.

Ditch bank vegetation types were: (1) canary grass; (2) herbaceous; and (3) woody. The canary grass type represented essentially pure stands of this grass which constituted over 50 percent of the total ditch bank acreage. Herbaceous cover consisted of aster, goldenrod, meadow rue, and frequently nettle.

Woody ditch banks were vegetated mainly by willow shrubs, red-osier dogwood, and elderberry, usually with a dense ground cover of canary grass.

Because of the linear configuration of strip cover, the number of nests observed per mile rather than the density per acre seemed to be a more realistic measure of the intensity of nesting use. Sample plots in strip cover varied considerably in length and usually contained more than a single vegetation type. At time of nest searching, data were recorded on the width of the strip and the percentage of each plot occupied by each cover type. Nest locations were classified accordingly, from which nest-per-mile figures could be calculated and compared between cover types and cover widths.

Nest occurrence in strip cover was lowest in grassy vegetation, intermediate in herbaceous cover, and highest in the woody and canary grass types (Table 11). Because strip cover was most important for early nesting (Fig. 6), these differences probably depended on characteristics of residual cover in spring. Grassy vegetation of most roadsides and fencelines tended to become severely flattened under winter snow, supplying poor cover before new growth in spring, whereas the denser cover of other strip cover types provided much improved opportunities for nest concealment during early stages of nesting.

Roadsides were usually 15 to 20 feet in width. Fencelines differed greatly in width, and a preference seemed to exist for wider strips (Table 12). Too few ditch bank data were available to test the relationship between cover width and nest occurrence independent of vegetation type, but for all types combined, the average number of nests per mile was 4.2 in strips less than 15 feet wide, 3.6 in strips 16 to 30 feet wide, and 11.3 in strips over 30 feet in width. The difference was highly significant (chi-square with 2 df = 15.39; reference value at 0.005 = 10.60).

Nesting in strip cover thus appeared to depend on cover density and cover width. Management practices that served to widen strip cover and to favor denser herbaceous and shrubby vegetation over grassy strips probably would result in greater nesting use by pheasants.

### NESTING IN PEAS AND SMALL GRAINS

Planting dates of green peas for canning were staggered between late April and early June. Roughly 60 days were required for maturity and harvests ordinarily extended from late June to early August. Out of 22 backdated clutches observed in this cover type, egg laying in only one preceded the 13-inch growth stage. This generally corresponded to the stage of first bloom reached about 35 days after planting.

**TABLE 11.** Comparison of nest occurrence in strip cover by vegetation type, 1959-64\*

Vegetation Type	Miles Searched	Nests Found	Nests Per Mile
Roadsides**			
Grassy	45.8	50	1.1
Herbaceous	4.7	10	2.1
Sedge-canary grass	4.9	14	2.9
Woody	3.0	11	3.7
Fencelines <sup>1</sup>			
Grassy	53.8	31	0.6
Herbaceous	13.6	15	1.1
Woody	12.5	28	2.2
Ditch banks <sup>2</sup>			
Herbaceous	3.9	12	3.1
Canary grass	7.4	37	5.0
Woody	1.6	11	6.9

\*Based on sampling results from Alto Study Area in 1959 and combined results from Alto and Mackford areas in 1960-64.

\*\*Difference in average number of nests per mile between roadside types highly significant (chi-square with 3 df = 21.49; reference value at 0.005 = 12.84).

<sup>1</sup>Difference in average number of nests per mile between fenceline types highly significant (chi-square with 2 df = 30.86; reference value at 0.005 = 10.60).

<sup>2</sup>Difference in average number of nests per mile between ditch bank types nonsignificant (chi-square with 2 df = 4.00; reference value at 0.05 = 5.99).

**TABLE 12.** Comparison of nest occurrence in fencelines by width of strip, 1959-64\*

Vegetation Type	Width in Feet	Miles Searched	Nests Found	Nests per Mile
Grassy**	1-6	44.5	16	0.4
	7-12	7.8	12	1.5
	13-18	1.5	3	2.0
Herbaceous <sup>1</sup>	1-6	8.4	6	0.7
	7-12	5.2	9	1.7
Woody <sup>2</sup>	1-6	0.8	0	0.0
	7-12	6.5	10	1.5
	13-18	5.2	18	3.5

\*Based on sampling results from Alto Study Area in 1959 and combined results from Alto and Mackford areas in 1960-64.

\*\*Difference in average number of nests per mile between fenceline widths highly significant (chi-square with 2 df = 18.05; reference value at 0.005 = 10.60).

<sup>1</sup>Difference in average number of nests per mile between fenceline widths nonsignificant (chi-square with 1 df = 2.17; reference value at 0.05 = 3.84).

<sup>2</sup>Difference in average number of nests per mile between fenceline widths nonsignificant (chi-square with 2 df = 5.21; reference value at 0.05 = 5.99).

Nest density in peas averaged 9 per 100 acres (Fig. 5), compared with 20 per 100 acres in mowed hay (Table 10). Peas were seldom harvested more than 25 days after they became available for nesting, whereas the mean date of hay cutting fell 35 days after the average date at which hayfields provided nesting cover (Table 9). Less frequent nesting in peas thus depended in part on the shorter period of time this crop was available to nesting hens.

The average date of establishment among seven backdated clutches in small grains was July 6, the earliest being started during the final third of June (Fig. 6). The average height of this crop at this season was approximately 30 inches. Virtually, the entire small grain acreage consisted of oats.

One of the real enigmas of our study was the extremely low number of nests found in small grains. Nest densities averaged only 3 per 100 acres (Fig. 5), and small grains contained less than 3 percent of total nest production. Either growth of small grains was simply too late for nesting or alternative late season cover, particularly hay, which was so much more preferred that small grains were for the most part avoided by nesting hens. In general, the latter seemed the more plausible interpretation. The fact that onset of nesting in small grains followed closely after the peak of first hay cutting implied that hens tended to use this cover type only while hayfields were temporarily unavailable as nest sites.

## ANNUAL VARIATION IN NEST DISTRIBUTION

Over 92 percent of all nesting attempts occurred in strip cover, wetlands, and hayfields. Strip cover contained a comparatively constant fraction of each year's nesting effort, but the distribution of nests between wetlands and hayfields showed a marked degree of annual variability (Fig. 10). The acreage of these cover types available to nesting birds fluctuated to some extent from year to year, but far too little to account for shifts in nest distribution of the magnitude observed.

## Influence of Hay Growth

How the phenology of nesting dovetailed with the earliness of hay growth appeared to be the predominant influence on nest distribution. Hay growth was early in 1962 and phenologically average in 1959 (Table 9). Nesting, however, in both years was considerably delayed. Figure 11 shows that large acreages of hay became available for nesting before establishment of initial clutches had been completed. As a result, hayfields attracted an unusually high percentage of the initial nesting attempts, accompanied by corresponding reduction in use of permanent cover. In 1959 and 1962, only 28 percent of all clutches were located in wetlands, compared with 45 percent as the average during all other years of study.

By comparison, nesting was phenologically advanced in 1961 and 1963, during which hay growth was retarded or near normal, respectively. Virtually all initial clutches had already been established before hay became available, and use of wetland cover was correspondingly high. Hayfields were used almost entirely for renesting and contained a comparatively small fraction of total nest production.

Hay growth and nesting phenologies were near normal in 1960. Although hayfields apparently attracted a small percentage of the initial nesting attempts, overall use of this cover type was nearly as high as the mean observed in 1959 and 1962. Comparatively heavy use of hay in 1960 could be explained by the long-delayed hay harvest of this season which prolonged the period of time that hay was available for nesting. Wetland cover was also wetter than normal in 1960, which may also have contributed to heavier nesting use of hayfields.

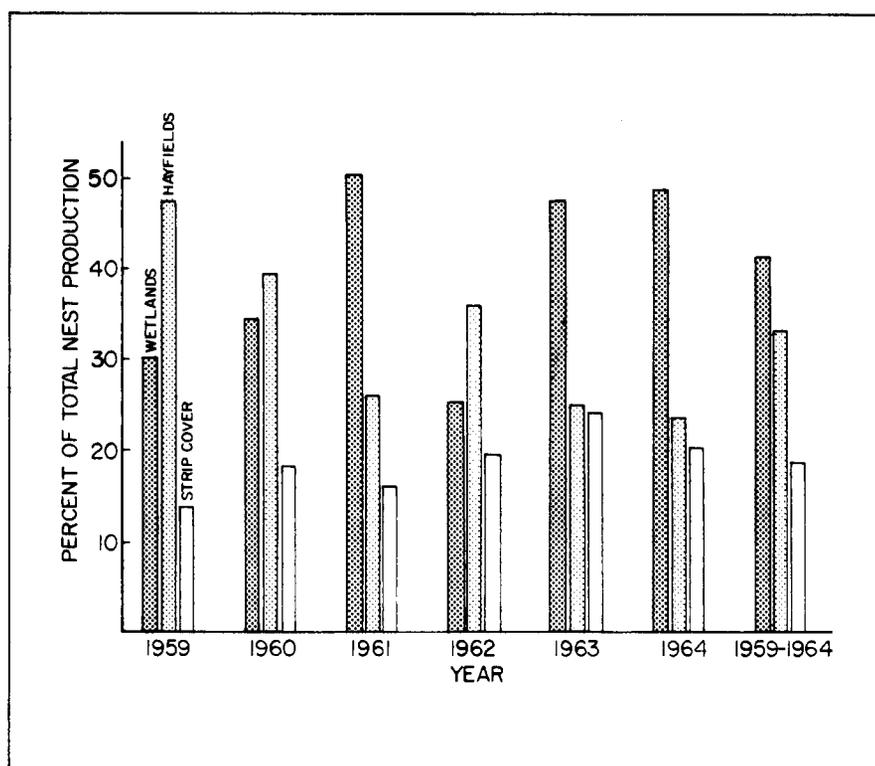
Onset of nesting was approximately normal in 1964, and hay growth was the earliest on record. Hayfields accordingly attracted a large proportion of early nesting attempts, but overall use of this cover was comparatively low. Nest success in permanent cover was appreciably higher in 1964 than in previous years, hence there was less need for renesting and consequently lower overall use of hay.

Our conclusion from these trends was that delayed onset of egg laying and/or advanced hay growth in spring was associated with higher use of hayfields for initial nesting attempts. This resulted in hayfields containing a larger fraction of total nest production than occurred when

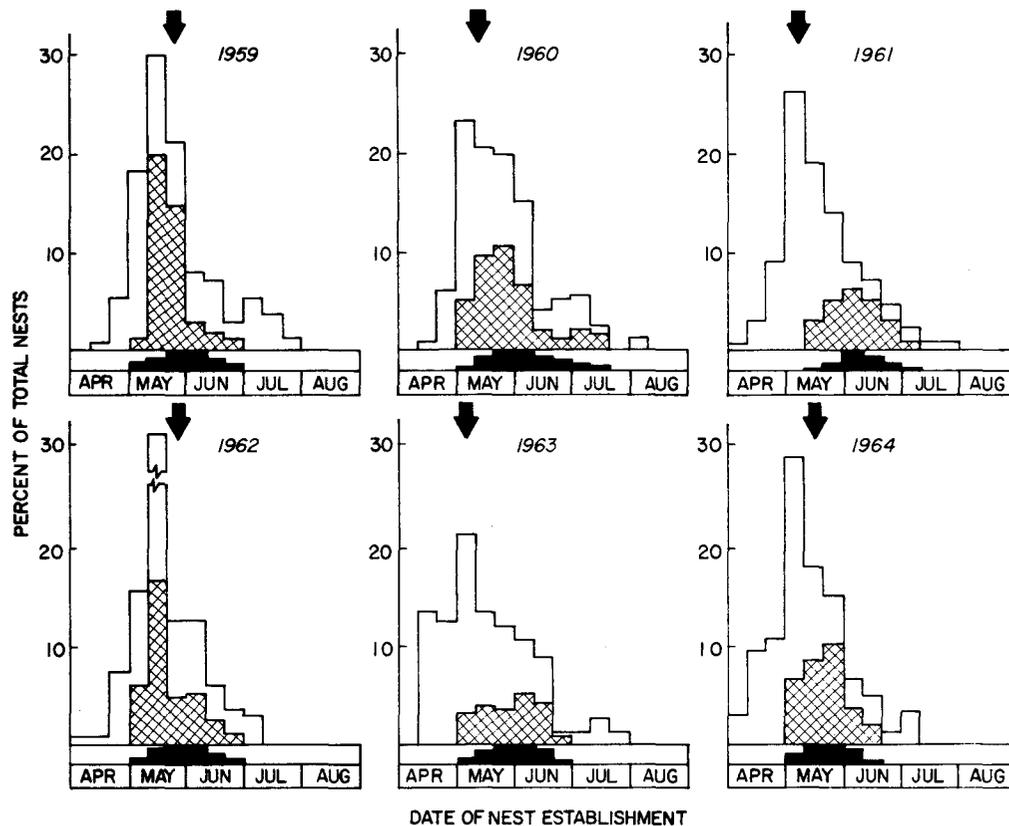
the majority of first nesting attempts had already been started before hay became available; in which circumstance, hay contained mainly renests. Nest distribution between hay and nonhay cover also appeared to be influenced by the schedule of hay cutting, which determined how long hay was available for nesting, and indirectly by rates of nest mortality which affected levels of renesting activity.

Two other generalizations could also be made from these trends: (1) Years when hayfields contained predominantly first nesting attempts were characterized by relatively large cohorts of nests established in hay soon after this cover type became suitable for nesting (Fig. 11). Years when hayfield nesting consisted mainly of renests were typified by more staggered distribution of nest starting dates. Evidence will be presented later showing that this basic difference in phenology of hay nesting had an important bearing on nest success, and very likely also contributed to yearly differences in brood survival.

(2) Early nesting years (1961 and 1963) were typified by proportionally heavier nesting use of wetlands and lower use of hay—late-nesting years (1959 and 1962) by the reverse (Fig. 10).



**FIGURE 10.** Annual variation in distribution of total nest production between major types of nesting cover. Based on sampling results from the Alto Study Area in 1959 and combined results from the Alto and Mackford areas in 1960-64. Information from Gates (1971:834-850).



**FIGURE 11.** Relationship between phenology of nest establishment representing total clutch production (open bars) versus phenology of nesting in hayfields (cross-hatched bars). The relative height of the latter to the former is proportional to the percentage of clutches established in hay by date of nest establishment. Excludes nests located in unharvested hayfields and second-growth harvested hay. Solid bars represent seasonal availability of hayfields for nesting. The left sides of the frequency

distributions based on the percentage of measured fields reaching the 10-inch growth stage and the right sides on the percentage of fields remaining uncut through completion of the first hay harvest. Arrows at the top of the graphs identify the date at which cumulative nest production by 10-day periods equaled the number of hens censused on study areas in early May and may be taken as a rough approximation of the separation point between initial nesting attempts and renesting efforts.

Because hatching success was consistently higher in wetlands, early nesting years were characterized by more favorable distribution of nests between cover types. Wagner et al. (1965) showed for Wisconsin that rates of pheasant reproduction tend to be higher when nesting is earlier. Differences in cover use between early and late nesting years may well contribute to this phenomenon.

### Influence of Population Density

The percentage of the hen population which remained in the vicinity of wetland cover to breed was density dependent, and with population increase proportionally more

hens were forced into nonwetland habitats for nesting (Gates and Hale 1974:34). An inverse relationship might therefore have been expected between population density and degree of wetland use for nesting. From gross inspection of spring population trends, however, no such trend was evident. Other variables affecting nest distribution, notably phenological differences in nesting and hay growth, apparently over-rode the expected relationship.

Closer scrutiny of the data was possible by comparing wetland use between pairs of years in which nesting phenology was similar. Even though hay growth was not necessarily comparable, the possible role of population density on nest dis-

tribution could be evaluated with other influences more nearly constant. Data were from the Alto Study Area only, which covered a longer span of years and greater range of population fluctuation (Table 13).

Nesting began early in 1961 and 1963, and although hay growth was earlier in 1963, nesting use of wetlands was not appreciably lower. Conceivably, this was a function of 1963's lower population density. Nesting phenology in 1964 was comparable to 1960, but hay growth was decidedly earlier. Notwithstanding, the percentage of all nests located in wetlands in 1964 was nearly 40 percent higher than 1960, perhaps in part determined by the

lower population level that prevailed in 1964. Nesting was delayed both in 1959 and 1962. Even though hay growth was considerably earlier in 1962, the percentage of nests in wetland cover was near comparable, again possibly influenced by 1962's lower density of nesting hens.

These comparisons indicate that population density may have exerted a subsidiary effect on nest distribution. Coupled with results of spring movement studies demonstrating density dependent egress of hens from wetland cover, we conclude that higher population levels on our study area should be subject to long-term lower reproductive success through heavier reliance on nonwetland cover for nesting.

### COMPARISON WITH OTHER NESTING STUDIES

Patterns of nest distribution in our study were compared with nesting studies conducted in Iowa (Baskett 1947; Weston 1953; Klonglan 1955; Wright and Otte 1962; and Klonglan 1962), Ohio (Dustman 1949), South Dakota (Trautman 1960), Nebraska (Linder et al. 1960), Illinois (Warnock and Joselyn 1964a, Minnesota (Chesness et al. 1968), and Pelee Island (Stokes 1954). From the generalized distribution of nests observed elsewhere in the midwest, Wisconsin findings demonstrated three notable departures: (1) unusually heavy dependence on permanent cover for nesting, particularly wetlands; (2) an unusually small percentage of the total nest production located in hayfields in

relation to the large amount of such cover available for nesting; and (3) near absence of nesting in small grains which in most other areas attracts a substantial percentage of total clutch production.

To interpret these differences, one must begin with the abundance of hay which typifies Wisconsin pheasant range. Dairy farming is the major farm enterprise of the state, and large acreages of hay characterize this type of agriculture. Hay acreages in the present study constituted 17 percent of the land area, nearly double the mean reported in all non-Wisconsin studies listed above. This abundance of hay was not unusual for Wisconsin pheasant range; hay acreages at Waupun tended to be somewhat lower than average.

The availability of hay as nesting cover in Wisconsin is markedly higher than is true of most other areas in the midwest. Few if any nesting hens in this state probably occupy home ranges in spring which do not include one or more hayfields as potential nest sites. This, coupled with an innate preference for hay, appears to account for virtual absence of nesting in small grains.

Rates of nest success in hay, however, were far too low (as will be shown in the next section) for a population to maintain itself if nesting is confined principally to this cover type. Alternative cover must therefore be present to raise the mean level of hatching success to whatever threshold is required for population maintenance. Small grains clearly do not serve the need under Wisconsin conditions, and

strip cover is neither abundant enough, nor is nest success high enough, to offset the heavy production losses sustained by hay mowing. Wetlands are the only cover type which is present in sufficient amounts, and in which nest success is adequate, to cushion the effects of heavy mowing mortality on reproductive success. As a result, populations are low or virtually nonexistent where wetlands are not present to draw a sufficiently high percentage of the nesting hens out of hayfield cover and thereby maintain the needed level of hatching success. Wagner et al. (1965:94) earlier reached essentially the same conclusion on the importance of wetlands in counterbalancing the large acreages of hay that typify Wisconsin pheasant range.

In other states, with lesser hayfield acreages and correspondingly heavier nesting use of small grains, need for permanent cover is apparently less. In contrast to Wisconsin, adequate levels of reproductive success are apparently maintained even though nesting is confined largely to cropland cover and less permanent cover is available to nesting birds.

### WETLAND MANAGEMENT IMPLICATIONS

The percentage of total nest production that occurred in wetland cover in our study was directly proportional to the acreage of wetland cover types (Fig. 8). The critical implication of this finding was that nest success in wetlands

**TABLE 13.** Summary of statistics on the relationship of nesting phenology, hay growth phenology, and population density to use of wetland cover for nesting, Alto Study Area, 1959-64.

Nesting Phenology	Phenology of Hay Growth								
	Early			Average			Late		
	Year	Hen Population	Percent Nests in Wetlands	Year	Hen Population	Percent Nests in Wetlands	Year	Hen Population	Percent Nests in Wetlands
Early	--	--	--	1963	250	56	1961	409	54
Average	1964	269	52	1960	317	37	--	--	--
Late	1962	255	33	1959	348	30	--	--	--

was considerably higher than the mean of all types of upland nesting cover combined. The net effect of wetland drainage on pheasants, accordingly, must be to force nesting hens into less secure nest sites with consequent reduction in overall hatching success. Wagner et al. (1965:95-97) reviewed a number of specific instances in Wisconsin in which intensive drainage enterprises were associated with virtually complete demise of local pheasant populations. Unquestionably, these declines can be attributed in large part to loss of wetland cover essential for reproduction.

Few areas within Wisconsin pheasant range still contain as high as 20 percent of the land area in wetlands, with the overall mean closer to 10 percent. Between the mid-1930's and late 1950's, approximately 26 percent of the wetland acreage in southeastern Wisconsin was lost through drainage (Wagner et al. 1965:94). As wetland habitat progressively disappears from the scene, there is every reason to expect that pheasant nesting will become increasingly dependent on nonwetland cover, that reproductive success will decline, and that population levels will drop accordingly. The fact that area-to-area differences in population density in this study tended to be proportional to the amount of wetland cover available suggests that population levels are roughly adjusted to the amount of wetland cover present, and that loss of such habitat must inevitably lead to population reduction. Without question, preservation of wetland nesting cover is the most critical management need for Wisconsin pheasants.

Gates and Hale (1974:51) suggested that scattered wetland preservation for pheasants would be most effective if key tracts of nesting and winter cover were acquired in discrete management units fulfilling year-round habitat requirements of local populations. The recommended size of these units was approximately 3 x 3 miles, with some form of traditionally used winter cover located near the center. According to this plan, highest priority for preservation should be given to nesting cover within a 2-mile radius of winter shelter. Only in areas where winter cover is well dispersed and management units

overlap should nesting cover be acquired more-or-less indiscriminately throughout the summer range.

Within this framework, those wetland types which afford the densest and driest cover in spring should be given first consideration. Herbaceous vegetation such as aster-goldenrod or canary grass deserve top ranking, followed by sedge meadow stands showing high representation of bluejoint grass, canary grass, and/or lowland forbs. Shrub-carrs with less than 50 percent shrub canopy may also be desirable, but those with complete or nearly complete shrub layers should be avoided in favor of less-shaded stands. Essentially monotypic stands of sedge, sedge-bluegrass, or sedge-redtop should be rated along with cattail as poor investments in nesting cover.

Strict attention should be paid to water levels in establishing acquisition plans. Areas which consistently retain surface water as late as the first of May in a normal year should not be acquired as nesting cover, nor should flood plain wetlands subject to overflow during the major period of pheasant nesting. Ideally, acquisition priorities should be based on field inspections made between winter breakup and spring greenup, the densest and driest cover at this season being of maximum value to nesting pheasants.

Although the ideal would be to preserve all high quality nesting cover within a given unit, we suggest as a more reasonable goal approximately 5 percent of the land area, or roughly 250 to 300 acres per 9-section unit. If this amount of cover does not exist or cannot be preserved in an area, then the area should be disqualified as a management unit or set aside as lower priority for future development. If, on a township basis, it is impossible to preserve at least 5 percent of the land area in high quality wetland cover, then the number of management units should be reduced so that each will meet minimum standards.

Nesting cover should be as well dispersed throughout the management unit as feasible. Blocks of cover 20 to 40 acres in size may be most attractive for nesting on a per acre basis, but smaller stands should not be rejected on size characteristic

alone. Cover composition and dryness should outweigh all other considerations in judging the potential value of a given stand. Wetland areas larger than 40 acres might better be acquired in part in order to promote as wide dispersion of the acquisition acreage as possible.

Many of the wetland types recommended for acquisition do not represent stable plant communities, and it should be recognized that certain types of management may be required to maintain desirable nesting cover. Shrub succession is a case at point. Sedge meadows protected from disturbance are commonly invaded by shrubs, and management to arrest shrub dominance may often become necessary. The herbaceous wetland type appears to be especially unstable, and in some instances may require disturbance at intervals as short as 5 years to retain optimum cover composition. Several herbaceous stands in our study were almost entirely replaced by bluegrass over a 6-year period, and thus became virtually worthless for nesting. Generally speaking, canary grass appears to be most stable of the preferred wetland types. On lowland sites accessible to farm machinery, the most economical form of management in the long run might be to artificially establish canary grass as nesting cover.

Finally, various types of management could be implemented to enhance the value of stands originally acquired as second-rate or inferior nesting cover. The simple expedient of excluding cattle from most sedge meadow stands would produce improved conditions for pheasant nesting. Shrub control might be used to open up closed-canopy shrub swamps and encourage higher rates of nesting use. Actual mechanical disturbance, for example, bulldozing or discing, should be explored as methods of initiating secondary successions on sedge meadow lands to provide more attractive nesting cover. An important research need in this connection is to obtain a clearer understanding of the response of all wetland vegetation types to various kinds of disturbance, to ascertain the stability of the various stages of secondary succession, and to develop and refine management techniques for maintaining those stages most

favorable to pheasant and other forms of wildlife production.

More detailed criteria for a scattered wetlands program of pheasant habitat preservation have been established and are reported in Gates (1970).

## SUMMARY

Pheasant densities were highest in strip cover, intermediate in wetlands and hayfields, and lowest in small grains and peas. Differences in nesting use of various cover types reflected differences in cover preferences, cover availability and time of nesting in relation to seasonal changes in cover condition. Preferred nesting cover consisted of residual cover in wetlands in early spring and new growth in hayfields as the season progressed.

Nest densities in wetlands were highest in secondary successions on drained sites formerly utilized as cropland. In the sedge meadow type, which made up the largest percentage of the wetland acreage, nest densities varied directly with the prevalence of adventive species representing invaders of the original sedge meadow community in response to past disturbance by overgrazing and drainage. Nest placement in wetlands was random with respect to edge. Heavier grazing pressure was generally associated with lower nest density.

Use of hay for nesting began at the 10-inch growth stage. Nest densities in hay were highest in

unharvested stands, intermediate in mowed stands, and lowest in stands that were used as rotational pasture. Nesting hens demonstrated no tendency for selective use of hayfield edges. Though evidence was not conclusive, a preference existed for field sizes larger than 10 acres. Nest occurrence in strip cover was lowest in grassy strips, intermediate in herbaceous cover, and highest in canary grass and woody cover. Use of strip cover appeared to be directly related to cover density and cover width.

Over 92 percent of all nesting attempts occurred in wetlands, hayfields, and strip cover, the relative distribution of nests between the former two showing a wide degree of annual variability. Years when nesting was delayed and/or hay growth early resulted in hayfields attracting a proportionally higher percentage of initial nesting attempts than in years when establishment of initial clutches had already been completed before hay became available, in which circumstance hay was used predominantly or solely for renesting. Changes in population density also appeared to have a subsidiary effect on nest distribution.

That pheasants are largely dependent on wetland cover for successful reproduction appears to be a basic principle of Wisconsin pheasant ecology. The abundance of hay which typifies Wisconsin pheasant range inevitably attracts a

high percentage of nesting hens. Nest mortality in hay, however, is too high for populations to maintain themselves unless alternative cover is also present to counterbalance the heavy production losses in hayfields. Wetlands appear to be the only cover type in which nest success is high enough, and which attracts sufficient numbers of nesting hens, to raise the mean level of nest success to what is needed for population maintenance. The generalized relationship between population density and wetland availability demonstrated by this and previous Wisconsin research leads inevitably to the conclusion that future trends in pheasant populations will depend on success or failure in preserving wetland nesting habitat.

Management recommendations were: (1) that wetland nesting and winter cover be preserved in planned management units aimed at meeting year-round cover requirements of local populations; (2) that first priority in wetland acquisition be given to herbaceous, canary grass, and sedge meadow nesting habitat affording the densest and driest cover available in spring; (3) that 250 to 300 acres of nesting cover per 9-section management unit be regarded as the minimum acquisition goal; and (4) that management techniques be developed and used as necessary to maintain wetland vegetation in optimum forms of nesting cover.

# NEST SUCCESS AND CAUSES OF FAILURE

## NEST SUCCESS BY COVER TYPE

Nest success was highest in unharvested hay (63%) and wetlands (46%), intermediate in small grains (31%) and strip cover (26%), and lowest in harvested hay (14%) and peas (0) (Fig. 12). These were best viewed as maximum rates owing to disappearance of nest sign and because of lower efficiency of search for unsuccessful clutches. Because the former bias was most pronounced in strip cover (Table 2), actual hatching success in strip cover was proportionally lower than indicated and may not have been appreciably better than that which prevailed in harvested hay.

Significant yearly differences in hatching success were demonstrable only in harvested hay (Gates 1971:851-861). Nest success on this cover type varied from 1 percent in 1961 to 30 percent in 1962. Hatching success did not show a significant degree of annual variability in any other cover type.

In 1964, however, the rate of success in wetlands and strip cover combined was 49 percent (79 nests), versus 34 percent (499 nests) as the 1959-63 mean. The difference was highly significant (chi-square with 1 df = 7.11; reference value at 0.01 = 6.63) and seemed to imply a marked reduction in levels of nest mortality in permanent cover. Because strip cover and wetlands were most important for early nesting, it appeared that nest success in permanent cover was substantially improved in 1964, with correspondingly fewer hens obliged to renest and consequent improvement in breeding success.

## CLUTCH LOSSES IN WETLANDS

Nest success in wetlands averaged 46 percent (Table 14). Whether this high rate of hatching success in wetlands prevails generally throughout Wisconsin is unfortunately obscure. Buss (1946:28-44) did not report nest success rates for each

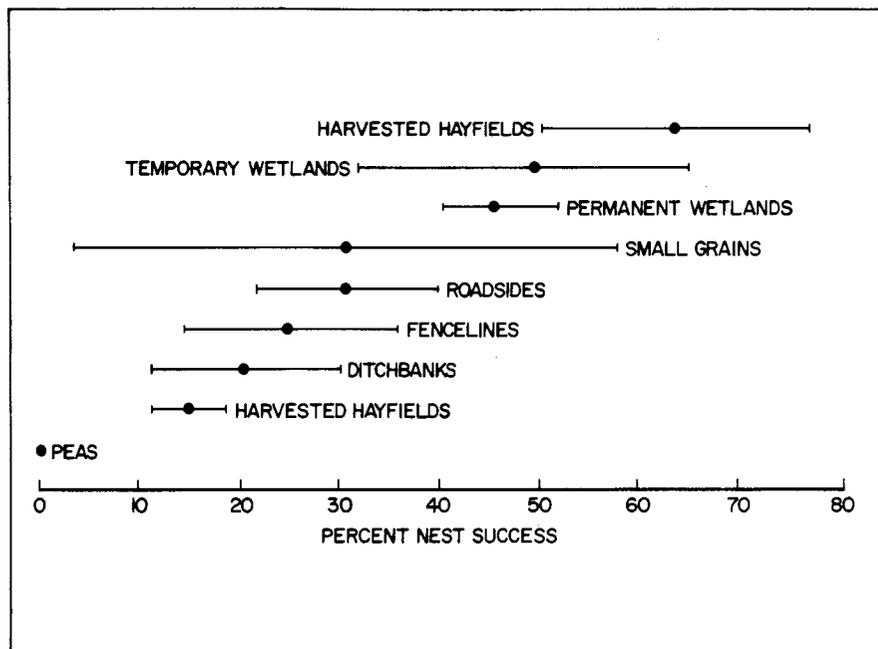


FIGURE 12. Weighted average rates of nest success and 95 percent confidence limits by individual cover types, 1959-64. Based on sampling results from the Alto Study area in 1959 and combined results from the Alto and Mackford areas in 1960-64. Information from Gates (1971:851-861).

cover type studied, but listed 39 percent success of 74 nonhay nests in 1941 at the Nevin Fish Hatchery Marsh in Madison. Eighty-four percent of the nonhay nests he observed were located in either pastured or unpastured marsh. From this we infer that hatching success in wetlands fell somewhere between 27 and 47 percent and may have been close to the rate that we observed.

Nest mortality in wetlands was chiefly the result of predation, which accounted for 69 percent of all nest destruction assigned to individual causes of failure (Table 14). Mammals were responsible for the majority of the losses, with skunks, raccoons, and foxes, in order listed, the most important in this regard.

Abandonment and burning ranked second as mortality factors and accounted for 13 percent of all observed nest loss in wetlands. Nest destruction by fire was restricted largely to 1961 and 1963. Both were

dry springs and years of early nesting, with large numbers of nests established in wetland cover before spring greenup was sufficiently advanced to preclude fire.

Water levels in most years gradually receded during the nesting season, and flooding losses were for the most part inconsequential. In 1960, this trend was reversed, with water levels in certain tracts rising as much as 12 inches after mid-May. However, only 5 percent of the wetland clutches were known to have been destroyed by flooding.

No relationship was detected between hatching success and nest placement in relation to edge. Success averaged 46 percent (174 nests) within the outermost 50 yards, compared with 43 percent hatching success (102 nests) elsewhere. Nor was any relationship demonstrable between wetland size and nest success. Success averaged 43 percent (57 nests) in tracts up to 20 acres in size, 48 percent (141

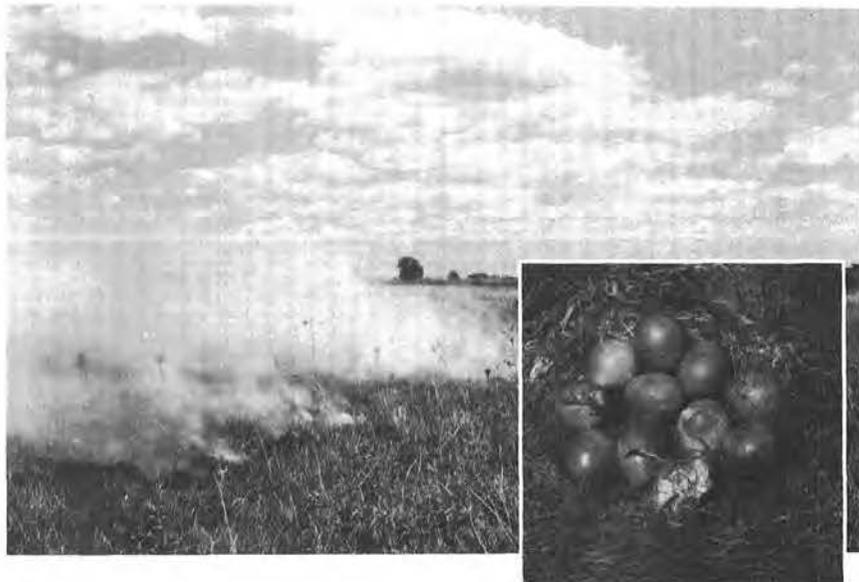
TABLE 14. *Weighted average nest success and causes of nest mortality by cover type, 1959-64\**

Cover Type	No. Nests	Percent Successful		Percent Unsuccessful by Cause of Failure							
		Mean	95 Percent Conf. Limits	Farm Mach.	Preyed Upon	Abandoned	Burning	Cattle	Flood-ing	Obser-ver	Undet.
Wetlands	323	46	41-52	1	34	6	6	1	1	1	2
Permanent	287	46	41-52	1	35	7	6	1	1	1	3
Temporary	36	49	32-66	8	26	0	14	0	0	3	0
Strip Cover	255	26	21-32	2	51	12	2	1	1	1	3
Roadsides	103	31	22-40	3	45	15	0	2	2	0	3
Fencelines	78	24	15-35	1	55	11	3	1	0	0	5
Ditch banks	74	20	12-30	0	59	10	3	2	2	5	0
Hayfields	691	18	16-21	69	3	7	0	2	0	0	1
Harvested	636	14	11-17	74	2	7	0	2	0	0	1
Unharvested	55	63	50-76	11	17	9	0	0	0	0	0
Small Grains	13	31	4-58	70	0	0	0	0	0	0	0
Peas	45	0	---	98	0	0	0	0	0	0	2

\*Based on combined results of supplemental nest searching and examination of sample plots on the Alto Study Area in 1959 and the Alto and Mackford study areas in 1960-64. Information from Appendix VI of Gates (1971: 851-861).



*Raccoons are important predators of pheasant nests in wetland cover*



*Destruction of pheasant nests by fire in wetland cover types is common in years with dry springs and early nesting.*

ests) in tracts 21 to 40 acres in size, and 40 percent (78 nests) in tracts larger than 40 acres. Success averaged 42 percent (161 nests) in sedge meadow cover, 43 percent (70 nests) in canary grass, 42 percent (55 nests) in herbaceous cover, and 56 percent (36 nests) in temporary wetland cover, demonstrating no significant difference between vegetation types. Since predation was the principal agent of nest destruction in wetlands (Table 14), the above comparisons suggested that activity of nest predators was unrelated to edge, size of wetland units, or vegetation type.

### CLUTCH LOSSES IN HAYFIELDS

The average rate of nest success was 3 percent in pastured hay, 16 percent in mowed hay, and 63 percent in hay left unharvested. Out of 637 nests in mowed stands, 13 occurred in second-crop hay, none of which succeeded.

Nest destruction in pastured hay resulted from predation, trampling by cattle, and desertion, all of which were ultimately related to heavy grazing pressure and rapid cover depletion typical of grazed stands. In May of 1961, 20 dummy clutches of 5 pheasant eggs apiece were concealed in 4 legume seedings several days before cattle were turned in. After 7 days exposure to grazing, 13 clutches had been trampled upon, 6 were preyed upon, and only a single clutch remained intact. Heavy grazing pressure was no less detrimental to pheasant nesting than hay mowing.

Hay mowers and forage choppers accounted for 87 percent of all observed nest mortality in harvested hay (Table 69). Doubtless, this represented an overestimate because of difficulties in distinguishing preyed upon from abandoned clutches after disturbance of nest sites by farm machinery; however, other evidence also indicated low rates of nonmowing mortality in hay. In unharvested stands, where interpretation of nest fates was more reliable, only 17 percent of all clutches were preyed upon and only 9 percent abandoned (Table 14). In 1961, 35 dummy clutches were placed in hayfields in late May and were revisited several days in ad-

vance of hay cutting. After 3 weeks exposure to disturbance, only 8 (23%) were preyed upon. Other studies have similarly demonstrated low rates of nonmowing mortality in hay (Leopold 1937; Buss 1946:38; and Wight 1950).

In mowed hay, hatching success was 18 percent in alfalfa, but only 10 percent in red clover, the difference being statistically significant (chi-square with 1 df = 4.53; reference value at 0.05 = 3.84). Alfalfa stands become available for nesting nearly 2 weeks earlier than red clover, but the mean date of harvest was only 5 days earlier in an average year. Clutches in alfalfa thus had a wider margin of safety between time of initial use for nesting and time of hay cutting.

Over 85 percent of all clutch production in the harvested hay stratum occurred in first-crop mowed stands. Nest success was highly variable, ranging from a low of 1 percent in 1961 to a high of 31 percent in 1962 (Table 15). Other workers have also reported highly variable rates of nest success in mowed hay, generally concluding that severity of mowing mortality depends on yearly differences in time of hay cutting (Dustman 1950; Wight 1950; Kimball et al. 1956:221; and others). In the present study, trends in nest success were unrelated to phenology of harvest. The correlation with the average date of hay cutting was -0.22. Other variables clearly exerted more profound influence on the outcome of hayfield clutches than the schedule of hay harvest per se.

How long hay was safe for nesting, and hence the apparent likelihood of nest success, actually depended on the phenology of hay growth, as well as hay harvest. The interval between the mean date of the 10-inch growth stage and the mean date of first hay cutting served as an index to the length of this period. While this index showed an improved correlation with nest success, the relationship was non-significant and suggested that only about 44 percent (0.66) of the variability in nest success from year to year could be explained by differences in the total length of time that hay was undisturbed.

A significant relationship between these variables would not exist unless the distribution of nest establishment dates in hay was comparable from year to year. Other things being equal, success would tend to be higher in years when hay nesting was concentrated during the initial stages of hay availability and would progressively decline as the curve of nest establishment in hay was skewed later into the nesting season and closer to the time of hay harvest. Differences in nesting phenology in hay appeared to account for the weakness of the correlation. A disproportionately large percentage of the hayfield clutches in 1959 and 1962 were begun shortly after hay became available for nesting (Fig. 11), and success was accordingly higher than might have been predicted from the length of time that hay was free of disturbance. Conversely, hayfield nesting in 1961 and 1963 was more evenly spread throughout the period of hay avail-

TABLE 15. Annual variation in nest success in first-crop mowed hay

Year	Number of Nests*	Percent Successful**
1959	89	15
1960	100	22
1961	91	1
1962	97	31
1963	107	15
1964	110	16
1965	30	13
Total and weighted mean	624	17

\*Includes nests in hayfields harvested by forage choppers for feedlot use.

\*\*Difference in nest success between years highly significant (chi-square with 6 df = 33.00; reference value at 0.005 = 18.55).

lability and nest success was considerably below expectation.

Differences in hay nesting phenology ultimately depended on how one onset of nesting meshed with availability of hay as nesting cover. Nest success in mowed fields thus depended on at least three variables: phenology of nesting, phenology of hay growth, and phenology of hay harvest. On such grounds, serious risks would be entertained if the severity of mowing mortality was inferred solely from yearly differences in the schedule of hay cutting. In the absence of information on other variables affecting nest success, such inferences might better be left undrawn.

Wagner et al. (1965:89-90) earlier postulated that hay mowing and nesting phenologies were related, both under control of spring temperature, which was said to minimize the degree of annual variation in mowing mortality. Warm springs according to these authors should favor early nesting as well as early hay growth, and the latter in turn should favor early hay harvest. While some relationship doubtless exists along this line, results of the present study suggest that on a given area it is too weak to obviate substantial variation in mowing mortality. Nest destruction in hayfields in our areas varied from 14 to 37 percent of total clutch production (Gates 1971:856-861).

## CLUTCH LOSSES IN OTHER COVER

Nest success averaged 31 percent in roadsides, 24 percent in fencelines, and 20 percent in ditchbanks (Table 14), the differences perhaps suggestive but not statistically significant (chi-square with 2 df = 2.23; reference value at 0.05 = 5.99).

Predation was the leading cause of nest failure in strip cover, accounting for 74 percent of all observed nest mortality excluding observer interference (Table 14). High rates of predation in these three cover types doubtless stemmed from well-known use of strip cover as travel lanes by nest predators. Fencelines and more particularly ditch banks in this study were often used as den sites and probably

received intensive hunting pressure by mammalian predators.

No difference in hatching success was detectable between strip cover vegetation types described earlier. In regard to fenceline width, hatching success averaged 20 percent (25 nests) in strips 1 to 6 feet wide, 23 percent (31 nests) in strips 7 to 12 feet wide, and 36 percent (22 nests) in strips 13 to 18 feet wide. Although the difference fell short of statistical significance (chi-square with 2 df = 1.93; reference value of 0.05 = 5.99), a possible relationship between nest success and cover width seemed indicated. Nest success in ditch banks was 23 percent (22 nests) in cover up to 15 feet in width, 33 percent (18 nests) in cover 16 to 30 feet wide, and 15 percent (34 nests) in wider strips. This difference fell short of statistical significance (chi-square with 2 df = 2.45; reference value at 0.05 = 5.99), but it should be noted that all but 5 nests in the latter category occurred in a single large ditch virtually honeycombed with predator dens. Only 2 clutches out of 29 in this cover were successful as result of concentrated activity of nest predators in the vicinity.

Nests in peas were universally unsuccessful and virtually all nest mortality resulted from harvest operations (Table 14). Nesting in this cover type began roughly 35 days after planting and harvesting followed less than 4 weeks later. Sufficient time was therefore never available for successful nesting. The lethality of this crop for nesting is doubtless an important depressant on reproductive success in localized areas of the state where canning companies lease or contract extensive acreages for pea production.

Nest success in small grains was 31 percent (Table 14), but sample sizes were small and no firm conclusions could be reached on the comparative success of nests in this cover type or on causes of nest destruction. Harvest operations were responsible for all observed nest mortality.

## PREDATION ON DUMMY NESTS

A total of 275 dummy clutches in 1961 and 1962 was concealed in permanent cover and periodically

checked as an index to nest predation rates. Each clutch consisted of five pheasant eggs freshly obtained from the Wisconsin State Game Farm. Placement of clutches was not entirely random, nor was it entirely subjective. In roadside cover, dummy clutches were concealed at 1-mile intervals along a predetermined transect. Eggs were placed in what appeared to be the most likely looking nesting cover within 50 yards or so of the stopping point. One dummy clutch was also placed in the nearest fenceline, usually within 200 yards of the stopping point.

Dummy clutches in ditch bank cover were spaced 200 paces apart. Three drainage ditches were studied in 1961 and two in 1962. Dummy clutches in wetland cover were similarly spaced, in sets of 5 clutches apiece, on seven transects selected at random in 1961. Six of the seven transects were reused in 1962. Transects were located in herbaceous, canary grass, and sedge meadow stands, the latter including both grazed and ungrazed cover.

Early and late season trials were conducted in 1961, the second set of clutches being located within several yards of the first. Eggs were placed in a slight depression and lightly covered with adjacent vegetation. Gloves were worn to minimize human scent. Clutches were checked at 1-week intervals for 4 weeks. Those from which all sign of eggs disappeared were considered to have been preyed upon. Eggs that disappeared or were destroyed by predators were not replaced.

Significant differences in predation rates existed between cover types, higher rates of destruction being observed in fencelines and ditch banks and lower rates in roadsides and wetlands (Table 16). The trend was similar to that demonstrated by natural clutches, lending support to our previous suggestion that nest success in roadsides was somewhat better than in other types of strip cover. The comparatively low rate of predation in wetlands was also consistent with the relatively high hatching success of natural clutches in this cover type.

Predation on dummy clutches in 1961 was significantly higher among clutches established in May than those established in June

**TABLE 16.** Rates of predation on dummy clutches compared with natural pheasant nests in permanent cover

Date Set Out	Percent Preyed Upon After 4-week Exposure to Predation				
	Roadsides	Fencelines	Ditch Banks	Wetlands	Totals
1961 May 12 to 13	52 (23)*	86 (22)	83 (12)	51 (35)	64 (92)**
June 19 to 22	30 (23)	43 (23)	58 (12)	34 (35)	39 (93)**
1962 May 22 to 26	45 (20)	60 (20)	65 (20)	50 (30)	54 (90)
Totals <sup>1</sup>	42 (66)	63 (65)	68 (44)	45 (100)	52 (275)
1961-62 natural clutches <sup>2</sup>	49 (37)	64(28)	65 (20)	42 (111)	49 (196)

\*Sample size shown in parentheses.

\*\*Difference in predation rates between early and late season trials significant (chi-square with 1 df = 5.86; reference value at 0.05 = 3.84).

<sup>1</sup>Difference in predation rates between cover types highly significant (chi-square with 3 df = 12.23; reference value at 0.01 = 11.34).

<sup>2</sup>Predation rates among natural clutches actually apply to somewhat longer period of exposure to predation than the 4-week interval over which dummy clutches were checked.

(Table 16). When the fate of natural clutches in permanent cover was compared by date of establishment, rates of nest success also demonstrated improvement after June 1. The success rate of 343 clutches started in April and May of 1959-65 was 45 percent, compared with 69 percent among 52 June and July clutches. Since predation was the predominant cause of nest failure in permanent cover, fates of both natural and dummy clutches implied a drop in predation loss during the latter stages of nesting.

Among dummy clutches set out in May, the rate of predation was 64 percent in 1961 and 54 percent in 1962. While the difference was not statistically significant (chi-square with 1 df = 1.76; reference value at 0.05 = 3.84), it too agreed in trend with data on natural clutches in strip cover and wetlands. These showed 45 percent predation in 1961 and 40 percent in 1962.

Although the above comparisons are only suggestive, further testing might well establish the dummy nest method as a reliable procedure under Wisconsin conditions for assessing comparative levels of predator pressure on pheasant nests. The method could be especially useful where pheasant densities are low and adequate information on nest success is unobtainable by means of direct search.

## SEASONAL AND ANNUAL VARIATIONS IN NEST SUCCESS

The average date of nest establishment representing overall clutch production was May 20 for the period 1959-64, compared with May 15 based on successful clutches only. The magnitude of the difference varied between years, but the direction was similar, indicating a generalized decline in nest success as the season advanced. During all years of study combined, 32 percent of the April clutches were successful, compared with 34 percent of the May clutches, 20 percent of June clutches, and 18 percent of the July and August clutches.

At first glance, this appeared inconsistent with the late season improvement of hatching success in permanent cover noted above. So few hens nested in such cover after the first of June, however, that improved nest success in permanent cover did not compensate for the high rates of clutch destruction which prevailed in cropland where most of the late season nesting was concentrated.

Higher success among early clutches in this study depended on the large acreage of wetland cover available, its selective use for early nesting, and the high rate of nest success therein. Other studies, in

areas with less abundant permanent cover, have generally reported the opposite trend (Randall 1939b, Robertson 1958:58, Nelson and Chesness 1964).

Because early nest success appears to be higher, and since early clutches are larger, Wisconsin pheasants may benefit to some extent from larger brood sizes at hatching. Survival of early hatched broods appears to be no poorer than those produced later in the season, hence the higher success rate of early clutches probably is some advantage to production.

The average rate of hatching success for all years of study combined was 30 percent (Table 17). Point estimates for individual years showed almost 2-fold variation, but *t* tests revealed that 1964 was the only year which differed significantly at the 5 percent level from any or all other years. Notwithstanding, it is our opinion that observed trends in nest success for the period 1959-63 also represented real annual differences which required explanation.

Nest success was lowest in 1959 at 24 percent (Table 17), the outcome of unusually heavy reliance on hay for nesting (Fig. 10) and above-average nest mortality in this cover type (Table 15). Nest success increased to 28 percent in 1960 with heavier nesting use of wetlands and

**TABLE 17.** Annual variation in overall average nest success and cause of nest mortality in all cover types combined\*

Year	Number of Nests	Percent Successful		Percent Unsuccessful by Cause of Failure							
		Mean	95 Percent Conf. Limits	Farm Mach.	Preyed Upon	Abandoned	Burning	Cattle	Flood-ing	Obser-ver	Undet.
1959	177	24	15-33	45	19	9	0	1	0	1	2
1960	237	28	19-38	34	21	8	0	2	3	1	4
1961	269	27	18-35	29	29	4	7	1	0	1	3
1962	209	30	21-38	36	23	8	1	2	0	0	1
1963	270	31	23-39	23	27	8	7	2	0	2	1
1964	201	46	37-55	20	25	8	0	0	0	0	1
Total and weighted means											
	1,363	30	22-38**	31	24	7	3	1	1	1	2
Percent of total nest mortality				46	36	10	5	2	1		

\*Based on sampling results from the Alto Study Area in 1959 and combined results from Alto and Mackford areas in 1960-64. Information from Appendix VI of Gates (1971:851-861).

\*\*Width of this confidence limit due to small sample of nests in small grains in relation to the large size of this stratum. With small grains excluded from consideration, the confidence limit was 27-33 percent.

lower mortality in hay.

The pattern of nest distribution in 1961 was basically favorable to pheasant production. Over 50 percent of all nesting occurred in wetlands and barely 25 percent in hay. However, nest success in wetlands was substantially less than average, in part the result of heavy burning losses, and only 1 percent of the clutches succeeded in hay. Overall hatching success in 1961 was 27 percent, slightly below the 6-year mean (Table 17).

Nest distribution in 1962 was nearly as unfavorable as 1959, but the disadvantage was offset by the above average success rate in mowed hayfields. Overall hatching success was 30 percent, actually better than 1961 despite the lower percentage of clutch production located in wetlands. Nest distribution in 1963 was roughly comparable to 1961. However, overall hatching success was higher, 31 percent, as a result of improved nest success in both wetlands and hay.

The 46 percent rate of hatching success in 1964 deserves special comment. Nest mortality in permanent cover in 1964 was unusually low. The relationship between nesting and hay growth phenologies was such that a sizeable percentage of the initial nesting attempts were drawn into hayfields (Fig. 11), but overall use of this cover type was

not appreciably higher than when hay contained predominantly re-nests. With lower nest mortality in permanent cover, there was less need for re-nesting and accordingly less nesting in hay. These events, coupled with near average nest success in hay, produced the highest overall rate of hatching success observed during the study.

A generalized increase in nest success from 1959 to 1964 (Table 17) also prevailed. Population densities were somewhat lower during the final 3 years of study than at its outset, and density dependent decline in hayfield nesting as the study progressed may have contributed to the trend. After 1961, substantial acreages of retired cropland were also present. Nest success in these cover types temporary wetlands and unharvested hay -- was well above average (Fig. 12), which probably contributed even more importantly to the increase.

Nest success appeared to be regulated by a complex of environmental influences, no one of which assumed singular importance. Given stable acreages of nesting cover and longer term study, we believe that trends in nesting phenology and population density would eventually emerge among the more important controls of nest success, both affecting the distribution of clutch pro-

duction between wetlands and hayfields. Over the short span of the present study, however, other annually varying influences obscured these relationships, and nest success more nearly resembled a random variable.

## MORTALITY FACTOR ANALYSIS

Agricultural operations, principally hay harvest, were the leading causes of nest mortality, followed in order by predation, abandonment, disturbance by cattle, and flooding (Table 17). This comparison, unfortunately, is misleading. Early nesting was for the most part confined to strip cover and wetlands where predation was the principal agent of nest destruction (Table 14). But because a large percentage of the nesting hens whose clutches were broken up in permanent cover moved into hayfields and other cropland to re-nest, much of the nest mortality attributed to agricultural operations was an indirect outcome of predation. The significance of nest predation in permanent cover far transcended the observed number of clutches actually destroyed. Hens forced to re-nest after such disturbance were much too long delayed to produce successful clutches in hay, since only those

**TABLE 18.** *Comparison of nest success in selected cover types on various pheasant study areas*

Area Studied and Years	Percent Nest Success						Percent Nest Success in All Cover Types Combined*	Authority
	Hay	Small Grains	Strip Cover	Pas-ture	Wet-lands	Other Permanent Cover		
Pelee Is., Ont., 1949-50	26	46	--	47	--	46	46	Stokes 1954
No. Cent. No. Dak., 1942	--	--	--	--	--	--	39	Bach 1943
NW Ohio, 1946-47	34	36	15	43	--	21	32	Dustman 1949
No. Cent. Iowa, 1939-41	21	46	13	31	20	67	31	Baskett 1947
No. Cent. Colo., 1948-50	--	--	--	--	--	--	31	Yeager et al. 1951
East Cent. Wis., 1959-64	14	31	26	--	46	--	30	This study
So. and SW Minn., 1939-41	23	54	28	22	--	--	29	Nelson and Chesness 1964
SE No. Dak., 1942	--	--	--	--	--	--	24	Bach 1943
Cent. Iowa, 1961	23	37	14	--	--	33	24	Wright and Otte 1962
East So. Dak., 1958-59	7	40	16	32	26	--	22	Trautman 1960
SE Penn., 1939	19	30	8	50	--	26	20	Randall 1939b
East Cent. Ill., 1963	13	20	26	33	--	8	20	Warnock and Joselyn 1964a
So. Cent. Minn., 1959-62	4	40	16	31	--	--	17	Nelson and Chesness 1964
No. Cent. Iowa, 1954	8	19	27	40	18	--	17	Klonglan 1955
SW No. Dak., 1953-54	--	--	--	--	--	--	17	Fischer 1955
SW Iowa, 1957-58	18	27	8	18	--	6	16	Klonglan 1962
So. Cent. Neb., 1955-59	4	25	17	7	--	5	15	Linder et al. 1960
West. N.Y., 1953	--	--	--	--	--	--	13	Robeson 1957
NW Iowa, 1933-35	14	47	27	30	18	--	--	Hamerstrom 1936
So. Wis., 1936	41	--	--	--	--	--	--	Leopold 1937
West. Ore., 1937	46	40	33	60	--	--	--	Eklund 1942
So. Wis., 1936-42	37	--	--	--	--	--	--	Buss 1946
SE Penn., 1949	11	--	--	--	--	--	--	Wight 1950
NW Iowa, 1948	0	27	--	--	19	--	--	Weston 1953
NW Ohio, no date	10	--	--	--	--	--	--	Thompson 1964

\*Listed only for those studies in which all available nesting cover was examined for nests.

**TABLE 19.** *Comparison of overall rates of nest success and the percentage of successful hens observed on various pheasant study areas*

Area Studied and Years	Overall Nest Success	Percent of Hens Successful in Brood Production	Authority
East. So. Dak., 1958-59	22	88	Trautman 1960
Pelee Island, Ont., 1949-50	46	81	Stokes 1954
SE Penn., 1939	20	52 to 55	Randall 1939a
East Cent. Wis., 1959-64	30	52	This study
No. Cent. Iowa, 1939-41	31	50	Baskett 1947
No. Cent. Colorado, 1948-50	31	50	Yeager et al. 1951
So. Cent. Neb., 1955-59	15	44	Linder et al. 1960
SW Iowa, 1957-58	16	43	Klonglan 1962

nests established soon after hay became available for nesting stood any chance of succeeding before the time of hay cutting.

Roughly 76 percent of all hay field clutches represented renesting efforts in an average year. If 76 percent of the nest mortality in hay ultimately resulted from nest destruction in permanent cover, chiefly predation, then it is clear that predation's impact on nest success far outweighed that of any other mortality factor. In summary, predation was viewed as the major depressant on nest success under conditions of the present study.

Apart from wetlands, rates of nest success in this study for each individual cover type differed little from information reported by other authors (Table 18). Hatching success in strip cover at Waupun was 26 percent, versus 19 percent as the mean observed elsewhere. In small grains the comparison was 31 and 36 percent, respectively. Nest success in hayfields in all areas has undergone a long-term decline. Among studies conducted prior to 1950, the mean was 27 percent; among those after 1950, 11 percent. Nest success of 17 percent in harvested hay in the present study perhaps was slightly higher than that which presently prevails in most other states.

The 46 percent rate of hatching success in wetlands was considerably better than that observed outside Wisconsin. Excluding Weston's (1953) study in Iowa, wetland habitat searched for pheasant nests in other states consisted of cover which was dry enough for nesting only on the edges (Hamerstrom 1936), or cover which occurred as scattered pockets comprising at most 3 percent of the landscape (Baskett 1947:12-13; Klonglan 1955; and Trautman 1960). More extensive wetland acreages on our area, coupled with absence of edge effect, may have led to greater security of nests from predation.

The 30 percent overall rate of hatching success observed by us was among the highest recorded in the literature (Table 18). Whether comparably high rates of hatching success typify all Wisconsin pheasants is difficult to determine. Although nest success is but one of several determinants of reproductive success, it is doubtful that produc-

tivity rates as high as we observed could be maintained elsewhere in Wisconsin without near comparable levels of hatching success. At least provisionally, we conclude that nest success in the present study was not atypically high.

In spite of good hatching success, Table 19 demonstrates that the percentage of hens that eventually succeeded in brood production was not commensurately high. Populations studies in many other areas have shown equally high or higher rates of hen success with lower levels of nest success, the implication being that renesting was less important in our study (Klonglan 1962, Linder et al. 1960, Randall 1939b). That Wisconsin pheasants seem to exhibit lower capacity for renesting may be a function of shorter nesting seasons or higher rates of hen mortality that apparently operate during the nesting season.

The only documented change in nest success affecting Wisconsin pheasants is the decline in clutch survival in mowed hay. Buss (1946:38) recorded 37 percent nest success in mowed hay in 1936-42 and Leopold (1937) 41 percent in 1936. Nest success in first-crop hay in the present study averaged 17 percent (Table 15), less than half the rate that prevailed in earlier Wisconsin studies.

In Buss' study, hayfield nesting must have been comparatively little disadvantage to pheasant production. Success of hayfield nests was not appreciably lower than nonhay nests, 37 versus 39 percent, whereas in the present study the success rate in mowed hay was no better than half the average of all other cover types combined. Wisconsin pheasants now appear to be even more dependent on wetland cover for successful nesting than was true 25 years ago.

Wagner et al. (1965:97) described several areas in Wisconsin with little wetland cover that once supported reasonably good pheasant densities. The Arlington prairie, north of Madison, produced huntable pheasant numbers during the 1940's, but in the 1960's was virtually without pheasants. Green County, on the Illinois border, maintained fairly good pheasant densities by Wisconsin standards through the mid-1950's, but popula-

tions in this area have since diminished to token levels of former abundance. That earlier hay cutting was responsible for population decline in these instances is mainly circumstantial. Other changes unfavorable to pheasants must have played contributory roles, but increasingly heavy hayfield mortality, with little alternative cover to cushion the effect on mean nest success, certainly must rank as one of the leading causes of population reduction.

Unfortunately, the outlook is for even heavier hayfield mortality in the years ahead. Agronomists now recommend the 5-15-30 schedule of alfalfa harvest for the southern two-thirds of Wisconsin, according to which plan the first cut is completed by June 5, the second by July 15, and the third before August 30. While many Wisconsin farmers have yet to adopt this practice, its economic benefits through improved forage quality make it a virtual certainty that hay cutting will steadily progress toward the recommended schedule.

Approximately 37 days are required to produce a successful pheasant clutch. The average date at which alfalfa became available for nesting in the present study was May 8, hence it was impossible for nests to succeed in alfalfa before mid-June. Hay cutting completed by June 5 would preclude all possibility of successful clutch production in alfalfa. Earlier first-crop cutting might be followed by higher levels of renesting, but the recommended interval between first and second cuts is only 40 days. Because nearly 2 weeks are required for second-growth alfalfa to again become suitable for nesting, too little time would also be available for completion of incubation before the second harvest.

Hence the 3-cut system of alfalfa management would completely eliminate pheasant production in hay. The closer that actual mowing practices approach this schedule, the greater the increase in nest mortality. It is reasonable to expect increased severity of mowing mortality in the future, even heavier dependence on nonhay cover for brood production, and further population declines in areas where wetland cover is not sufficiently abundant to offset the disadvantage

of large hayfield acreages.

One other long-term change on the Wisconsin scene probably has also been a detriment to pheasant production. Between the early 1940's and the mid-1950's, notable population increases were recorded among raccoons (Woehler 1956), opossums (Knudsen 1953), and red foxes (Richards and Hine 1953), densities of which remained generally high into the 1960's. Nest mortality from predation, and indirectly from hay mowing, very likely increased as result. Higher predator populations doubtless rank with wetland drainage and earlier hay mowing as long-term changes unfavorable to pheasant production since the early years of pheasant abundance in the state.

## SUMMARY

Nest success was highest in unharvested hay, followed in order by wetland cover, strip cover, small grains, harvested hay, and peas. Hatching success in wetland cover averaged 46 percent and was inde-

pendent of nest location with respect to edge, size of wetland tracts, or vegetation type. In hayfields, 3 percent hatching success prevailed in pastured stands, 16 percent in mowed stands, and 63 percent in unharvested stands. Yearly variation in nest success was most pronounced in first-crop hay and was jointly dependent upon phenology of hay growth, phenology of hay harvest, and time of nest establishment in hay. Trends in nest success from year to year could not be inferred from hay cutting dates alone. Hatching success in strip cover averaged 26 percent, suggestively higher in roadsides (31%) than fencelines (24%) or ditch banks (20%). An association between cover width and nest success was also suggestive but not statistically significant. Nest success was 0 in peas and 31 percent in small grains.

Overall nest success varied from 24 to 46 percent per annum and averaged 30 percent for all years of study combined. Yearly differences in overall hatching success were the outcome of a number of interacting

variables. Changes in nesting phenology, population interacting variables, changes in nesting phenology, population density, phenology of hay growth, schedule of hay cutting, and rates of nest predation all played contributory roles.

Agricultural operations and predation were leading causes of nest failure; however, predation was viewed as the major depressant on nest success because much of the mortality from farm machinery ultimately stemmed from necessity for renesting after nest destruction by predators. Although hatching success of 30 percent in the present study ranked among the highest reported in the literature, the percentage of successful hens in the population was not commensurately high, suggesting lower importance of renesting under Wisconsin conditions. Long-term changes in nest success in Wisconsin include greater severity of hay mowing mortality and higher rates of nest predation inferred from recent increases in nest predator densities.

# CLUTCH SIZE AND PRODUCTION RATES

## VARIATIONS IN CLUTCH SIZE

Completed clutch size averaged 11.2 eggs based on a sample of 574 incubated clutches observed in 1959-65 (Table 20). These included all clutches for which it was believed complete egg counts had been obtained and excluded all apparent instances of dump nesting. Clutches found during supplemental searching were included as well as clutches found on sample plots.

It has been shown in numerous single-brooded species that clutch size declines as the breeding season advances because of the small size of reneest clutches (Lack 1954:32). The trend has been amply demonstrated in pheasants both from

seasonal decline in average clutch size (Hamerstrom 1936; Randall 1939b; Dustman 1949:79; and Stokes 1954:26) and from the smaller size of reneest clutches of individually marked hens (Seubert 1952; Warnock and Joselyn 1964b; and Gates 1966c). The seasonal change in clutch size in our study is shown in Figure 13. Using May 15 as the approximate separation date between initial and reneest clutches in an average year, first nesting attempts averages 12.5 eggs per clutch, compared with reneest clutches which averages 10.0 eggs. Though the means differed from each other at a high level of significance ( $t$  with 466 df = 5.68; reference value at 0.01 = 2.58), overlap was far too great to dis-

tinguish between initial and reneest attempts on the basis of clutch size alone.

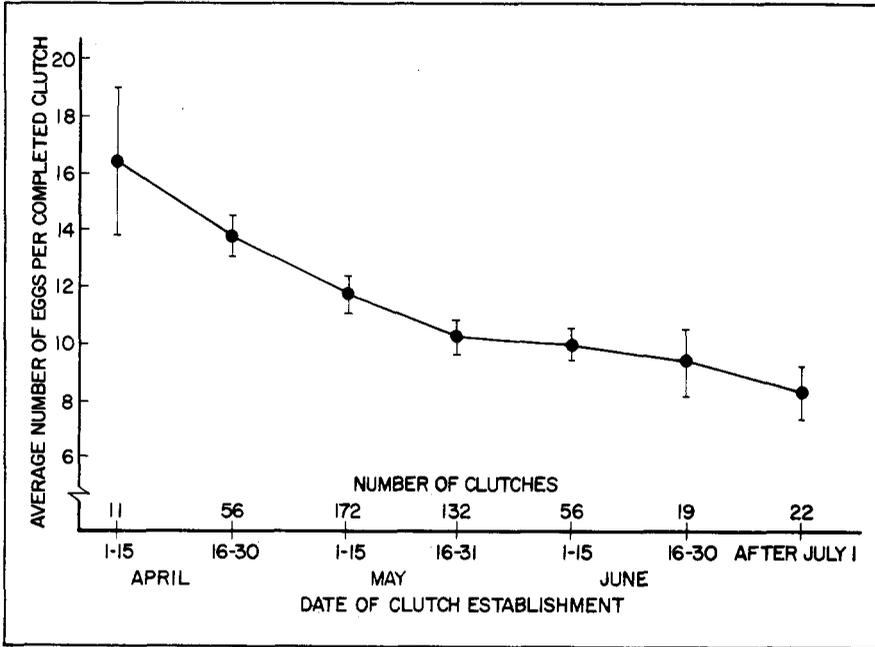
Yearly differences in clutch size during the period 1959-65 were highly significant (Table 20). Clutch sizes in 1959 and 1962 were significantly lower than all other years. Average clutch size in other years showed comparatively minor variation.

During the years 1959-65, average clutch sizes were significantly correlated with the average weight of hens in March (Fig. 14). The approximate size of initial clutches could be estimated only in 1959-64 (Table 21). When these were compared with March hen weights, the relationship was suggestive but not statistically significant ( $r = 0.68$

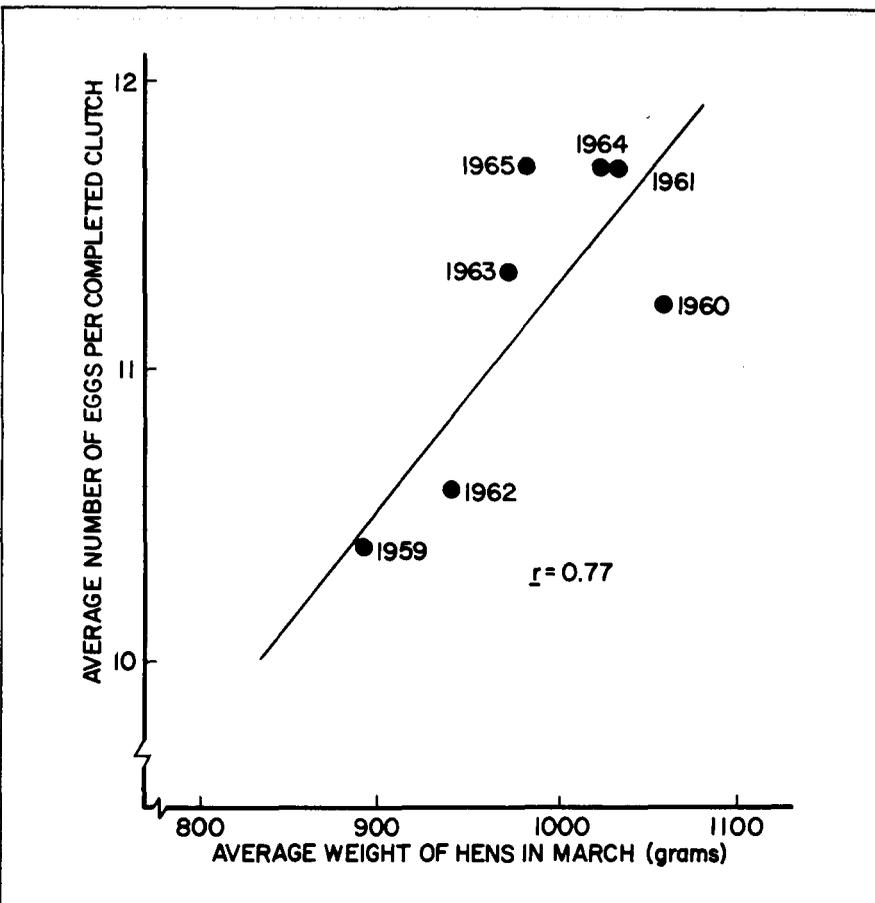
**TABLE 20.** Annual variation in completed clutch size based on the number of eggs observed in incubated clutches

Year	Number of Clutches by Clutch Size																		Total	Mean*	95 Percent Confidence Limits
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22			
1959	0	0	7	8	12	24	18	9	4	1	1	1	3	0	0	0	0	0	88	10.4	9.9-10.9
1960	0	0	2	9	8	15	21	14	9	3	3	3	1	0	1	0	0	0	89	11.2	10.7-11.7
1961	1	0	0	2	7	16	18	11	13	6	3	1	1	0	2	1	0	0	82	11.7	11.2-12.2
1962	1	1	3	4	18	13	13	13	8	3	0	0	0	0	0	0	0	1	78	10.6	10.1-11.1
1963	1	0	1	11	19	25	14	17	9	5	5	2	0	1	1	2	1	0	114	11.3	10.8-11.8
1964	2	0	1	5	9	12	16	22	12	8	10	2	0	2	5	0	0	0	106	11.7	11.1-12.3
1965	0	0	0	0	2	3	1	6	3	2	0	0	0	0	0	0	0	0	17	11.7	10.9-12.5
Totals	5	1	14	39	75	108	101	92	58	28	22	9	5	3	9	3	1	1	574	11.2	11.0-11.4

\*Difference between years in mean clutch size highly significant by analysis of variance ( $F$  with 6 and 567  $df = 3.34$ ; reference value at 0.005 = 3.09). From multiple range tests (Steel and Torrie 1960: 114), average clutch size in 1959 and 1962 differed significantly from all other years at the 5-percent level. No other years showed significant differences from each other.



**FIGURE 13.** Seasonal trend in clutch size based on the average number of eggs observed in incubated clutches, 1959-65. Means shown with 95 percent confidence limits.



**FIGURE 14.** Relationship between the average weight of hens in March and the subsequent size of completed clutches. Correlation significant at the 5 percent level (reference value with 5  $df = 0.75$ ).

**TABLE 21.** Comparison of completed clutch sizes between initial nesting attempts and renesting efforts

Year	Approximate Separation Date between Initial and Renest Clutches	Initial Clutches		Renest Clutches	
		Mean	95 Percent Confidence Limits	Mean	95 Percent Confidence Limits
1959	May 20	11.3 (42)*	10.6-12.0	9.7 (29)	9.2-10.3
1960	May 12	12.4 (36)	11.6-13.2	10.2 (45)	9.7-10.7
1961	May 9	13.0 (31)	12.1-14.0	10.5 (29)	9.9-11.1
1962	May 24	11.4 (37)	10.0-12.9	8.7 (22)	8.1- 9.3
1963	May 7	13.4 (32)	12.3-14.6	10.1 (60)	9.7-10.5
1964	May 16	13.3 (54)	12.6-14.1	10.7 (36)	10.1-11.4

\*Sample size shown in parentheses.

**TABLE 22.** Seasonal variation in egg fertility and hatchability based on egg fates in successful clutches, 1959-65

Month of Clutch Establishment	Number of Eggs in Successful Clutches	Percent of Eggs Fertile*	Percent of Fertile Eggs Hatching**	Percent of All Eggs Hatching <sup>1</sup>
April	576	91	96	87
May	2,066	95	95	91
June	247	97	97	94
July	127	93	96	89

\*Difference between months in egg fertility highly significant (chi-square with 3 df = 17.32; reference value at 0.01 = 11.34).

\*\*Difference between months in egg hatchability nonsignificant (chi-square with 3 df = 1.54; reference value at 0.05 = 7.81).

<sup>1</sup>Difference between months in the percentage of all eggs hatching significant (chi-square with 3 df = 11.00; reference value at 0.05 = 7.81).

**TABLE 23.** Annual variation in egg fertility and hatchability based on egg fates in successful clutches

Year	Number of Eggs in Successful Clutches	Percent of Eggs Fertile*	Percent of Fertile Eggs Hatching**	Percent of All Eggs Hatching <sup>1</sup>
1959	365	92	93	86
1960	529	94	96	90
1961	375	96	95	92
1962	474	94	98	92
1963	542	95	94	89
1964	616	95	96	95
1959-64	2,901	94	96	91

\*Difference between years in egg fertility nonsignificant (chi-square with 5 df = 3.74; reference value at 0.05 = 11.1).

\*\*Difference between years in egg hatchability highly significant (chi-square with 5 df = 26.69; reference value at 0.01 = 15.1).

<sup>1</sup>Difference between years in percentage of all eggs hatching highly significant (chi-square with 5 df = 27.03; reference value at 0.05 = 11.1).

**TABLE 24.** Comparison of egg fertility and hatchability based on egg fates in successful clutches on various study areas

Area Studied and Years	Percent of Eggs Fertile	Percent of Fertile Eggs Hatching	Percent of All Eggs Hatching	Authority
East Cent., Wis., 1959-64	94	96	91	This study
NW Ohio, 1946-47	--	--	91	Dustman 1949
SE Penn., 1939	94	96	90	Randall 1939b
No. Cent. Iowa, 1954	95	93	88	Klonglan 1955
So. Dak., 1946-49	93	94	87	Nelson 1950
SW Iowa, 1957-58	95	88	84	Klonglan 1962
No. Cent. Iowa, 1939-41	--	--	83	Baskett 1947
NW Iowa, 1933-35	93	88	82	Hamerstrom 1936
So. Cent. Neb., 1955-59	90	86	77	Linder et al. 1960
Pelee Is., Ont., 1949-50	89	85	75	Stokes 1954

with 4 df; reference value at 0.05 = 0.81). Our conclusion was that clutch size reduction in 1959 and 1962 was somehow related to poorer physical condition of hens in late winter and early spring.

The extent to which weight deficiencies at winter's end influenced hen condition during egg laying is unfortunately unknown. In experiments with captive pheasants, however, Gates and Woehler (1968) observed that hens sustaining progressively greater weight loss in winter tended to remain below normal in body weight throughout the subsequent period of egg production. On such grounds, it seems probable that hens actually entered reproduction in substandard body condition in 1959 and 1962, which was reflected in the smaller size of incubated clutches.

## UNHATCHED EGGS

Rates of egg fertility and embryonic mortality were calculated from egg fates in successful clutches only. In instances where clutches were discovered long after hatching or had been crushed by farm machinery, it was often impossible to identify the status of unhatched eggs. All such eggs were prorated according to the status of unhatched eggs of known fates. Eggs containing embryos which had died during the very early stages of incubation obviously were indistinguishable from infertile eggs, and observed rates of egg fertility and embryonic mortality may have erred accordingly. In subsequent discussion, egg hatchability will refer to the percentage of all fertile eggs that hatched.

The percentage of all eggs hatching was highest during the middle stages of nesting. The difference was attributable to seasonal change in egg fertility. Rates of egg hatchability showed no consistent trend during the nesting season (Table 22). Essentially the same phenomena prevailed among captive-reared pheasants at the Wisconsin State Game Farm, where egg fertility was highest near the midpoint of egg production, but hatchability remained nearly constant from beginning to end. Neither set of data suggested a seasonal decline in egg quality judged by trends in prehatching survivability.

Egg fertility did not exhibit a significant degree of yearly variability, but annual differences in the percentage of fertile eggs hatching were highly significant (Table 23). The reason for the latter trend was unclear. The lowest rate of hatchability was observed in 1959, a year when the spring condition of hens was believed to have been suboptimum. But highest hatchability prevailed in 1962, a year when hen condition must have been equally substandard. No consistent relationship was apparent between these variables. Experiments with captive pheasants also failed to detect a relationship between winter weight loss and subsequent levels of hatchability (Gates and Woehler 1968).

Overall egg fertility of 94 percent in the present study was about comparable to other wild population (Table 24), but substantially better than the 90 percent rate observed under game farm conditions. This should be of interest to Wisconsin sportsmen, among whom concern is often expressed that high rates of cock harvest may have an adverse effect on egg fertility. In captive pheasants, Shick (1947) found that a single cock could inseminate as many as 50 hens without loss of fertility and concluded that sex ratios in the wild of 10 to 12 hens per cock would not be detrimental to reproduction.

Egg hatchability in the present study was somewhat higher than that generally recorded elsewhere (Table 24). Possibly this was related to the low level of random egg dropping and infrequent dump nesting that characterized our population. At the opposite extreme, the comparatively low rate of hatchability observed by Stokes (1954:29) on Pelee Island was associated with much greater prevalence of promiscuous egg laying.

## RATES OF EGG, CLUTCH, AND CHICK PRODUCTION

Estimates of the total number of eggs produced each year (Table 25) were based on the sum of three separate calculations: (1) Total clutch production was first subdivided into the number of clutches that reached incubation versus the number that did not, relying on the

percentage of observed clutches that showed evidence of incubation. The total number of eggs laid in incubated clutches was then calculated from the average completed clutch size. (2) The average number of eggs laid in clutches that did not reach incubation was estimated at half the average size of completed clutches, our assumption being that clutch failure prior to incubation was evenly distributed over the period of egg laying. (3) The number of randomly dropped eggs was estimated from the density of single eggs on study plots. Searching efficiency for single eggs was arbitrarily estimated at 20 percent, and occurrence of random eggs on study plots was adjusted accordingly. Egg production calculated in this manner obviously left considerable room for error, but furnished at least a rough indication of the number of eggs produced per hen. Estimates were clearly minimum values, but the degree of error was not believed to be greater than 10 or 15 percent.

The definitive yardstick of annual production was the eventual number of chicks produced per hen. This showed extreme variation, ranging from four chicks or fewer per hen in 1959 and 1962 to more than seven chicks per hen in 1964. Chick production in other years averaged 5.7 to 5.8 per hen (Table 25).

The average rate of chick production per breeding hen was singularly dependent on the percentage of successful hens ( $r$  with 4 df = 0.96; reference value at 0.01 = 0.91). Clutch size, egg fertility, and egg hatchability differed too little from year to year to constitute significant influences on chick production. The percentage of successful hens, in turn, was the product of the number of nesting attempts per hen and the average rate of nest success. Neither showed a very strong correlation with hen success ( $r$  with 4 df = 0.35 and 0.65, respectively; reference value at 0.05 = 0.81), suggesting that both contributed to yearly differences in chick production rather than one or the other assuming dominant importance.

The percentage of breeding hens alive in spring which succeeded in brood production was highest in 1964 at 64 percent. This was largely the result of unusually high nest success. The relatively low rate of

**TABLE 25. Summary of annual rates of pheasant production derived from nesting studies\***

Item	May 1 Hen Population Estimates by Individual Years						
	1959 (348)	1960 (427)	1961 (524)	1962 (353)	1963 (333)	1964 (353)	1959-64 (2,338)
<b>Clutch production</b>							
Total clutch production	554	881	1,065	487	638	495	4,120
Percent clutches incubated	82.9	75.9	81.5	83.2	80.9	86.1	81.1
No. incubated clutches	459	669	868	405	516	426	3,343
No. unincubated clutches	95	212	197	82	122	69	777
Total successful clutches	132	250	284	144	198	227	1,235
<b>Egg Production</b>							
Avg. eggs per inc. clutch	10.5	11.1	11.6	10.7	11.5	11.7	11.2
No. eggs in inc. clutches	4,820	7,426	10,069	4,334	5,934	4,984	37,567
Avg. eggs per uninc. clutch	5.3	5.6	5.8	5.4	5.8	5.9	5.6
No. eggs in uninc. clutches	499	1,177	1,143	439	702	404	4,364
No. of randomly laid eggs	295	115	240	285	245	260	1,440
Total egg production	5,614	8,718	11,452	5,058	6,881	5,648	43,371
<b>Chick production</b>							
Avg. eggs per succ. clutch	10.1	11.0	11.4	10.7	10.9	12.1	11.1
No. eggs in succ. clutches	1,333	2,750	3,238	1,541	2,158	2,747	13,767
Percent of eggs hatching	85.5	90.4	91.5	91.7	88.5	94.5	90.7
Total chick production	1,140	2,486	2,963	1,413	1,910	2,596	12,508
<b>Production rates</b>							
Percent succ. all clutches	23.8	28.4	26.7	29.6	31.0	45.9	30.0
Percent succ. inc. clutches	28.8	37.4	32.7	35.6	38.4	53.3	36.9
Percent succ. all eggs	20.3	28.5	25.9	27.9	27.0	46.0	28.8
Percent succ. eggs in clutches	21.4	28.9	26.4	29.6	28.8	48.2	29.8
Clutches produced per hen	1.6	2.1	2.0	1.4	1.9	1.4	1.8
Incubated clutches per hen	1.3	1.6	1.7	1.1	1.5	1.2	1.4
Total eggs produced per hen	16.1	20.4	21.9	14.3	20.7	16.0	18.6
Percent hens producing chicks	37.9	58.5	54.2	40.8	59.5	64.3	52.8
Chicks produced per hen	3.3	5.8	5.7	4.0	5.7	7.4	5.3

\*Based on results from the Alto Study Area in 1959 and combined results from the Alto and Mackford study areas in 1960-64. Estimates of total clutch production and production of successful clutches from Appendix V of Gates (1971:834-850).

**TABLE 26. Calculated production of successful clutches by cover type\***

Cover Type	Estimated Production of Successful Clutches and Percent of Total						
	1959	1960	1961	1962	1963	1964	1959-64
<b>Wetlands</b>							
Permanent	82 (62)	140 (56)	217 (76)	55 (38)	129 (65)	150 (66)	773 (63)
Temporary	0	0	35 (12)	10 (7)	14 (7)	1	60 (5)
<b>Strip Cover</b>							
Roadsides	14 (11)	32 (13)	45 (16)	33 (23)	34 (17)	40 (18)	198 (16)
Fencelines	5 (4)	15 (6)	30 (11)	15 (10)	19 (10)	18 (8)	102 (8)
Ditchbanks	3 (2)	15 (6)	8 (3)	15 (10)	10 (5)	12 (5)	63 (5)
	6 (5)	2 (1)	7 (3)	3 (2)	5 (3)	10 (4)	33 (3)
<b>Hayfields</b>							
Harvested	36 (27)	69 (28)	13 (5)	47 (33)	35 (18)	32 (4)	232 (19)
Unharvested	34 (26)	69 (28)	0	32 (22)	18 (9)	12 (5)	165 (13)
	2 (2)	0	13 (5)	15 (10)	17 (9)	20 (9)	67 (5)
<b>Small Grains</b>							
	0	9 (4)	9 (3)	9 (6)	0	5 (2)	32 (3)

\*Based on results from the Alto Study Area in 1959 and combined results from the Alto and Mackford study areas in 1960-64. Data from Appendix V of Gates (1971:834-850).

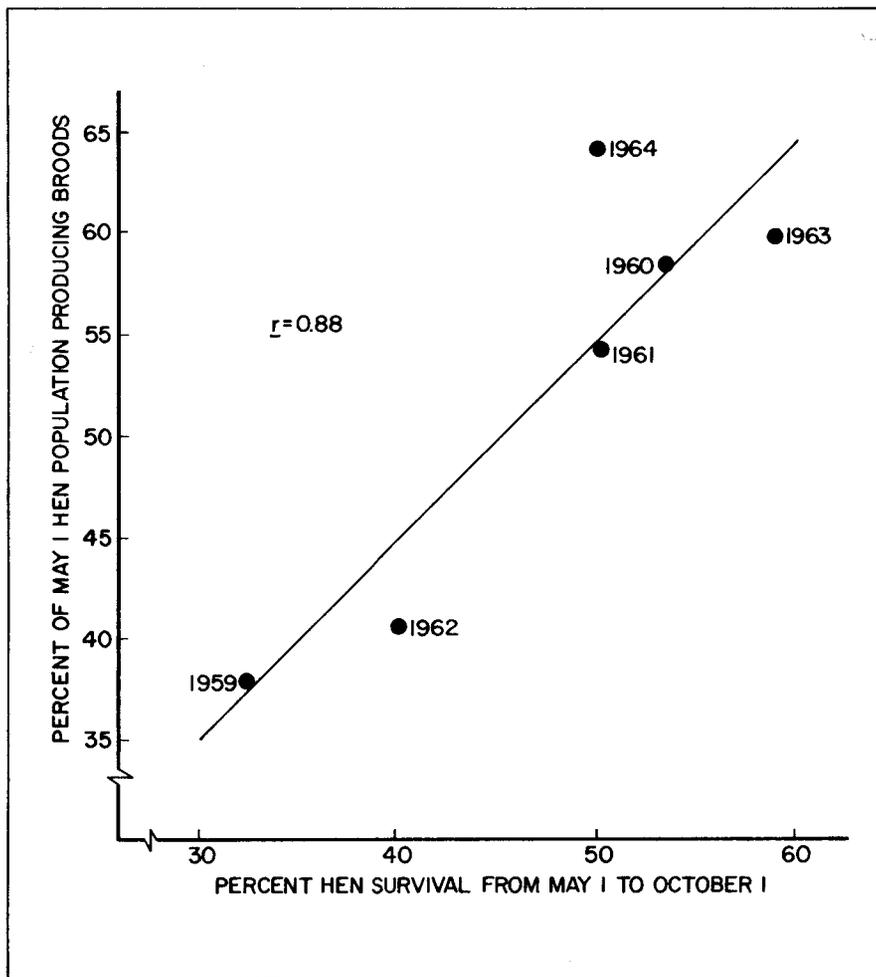
clutch production in 1964 (1.4 per hen) reflected a high rate of nest survival and correspondingly less need for renesting than was true of other years. Intermediate rates of hen success prevailed in 1960, 1961, and 1963 under near normal rates of nest success (28%) and clutch production (2.0 per hen). The percentage of successful hens was lowest in 1959 at 38 percent. Nest success in 1959 was 24 percent, well below the 6-year mean, but not appreciably lower than 1960 and

1961 when the percentage of successful hens averaged 57. In 1962, nest success averaged 30 percent, but only 41 percent of the hens produced young. The common denominator of the low rate of hen success in 1959 and 1962, and hence the reduced rate of chick production, was the smaller number of nesting attempts per hen.

The percentage of hens producing young was significantly correlated with hen survival from May to October (Fig. 15). In turn, annual

survival differences over this interval depended mainly on survival trends during nesting (Gates 1971:709). From these relationships, we conclude that lower hen survival was responsible for the reduced rate of clutch production and ultimately for the low rate of chick production that prevailed in 1959 and 1962.

Compared with other studies, we have already noted that the high rate of nest success was not associated with a correspondingly high



**FIGURE 15.** Relationship between spring-to-fall hen survival and the percentage of the spring hen population ultimately succeeding in brood production. Correlation significant at the 5 percent level (reference value with 4 df = 0.81).

percentage of successful hens (Table 19), the apparent difference being the smaller number of clutches produced per hen. The overall contribution of reneating in our study thus appeared to be less than that in many other areas. We doubt that incidence of nonbreeding, if it occurs at all, is any higher in Wisconsin than elsewhere, and while this can hardly be proven, it is pertinent that ovarian examinations in this state have not revealed evidence of wild hens failing to produce eggs (Kabat et al. 1948:106). Nor does it seem likely that Wisconsin pheasants have intrinsically lower capacity for reneating. A very high fraction of the postnesting hen population in this study, 90 percent in an average year, was accompanied by young. With due allowance for observability differences between successful and broodless hens, this still indicates that a large majority of the surviving hens eventually produced

broods each season, which would require rather persistent reneating with rates of nest success averaging 30 percent.

#### DISTRIBUTION OF SUCCESSFUL CLUTCHES BY COVER TYPE

During the years 1959-64, wetland cover types contained 41 percent of total clutch production and 63 percent of all clutches that succeeded (Table 26). Ninety-two percent of the successful wetland clutches occurred in permanent wetland types, the remainder in temporary cover on lowland sites normally used as cropland. Strip cover contained 19 percent of total clutch production in an average year and 16 percent of all which succeeded. Hayfields contained 33 percent of all clutches established and 19 percent of those producing young. Unharvested stands comprised only

6 percent of the aggregate hayfield acreage, yet accounted for 29 percent of the successful clutch production in hay. Small grains were the only other nesting cover in which successful nesting occurred, but production from this cover type amounted to less than 3 percent of the total in an average year.

In all but one year of study (1962), the number of successful clutches in wetlands exceeded the production of all other cover types combined. The critical importance of wetland cover for reproduction was best exemplified in years when hatching success in hay was minimal. In 1961, with only 1 percent of the clutches in harvested hay succeeding, 76 percent of all nesting attempts that terminated successfully were situated in wetlands.

#### SUMMARY

The average size of completed clutches was 11.2 eggs. Clutch sizes showed significant annual variation which could not be explained by influences operating after the start of egg laying. A significant relationship between the average size of incubated clutches and the mean weight of hens in late winter led to the conclusion that condition of the nesting hen was the chief variable affecting egg production under conditions of the present study.

Egg fertility was highest during the middle stages of nesting, but the percentage of fertile eggs hatching did not vary seasonally. Similar trends were identified in captive-reared populations.

The average number of chicks produced per hen showed extreme variation between years. Production was lowest in 1959 and 1962 at 4 chicks or fewer per hen and highest in 1964 at over 7 chicks per hen. Yearly variation in chick production ultimately stemmed from annual difference in nest success and the rate of hen survival during nesting. No indication could be found that extent of nonbreeding or capacity of unsuccessful hens for reneating was subject to annual variation. Under Wisconsin conditions, reneating apparently contributes less to annual production than is true in many other areas.

Wetland cover types contributed 63 percent of successful clutch

production in an average year, hayfields 19 percent, strip cover 16 percent, and small grains 3 percent.

In 1961, with hatching success in harvested hay only 1 percent, wetlands accounted for 76 percent

of overall brood production.

## HATCHING DISTRIBUTIONS

### METHODS OF SAMPLING AND ANALYSIS

The most reliable data from which to construct hatching distributions are those based on actual nest observations. In the present study, fewer than 50 successful clutches were available for this purpose in an average year (Table 27). These were believed to be a representative sample of hatching dates, but sample sizes were inadequate to reveal the actual shape of each year's hatching distribution. Nest data were thus used only to calculate average hatching dates and to estimate the percentage of each year's hatch produced during respective thirds of the hatching season. In all cases, data were appropriately weighted to account for unequal rates of nest searching between cover types.

The bulk of our summer brood data consisted of early morning

roadside observations. Occasional counts were also made in evening, and records were kept of all broods incidentally encountered at other times of day. Morning counts were made between 6:00 a.m. and 9:00 a.m. In most years, observations began in mid-July and terminated at the end of August. Counts in 1959 and 1960 extended through mid-September. We did not follow predetermined routes, but systematically covered the Waupun Study Area and vicinity (Fig. 2), all roads of which were driven at least once weekly. Meteorological conditions were noted at the start and conclusion of each count, including temperature, dewfall, wind velocity, and cloud cover. The mileage driven each morning was also recorded.

Aging of young pheasants was based on criteria used by Wagner et al. (1965:160). All age determinations were made through binoculars or spotting scopes. At least 90

percent were made or confirmed by the senior author each year, assuring that age criteria were applied in a consistent manner throughout the study. Among broods older than 10 weeks, young cocks were commonly found that differed by as much as 2 weeks in apparent stage of the postjuvenile body molt. Unless plumage differences of this sort were accompanied by appropriate size differences, the final age estimate represented an abstraction based on the average size and stage of molt of all chicks present in the brood. Comparison between wing molts and body molts among dead chicks variously encountered provided constant checks on aging accuracy.

It is well known that the observability of pheasant broods changes with age. Because the seasonal distribution of our brood observations was not constant from year to year, bias would have existed had we relied on uncorrected data in annual comparisons of hatching phenologies.

To develop an appropriate correction for this bias, we first assigned each brood observed to a weekly hatching cohort and assumed it had hatched on the mid-date of that week. The interval over which brood observations were conducted was next divided into semimonthly periods between July 15 and August 31. We then assumed that the relative observability of a given cohort during a particular observation period was proportional to the length of time during that period that broods making up this cohort were between the ages of 5 and 11 weeks, these age classes comprising over 75 percent of all brood observations made.

TABLE 27. Comparison of mean hatching dates between various methods of constructing hatching distributions

Year	Mean Hatching Date in June			
	Nest Records	Brood Observations		Postjuvenile Primary Molts
		Uncorrected	Corrected	
1959	20 (32)*	22 (170)	17	14 (530)
1960	26 (52)	28 (297)	25	17 (280)
1961	20 (36)	20 (328)	18	15 (328)
1962	17 (40)	17 (280)	18	19 (373)
1963	19 (45)	16 (267)	18	15 (375)
1964	12 (49)	11 (323)	13	10 (455)
1965	---	15 (313)	14	16 (195)
Unweighted means	June 19	June 18	June 18	June 15

\*Sample size shown in parentheses.

Broods produced near the middle of the hatching season, particularly those born in June, were most likely to be encountered on brood observations run between mid-July and late August. Earlier hatched broods were under-represented because of their advanced age at the start of brood observations, whereas later hatched broods were under-represented because they had not yet reached the most observable age classes by the time our observations terminated.

The final step was to weight the observability ratings for each cohort in each observation period by the number of miles driven in search of broods during that period. These values were then summed for each cohort. The result was a set of index values showing the relative probability of observation of each cohort according to the particular schedule of brood observations undertaken in a given year. These values were then applied as correction factors to the observed number of broods in each cohort.

Corrected hatching curves tended to be highly erratic near the tails of the distributions, the result of large correction factors which tended to exaggerate inherent sampling error associated with the smaller number of early and late-season broods observed. For this reason, corrected hatching distributions were used solely to calculate mean hatching dates and to estimate the percentage of each year's brood production during respective thirds of the hatching season. The validity of this correction procedure was demonstrated by the strength of the correlation between mean hatching dates based on corrected brood observations versus actual nest records ( $r$  with 4  $df$  = 0.94; reference value at 0.01 = 0.92). By comparison, the correlation between nest data and uncorrected brood data was only 0.74 (reference value at 0.05 = 0.81).

Comparison of mean hatching dates (Table 27) showed that hatching distributions tended to be shifted left or right from their actual placement along the x-axis by variable scheduling of brood observations. We doubt, however, that the generalized configuration of the curves was affected to any appreciable extent, except possibly near the tails. Subsequent attention



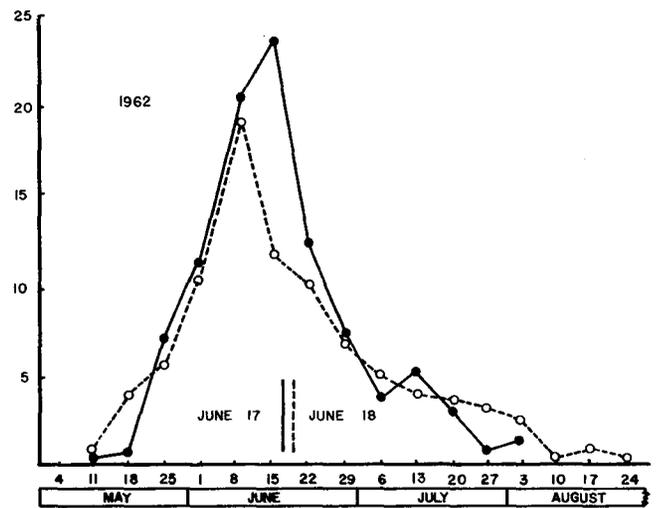
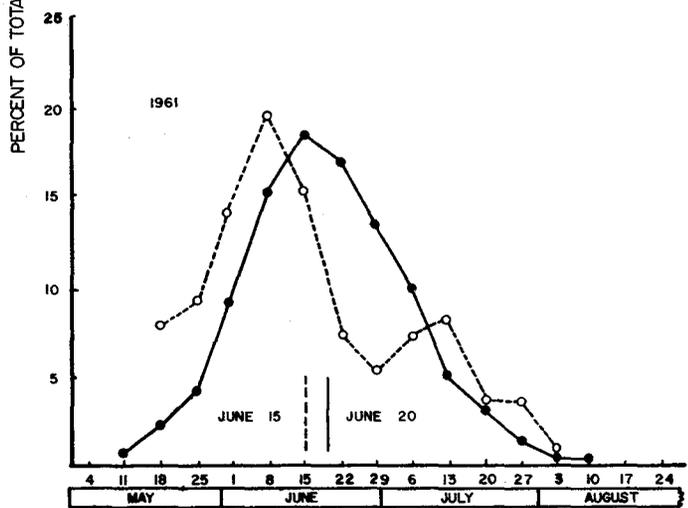
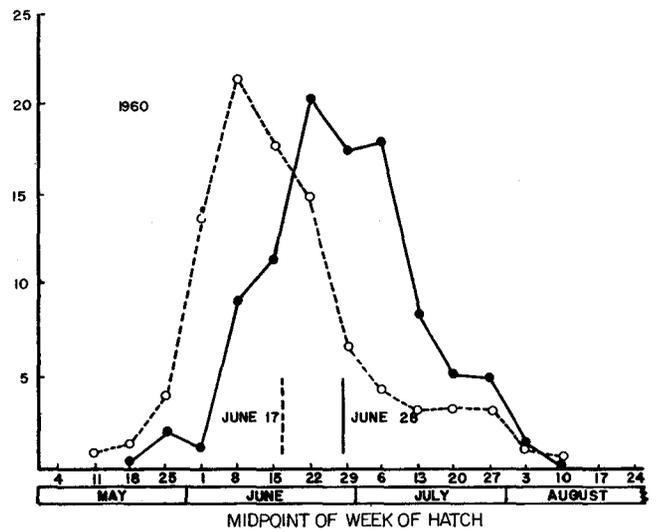
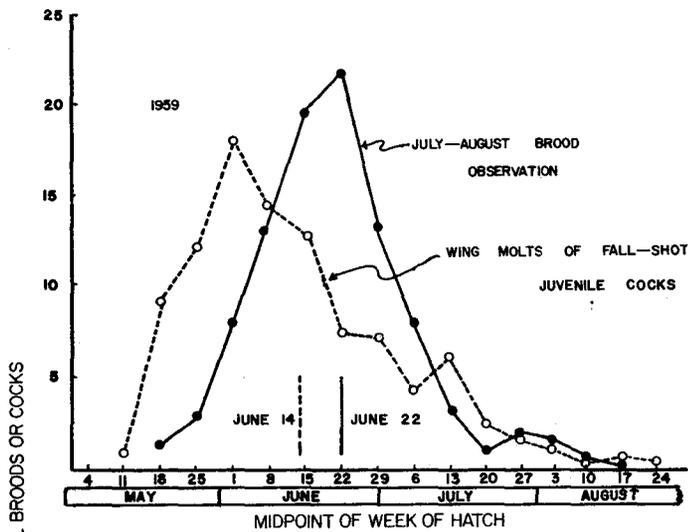
will therefore concentrate on the model portions of the curves and all reference to mean hatching dates will be based on corrected observations exclusively.

One set of primary feathers was collected from each juvenile cock examined during hunter bag checks. Wings were also obtained through cooperation of study area hunters in conjunction with spur collections. Age determination through 23 weeks of age was possible from progress of the postjuvenile primary molt according to criteria developed for Wisconsin pheasants by Woehler (1953). In the present study, hatching dates were late enough, and hunting seasons early enough, so that less than 8 percent of the juvenile cocks had already completed the molt by the time of collection and could not be aged. Such birds were arbitrarily assigned an age of 23 weeks and backdating proceeded accordingly.

With only a single exception (1961), brood and wing molt hatch-

ing curves exhibited minor configurational differences. The wing molt distributions, however, were generally broader at the base (Fig. 16), indicating a proportionally larger percentage of the hatch coming off near the beginning and the end of the hatching season. In general, this bore out our earlier conclusion that brood counts tended to oversample the mid-season cohorts.

In most years, wing molts also produced an earlier hatching distribution (Table 27). A similar trend was reported by Stokes (1954:46) on Pelee Island. Our conclusion was that later hatched chicks matured faster and thus were actually younger than their wing molts indicated at time of collection. E. E. Woehler (Pers. comm.) compared growth rates of pen-reared chicks at the Wisconsin State Game Farm in 1952 and observed that birds hatched in late June reached the half-way point in the postjuvenile primary molt roughly



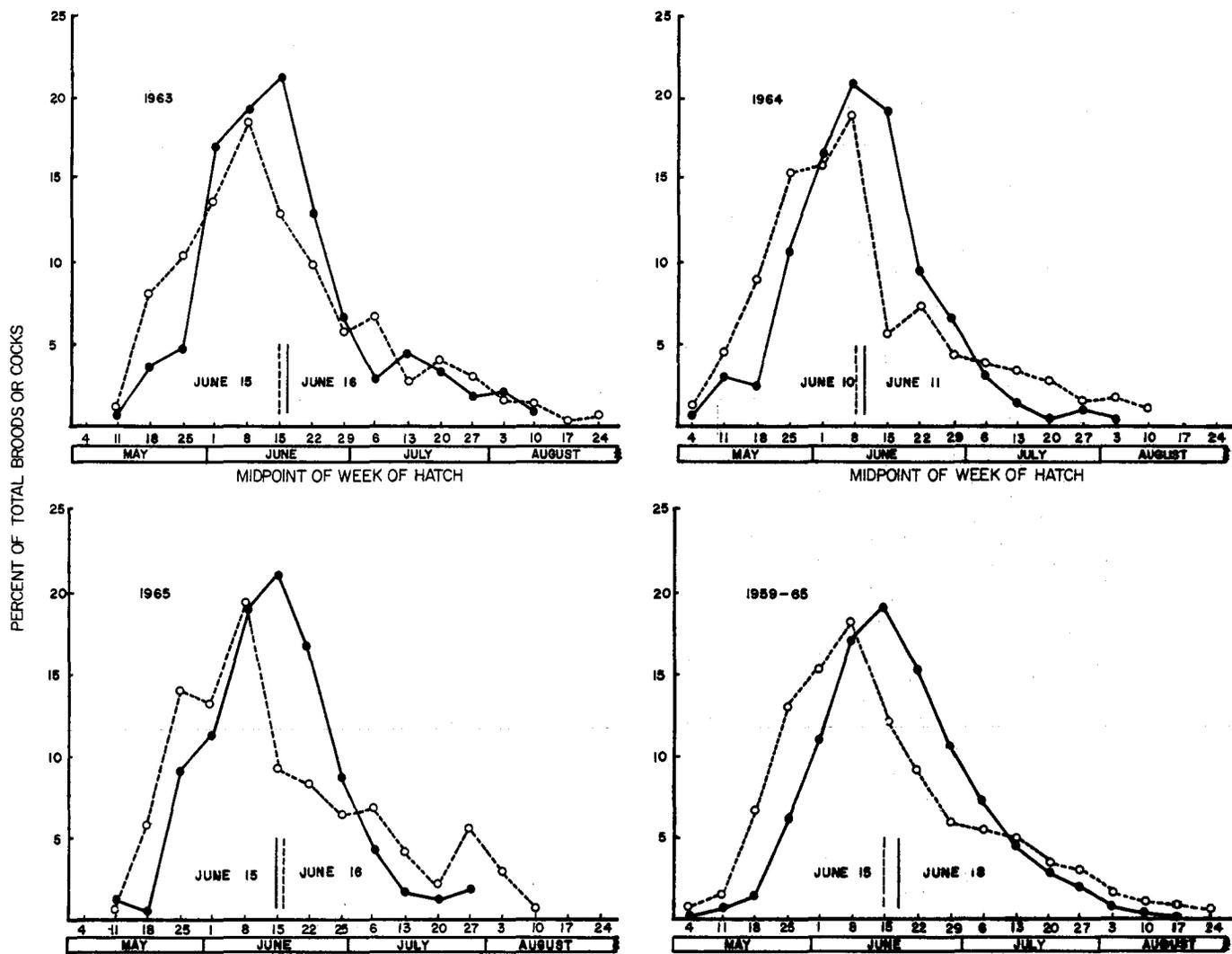


FIGURE 16. Hatching distributions based on summer brood observations and postjuvenile primary molts of fall-shot juvenile cocks. Sample sizes shown in Table 27. Mean hatching dates shown by vertical lines under each distribution.

10 days younger than chicks born in mid-May. By contrast, Stokes (1954:120), on Pelee Island, observed that late-hatched chicks matured slower, though in Stokes' study delayed growth appeared to be a function of summer shortage in food supply. We doubt that food shortage was a factor in our study, and the fact that Woehler's late-hatched chicks molted faster on the same diets as early-hatched chicks suggests that accelerated feather replacement as the brood season progresses may be the ordinary circumstance where food is not limiting. The reason why brood and wing molt curves in the present study departed farthest from each other in 1959 and 1960 was unclear. Possibly the growth differential was more pronounced in these years, or possibly we were under-aging broods during the initial 2 years of field study.

On first consideration, the earliness of our wing molt curves seemed attributable to the larger number of chicks per brood among early-hatched clutches. But when brood observations were segregated and hatching distributions were compared using brood ages versus chick ages, no appreciable difference in hatching phenology was observed. At least through the period that brood observations were being conducted, the longer period of time that early hatched broods were exposed to mortality apparently counterbalanced their larger average number at hatching. Extrapolating this trend into the hunting season suggested that the seasonal decline in brood size probably was not the sole factor accounting for the earliness of the wing molt curves.

Finally, earlier wing molt curves may also have stemmed from poorer survival of late-hatched broods or because chicks produced later in the season were for some reason less vulnerable to hunters and therefore under-represented in our samples. The reliability of any posthatching method of determining hatching phenology rests on the assumption that survival is constant between hatching cohorts, and the closer to the time of hatching that a sample is drawn, the less the risk that this assumption will not be met. For these reasons, hatching curves based on fall wing molts were believed to

be inherently less reliable than results obtained from brood observations. Subsequent discussion of hatching phenology, unless otherwise noted, will thus be restricted to brood aging alone.

## ANNUAL VARIATIONS

The average date of hatch for all years of study combined was June 18 (Fig 16). In an average year, 12 percent of the broods came off in May, 67 percent in June, 19 percent in July, and 2 percent in August. This comparison was based on uncorrected brood data, hence the actual percentage of brood production for June was something less than indicated in relation to other months.

Hatching phenologies at Waupun compared closely with statewide information reported by Wagner et al. (1965:45). A composite of the 1947-56 hatching distribution reported by these authors also showed an average hatching date of June 18. The modal point of their curve was a week later than ours, but its shape was similar.

The most striking difference in hatching distributions from year to year was in the relative sharpness of the peaks (Fig. 16). Steepest curves occurred in 1959 and 1962. In each of these years, two points shared dominance at the peak, whereas in all other years there were at least three points of near equal rank contributing to the modal portion of curve.

In order to quantify these configurational differences, the range of the three highest points was expressed as a percentage of their mean. Values for individual years were 46, 13, 14, 57, 23, 25, and 22 percent, respectively, for the period 1959-65. Whether the unusually high values for 1959 and 1962 represented real annual departures from the norm or simply errors in sampling was unclear. An attempt was therefore made to establish a set of empirical confidence limits for these percentages.

An artificial population of 1,500 hatching dates was constructed representing the composite 1959-65 hatching curve in Figure 16. Twenty samples of 300 each were next drawn at random from this population. This sample size was decided

upon because it approximated the actual number of brood observations on which each year's hatching curve was based. Each of the 20 samples was then plotted graphically, and values for each were calculated as described above. The 20 sample distributions showed a mean value of 24 percent with a range of 8 to 41 percent. Hence, in samples of 300 drawn at random from this population, the range of the three highest points did not exceed 41 percent of their mean once in 20 times. This left little room for doubt that hatching curves in 1959 and 1962 were significantly sharper than the generalized type of distribution which otherwise characterized the study.

The common feature of these two nesting seasons was that nesting was delayed and that hayfields attracted an above-average percentage of total clutch production (Fig. 10), in addition to an inordinately high percentage of initial nesting attempts (Table 28). In 1959, clutch establishment in hay was concentrated between May 10 and May 31. In 1962, it was largely compressed between the dates of May 1 and May 20 (Fig. 11). These particular clutches comprised a substantial fraction of the overall reproductive effort—39 and 28 percent, respectively, and a corresponding high level of brood production would have been expected in the absence of hay mowing between June 18 and July 9 in 1959 and between June 9 and June 28 in 1962. But hatching distributions peaked well ahead of these periods and dropped abruptly (Fig. 16). Evidently all but the earliest of these clutches were wiped out by hay cutting, in line with our earlier conclusion that under normal mowing schedules only the earliest clutches established in hay stood any chance of succeeding.

Sharpness of hatching curves appeared to depend on the degree to which hayfields attracted initial nesting attempts. In springs during which an unusually large percentage of the breeding hens established first clutches in hayfields, nest starting dates in this cover type were tightly clustered during the month of May. These clutches were sufficiently numerous that their fates tended to dominate the eventual hatching distributions, which ex-

TABLE 28. Calculation of the percentage of hens establishing first nesting attempts in hayfield nesting cover\*

Year	Approximate Separation Date between Initial and Renest Clutches	Percent of Hayfield Clutches Established Prior Thereto**	Total Number of Hayfield Clutches <sup>1</sup>	Indicated Number of Hayfield Clutches Representing First Nesting Attempts	Spring Hen Population	Calculated Percent of Spring Hen Population Establishing Initial Nesting Attempts in Hay
1959	May 20	46	265	122	348	35
1960	May 12	18	329	59	427	14
1961	May 9	0	257	0	524	0
1962	May 24	59	151	90	353	26
1963	May 7	10	159	16	333	5
1964	May 16	31	116	36	353	10

\*Based on results from Alto Study Area in 1959 and from combined results from Alto and Mackford study areas in 1960-64.

\*\*Based on nest starting dates among backdated hayfield clutches.

<sup>1</sup>Data from Appendix V of Gates (1971:834-850).

hibited steep declines when these nests were exposed to mowing mortality. Flatter hatching distributions were observed in years when there was greater spread of nest establishment dates in hay, or when a smaller percentage of total clutch production occurred in this cover type. In 1961, when nest success in hay was only 1 percent, there was not major dropoff in the hatching distribution (Fig. 16) because mowing mortality was borne by clutches begun over a wider span of time (Fig. 11).

Wagner et al. (1965:44-45) divided statewide hatching curves into dual categories depending on the mean date of hatch. In late-hatching years, the hatching distribution tended to be higher and sharper with only a single dominant point at the peak, whereas in early years there were typically one or more subdominant points on either side of the mode. Mean hatching dates were regarded as valid indices to nesting phenology, from which these authors concluded that delayed nesting seasons were somehow associated with steeper hatching curves. Their hypothesis was that clutch production in late nesting years was compressed into a shorter period of time because of a more-or-less fixed terminal date for egg laying which allowed less time for renesting.

Results from our study suggested an alternative explanation for this phenomenon. Delayed nesting on our area was associated with heavier reliance on hay as nesting cover.

Effects of mowing mortality operating against a proportionally larger percentage of total clutch production gave rise to a sharper hatching curve than in years when nesting was earlier and hayfields attracted mainly renesting hens whose clutches were staggered over a broader range of starting dates. The sharper hatching distributions observed by Wagner et al. in late-nesting years suggest that the mechanism described for our study may be of general application to Wisconsin pheasant range.

Average hatching dates in this study were unrelated to trends in onset of nesting or mean date of clutch establishment. Because of the seasonal decline in nest success, all years of study demonstrated an advance in hatching phenology relative to nesting phenology, but the difference was more pronounced in certain years than others. The correlation between the average date of hay harvest and the mean date of hatch was at best suggestive ( $r$  with 4 df = 0.68; reference value at 0.05 = 0.81), indicating that time of hay cutting was but one of several influences upsetting a possible relationship between nesting and hatching phenologies. Other variables affecting the amount of nest destruction in hay, and hence the impact of hay cutting on hatching dates, included the percentage of total clutch production that occurred in hay, as well as the timing of nest establishment in this cover type.

In 1959 and 1962, with a large

proportion of the total nesting effort in hay, earlier than average hay harvest was associated with a 15- and 10-day advance, respectively, in mean hatching dates. But in 1964, with even earlier hay harvest, the advance in hatching dates was considerably less because so few hens nested in hay. In 1961, hay cutting was comparatively late, but a wide gap still prevailed between nesting and hatching phenologies because virtually all hayfield clutches were begun too late to benefit from delayed harvest.

Other influences on nest success also entered the picture. Onset of egg laying was approximately normal in 1964, yet the hatching curve was the earliest on record, the result of unusually low nest predation in permanent cover and less need for renesting. It was clear that hatching dates depended on a multiplicity of individual factors, among which annual differences in time of nesting were comparatively unimportant. Under conditions of the present study, trends in mean hatching dates from year to year would have been virtually meaningless as indices to the relative earliness of nesting.

Wagner et al. (1965:89-91) compared statewide average hatching dates with annual trends in hay mowing phenology. The correlation fell short of statistical significance from which it was concluded that mean hatching dates were not simply artifacts of mowing determined by the schedule of hay harvest. Instead, hay mowing and nesting

phenologies were said to be related, each under influence of spring temperature, so that hay harvest had a relatively nonvariable influence on pheasant production from year to year.

Results from our particular study area contrasted sharply with this statewide picture. The schedule of hay cutting at Waupun depended on early summer precipitation and whether or not other agricultural operations which took precedence over hay harvest were completed on time. These factors were extrinsic to those regulating nesting phenology, and hay mowing affected a highly variable fraction of each year's nest production. As high as 37 percent of total clutch production was destroyed by mowing in 1959 and as low as 14 percent in 1964 (Gates 1971:856-861). Although earliness of hay cutting was not the sole factor accounting for variable rates of nest destruction in hay, it was clearly a contributing influence, which in certain years had a marked effect on both the shape and the timing of the ultimate hatching distribution.

Many of the variables affecting nest success in our study represented small area influences that would cancel each other on a statewide basis. The conclusion of Wagner et al. that mean hatching dates are determined by time of nesting obviously applied to statewide populations. The relationship they observed between hatching phenology and prenesting temperatures clearly demonstrates that the former were varying with more fundamental influences on hatching dates than events affecting reproduction after nesting was already underway.

## CONCLUSIONS ON RENESTING

Seubert (1952) observed a terminal date in early July after which captive pheasants whose clutches were disrupted did not attempt to renest. On Pelee Island, delayed onset of nesting in 1950 was not offset by compensatory extension of nesting later into the season, so Stokes (1954:44) therefore proposed that the length of the nesting season, and hence the amount of time available for renesting, might

depend on the time at which nesting began. Essentially the same hypothesis was suggested by Wagner et al. (1965:45) to explain the observation that late-nesting years in Wisconsin were characterized by steeper, more singlemoded hatching curves. A pertinent question, however, is what relationship the shape of the central portion of a hatching curve has to the total length of the nesting season. Actually, early and late nesting years in the study of Wagner et al. showed no clear-cut differences in the overall spread of hatching dates.

In our study, 1961 and 1963 were early nesting years, while 1959 and 1962 were late. Hatching distributions suggested no difference in the time at which nesting terminated, however (Fig. 16). Roughly 90 percent of the hatch was off by July 15 during early and late nesting years alike.

At first, these findings appeared consistent with the view that renesting potential was lowered when nesting began later. But lower rates of hen survival also prevailed in 1959 and 1962 (Gates 1971:709-746), and apparent telescoping of the nesting season into a shorter period of time may simply have been the outcome of fewer hens surviving long enough to renest successfully. The percentage of the late summer hen population observed with broods in these years was not below normal, implying equally persistent renesting by surviving hens despite the fact that nesting began later.

It is therefore possible that late seasons appeared to be foreshortened because of other factors that curtail the amount of successful renesting. Even during the late nesting years of 1959 and 1962 in our study, egg laying continued another 6 to 8 weeks after the approximate date separating initial from renest clutches (Fig. 11), seemingly ample time for renesting by hens still surviving during this season.

First-crop hay harvests at Waupun generally began in early June and were completed by early July. The average date of mowing for all years of study combined was June 17 (Table 9). If clutch destruction in mowed hay was followed by an appreciable amount of successful renesting, a secondary

or minor peak on the hatching curve might have been expected between late July and mid-August. Because the amount of time required to begin a second clutch varies with stage of incubation (Seubert 1952), it seems reasonable to suppose that this peak would have been most pronounced in 1959 and 1962, seasons when hayfield nesting was more nearly synchronized (Fig. 11) and clutches were at near comparable stages of incubation when destroyed. The wider spread of nest starting dates in hayfields in other years, if followed by successful renesting, would more likely have been associated with attenuation of hatching curves rather than definite subpeaks.

Neither the brood nor wing-molt curves in 1959 or 1962 demonstrated significant resurgence in hatching dates at the expected time (Fig. 16). Hence it did not appear that mowing mortality was followed by a substantial amount of successful renesting. The large majority of hayfield clutches in these years were begun in the month of May, and accordingly were in advanced stages of incubation when destroyed. Since renesting ability declines as incubation progresses (Seubert 1952), time of clutch destruction may have been particularly ill-suited for production of a subsequent clutch.

Herein may lie a crucial disadvantage of delayed nesting seasons or other factors which promote heavier reliance on hayfields for initial nesting. Such nests are more-or-less secure from disturbance until time of hay harvest, but are then destroyed so late in incubation that renesting ability is seriously impaired.

Data for all years of study combined similarly revealed that renesting after hay harvest contributed insignificantly to brood production. The composite 1959-65 hatching curves suggested that about 5 percent of all broods were produced after July 25 in an average year. Late-hatched cohorts appeared to be under-represented in our hatching distributions, but not all hens producing young after July 25 had necessarily been disturbed in hay. Five percent thus appeared to be a reasonable estimate of the fraction of brood production contributed by renesting after hay mowing.

The number of nesting hens killed by hay mowers in 1959-64 amounted to 17 percent of the spring population (Gates 1971:709-746). Nest searching in hayfields suggested that roughly half of the hens with active clutches in hay at time of mowing were killed outright or seriously injured in mowing accidents. It follows, then, that approximately 17 percent of the hens alive in spring must have survived clutch destruction in hay and accordingly were available for renesting. Since 53 percent of the hen population produced broods in these years (Table 25), less than 3 percent of the number alive in spring must have succeeded by virtue of successful renesting after clutch destruction in hay (5% of 53 = 2.8).

This low rate of production did not necessarily depend on lack of renesting effort. The success rate of clutches began after June 1 was only 20 percent, from which it might be inferred that approximately 88 percent of the unsuccessful hens tried again ( $3\% \div 20\% = 15$ ;  $15 \div 17 = 88\%$ ). Many hens evicted by hay mowers moved into other hayfields to renest, into second-growth hay, or into peafields. In all of these cover types, rates of nest success were extremely low.

For all practical purposes, then, clutch destruction by hay mowing virtually finished a hen's chances for successful reproduction that year. This may explain in part why Klonglan et al. (1959) in Iowa failed to detect a significant population response despite 38 percent reduction in hen mortality in hayfields over a 3-year period through use of flushing bars. Several studies have demonstrated the efficacy of flushing bars in reducing hen casualties in mowed hay (Warvel 1950; Swagler 1951; Bue and Ledin 1954; Nelson 1955; Robertson 1958:84; and Klonglan et al. 1959), but the benefits of such a practice are open to suspicion. At least under Wisconsin conditions, the contribution of renesting after hay mowing appears to be inconsequential, and because of the high turnover rate of pheasants, hens saved one year probably contribute little to the subsequent year's production.

It is often supposed that hatching

curves skewed farther to the right indicate better reproductive success because they reflect a high degree of successful renesting. On such grounds, one might infer that 1960 and 1961 represented lower and upper levels of renesting activity in this study (Fig. 16). From actual nest-per-hen figures, however, the rate of renesting was actually comparable between the two, and the percentage of hens that succeeded in brood production was nearly the same (Table 25). The season of highest overall reproductive success, 1964, showed comparatively little evidence of renesting because of the high rate of nest success which required fewer hens to nest a second time.

Although more skewed hatching curves indicate higher prevalence of renesting, it does not follow that reproductive success is necessarily higher. Frequent renesting may be the outcome of higher nest mortality which results in a net reduction in reproductive success. The 1961 and 1964 nesting seasons at Waupun were cases in point. Even though 1961 showed more extensive renesting, this did not compensate for the higher rate of nest mortality which prevailed that year. Only 54 percent of the hens nested successfully in 1961, compared with 64 percent in 1964 (Table 26).

Hatching distributions in this study did not shed useful light on the relative success of the nesting season, nor did they accurately reflect yearly differences in phenology of clutch production, onset of nesting, or extent of renesting. Our conclusion was that hatching curves must be interpreted with caution, and that they provided at best highly imperfect clues to actual mechanisms affecting reproductive success.

## SUMMARY

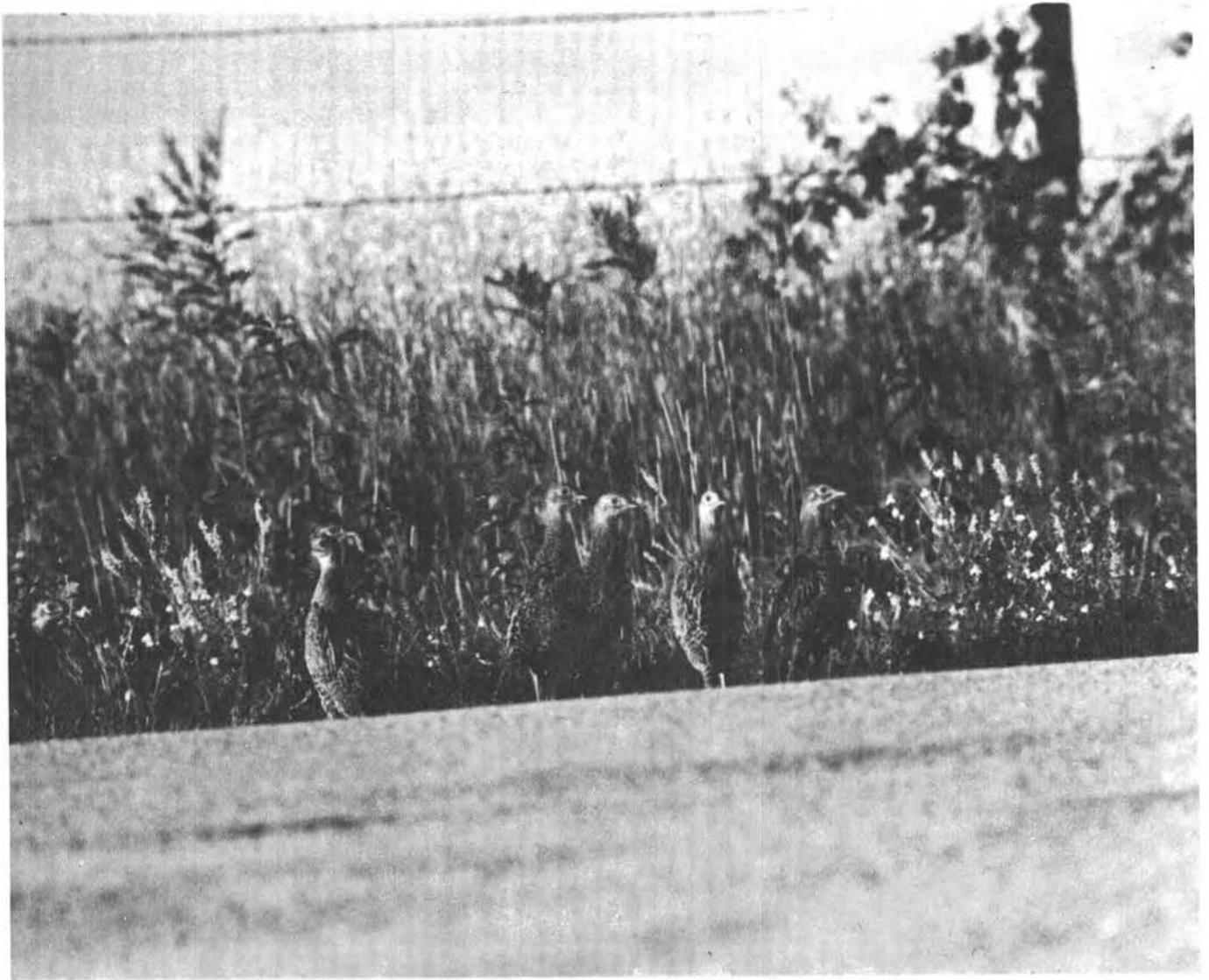
Three sources of data provided information on hatching phenology: (1) nest records; (2) summer brood observations; and (3) aging based on postjuvenile primary molts. Nest samples were inadequate to reveal configurational differences in hatching distributions, and wing molt curves were regarded as inherently less reliable than those based on brood aging. Brood observations were thus relied upon as the princi-

pal method of determining hatching phenology.

The most conspicuous annual difference in hatching curves was in the relative sharpness of the peaks. Sharper, more nearly singlemoded distributions characterized years of delayed nesting when hayfields attracted unusually large numbers of initial nesting attempts. The fates of these clutches tended to dominate the subsequent hatching curves, which showed sharp dropoffs at the time these clutches were exposed to mowing mortality. Flatter curves prevailed when hay cutting losses were borne by clutches begun over a wider range of starting dates, or when the total volume of hayfield nesting was less. It was concluded that sharpness of hatching curves under Wisconsin conditions may depend on the extent to which hayfields attract initial nesting attempts, and that the attraction is stronger when nesting is delayed.

Average hatching dates demonstrated no relationship with onset of clutch production or with average date of nest establishment. Variable magnitude of nest destruction in hay, in part the outcome of variable hay harvest, was most prominent in precluding a relationship between nesting and hatching phenologies. Under conditions of the present study, mean hatching dates were highly imperfect as annual indices to nesting phenology.

Delayed onset of nesting was not offset by compensatory extension of clutch production later into summer; however, late nesting seasons were associated with higher hen mortality which tended to curtail the extent of renesting. Renesting ability of surviving hens did not appear to be less in delayed seasons, raising doubt against the hypothesis that late nesting seasons are less favorable to pheasant production because of lesser time for renesting. Only about 3 percent of the spring hen population succeeded in brood production by virtue of successful renesting after hay cutting. The large majority of hens that survived hay mowing apparently nested again, but few were successful owing to high nest mortality late in the season. Relative rates of renesting and reproductive success from year to year could not be inferred by comparison of hatching distributions.



# BROOD SIZE AND JUVENILE MORTALITY

## BROOD SIZES

Most of our information on brood size was obtained from July and August brood observations. Use was also made of broods counted outside this period, as well as broods encountered during other field work. Analysis of brood size was restricted to completely counted broods only.

When groups of chicks were accompanied by two hens, they were recorded as two broods if two age classes were distinguishable; otherwise they were recorded as a single brood and the extra hen was regarded as broodless. Chicks without hens were also recorded as broods depending on the number of age classes recognized. All broods of 14 or more chicks of the same age were halved and treated as two broods; if only one hen was present, half were recorded as orphans. Single chicks, with or without hens, if listed as complete counts, were also treated as broods. Broods consisting of mixed age classes were recorded as separate broods, but were not treated as complete counts.

For the years 1959-65, the average brood size at hatching was 10.0 chicks, and the mean of all posthatching age classes was 6.6 chicks (Table 29). The latter compares with 7.4 young per brood reported by Wagner et al. (1965:53) as the statewide average in 1946-56. The difference was perhaps a real one, but whether it represented an actual population characteristic or simply a difference in methods cannot be stated.

The average number of young per brood at hatching demonstrated a significant degree of annual variation, as did the average of all posthatching age classes (Table 29), but the two were not correlated with each other ( $r$  with 5 df = -0.02). During the period 1959-64, the correlation between the average brood size at hatching and the earliness of nesting (Table 4) was only suggestive ( $r$  with 4 df = 0.58; reference value at 0.05 = 0.81), but a relationship seemed likely because of a significant relationship between

**TABLE 29.** Annual variation in average brood sizes at hatching versus the average of all posthatching age classes

Year	Average Size at Hatching (No. Chicks/Brood)*	Average All Older Age Classes (No. Chicks/Broods)**
1959	9.1 (36) <sup>1</sup>	6.3 (210)
1960	9.8 (48)	6.7 (252)
1961	10.2 (33)	6.3 (213)
1962	9.7 (44)	7.1 (188)
1963	9.9 (50)	7.2 (148)
1964	10.8 (51)	6.6 (176)
1965	10.1 (8)	6.6 (189)
1959-65	10.0 (270)	6.6 (1,376)

\*Difference between years in average brood size at hatching highly significant by analysis of variance ( $F$  with 6 and 263 df = 2.65; reference value at 0.025 = 2.41).

\*\*Difference between years in average size of all posthatching age classes highly significant by analysis of variance ( $F$  with 6 and 1,374 df = 3.56; reference value at 0.005 = 3.09).

<sup>1</sup>Sample sizes shown in parentheses.

onset of nesting and average clutch size (Table 77) ( $r$  with 4 df = 0.85). Average brood size after hatching (1959-64) was not correlated with the phenology of nesting ( $r$  with 4 df = 0.37), the mean date of hatching ( $r$  with 4 df = 0.15), nor with average clutch size ( $r$  with 4 df = 0.02), from which we infer that brood size at hatching was partly a function of clutch size, and in turn earliness of nesting, but that posthatching influences on chick survival were sufficiently variable from year to year to obscure these relationships.

The mean number of chicks per brood showed a declining trend over the first 4 weeks of life, an increasing trend between the sixth and eleventh weeks, and a final decline as family organization weakened and broods began disbanding (Fig. 17). The pattern of change was virtually identical to that reported by Wagner et al. (1965:48) from statewide observations. It seems reasonable to attribute the initial decline to mortality and the increase to brood combination, the latter

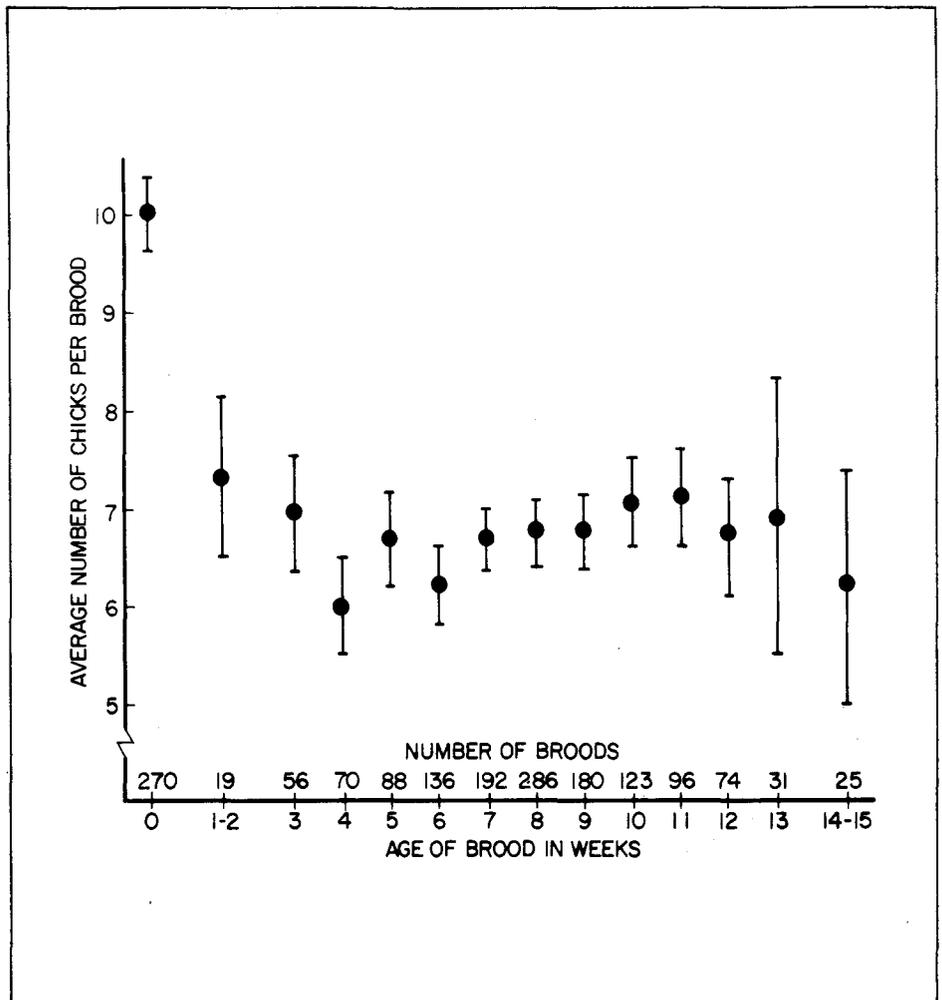
being commonly observed in pheasants (Erickson et al. 1951; Stokes 1954:52; Baskett 1947:24; Robertson 1958:88; and others).

Rates of brood shrinkage would have been most valuable as annual mortality indices had it been possible to compare brood size at hatching with the average number of surviving chicks per brood at 4 to 6 weeks of age. Unfortunately, these three age classes made up such a small segment of each year's observations that comparison would have depended on extremely small samples. Larger sample sizes were available by taking the mean for all age classes combined, but this entailed the risk of variable effects of brood combination from one year to the next.

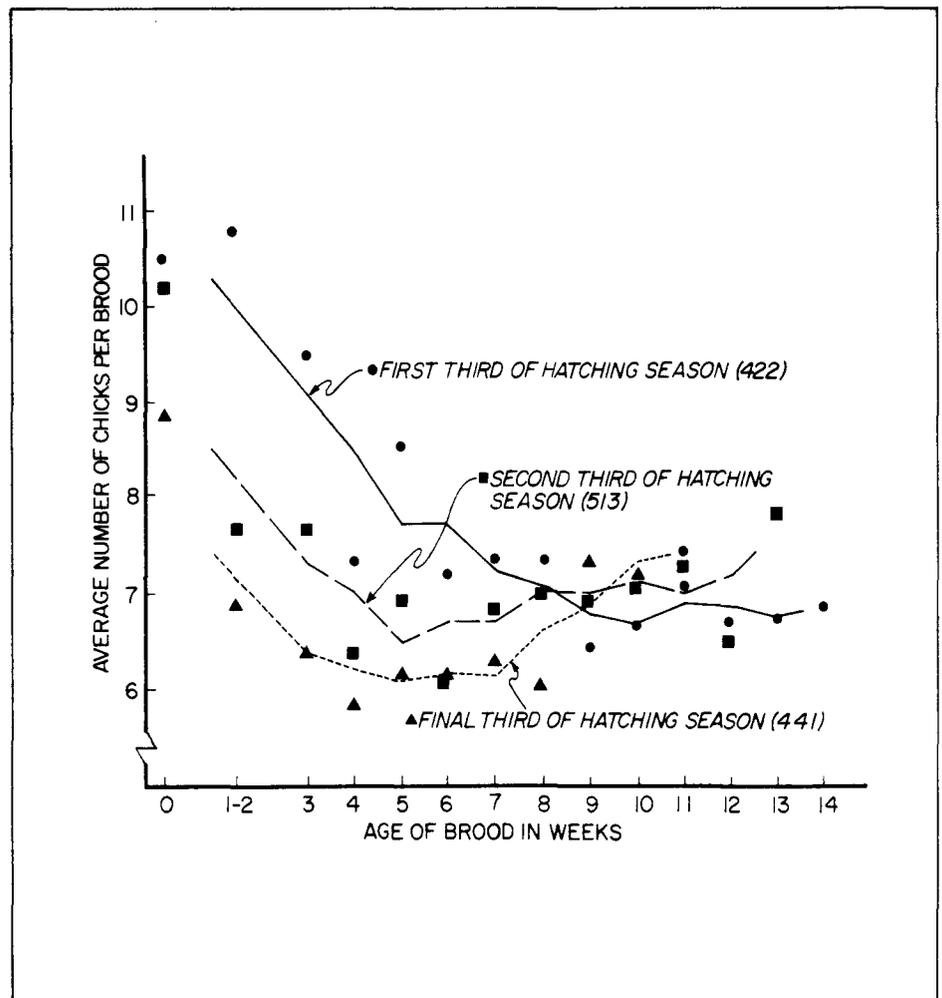
Trends in brood size versus brood age were therefore plotted by individual years. The resultant curves were so highly erratic, however, that no decision could be reached as to whether brood combination was subject to annual variation.

The frequencies of mixed-age and orphaned broods were next examin-

**FIGURE 17.** Relationship between average brood size and brood age based on completely counted broods, Waupun Study Area and vicinity, 1959-65. Means bracketed by 95 percent confidence limits. Average brood size at hatching based on the number of hatched eggs recorded in successful clutches.



**FIGURE 18.** Relationship between average brood size and brood age segregated by date of hatch, Waupun Study Area and vicinity, 1959-65. Dates used to divide the hatching season into approximately equal thirds (June 10 and June 24) were taken from the composite 1959-65 hatching distribution (Fig. 16). Lines fitted by 3-point moving averages. Sample sizes shown in parentheses.



ed (Table 30). These showed a highly significant difference between years in the percentage of broods comprised of more than one age class. If the frequency of recognized instances of brood combination varied, then it is reasonable to suppose that the frequency of brood mixing between chicks too similar in age to be distinguished as young from separate broods must also have varied. It also was evident that the frequency of orphan broods was subject to yearly fluctuation (Table 30). The likelihood that parentless chicks might be especially prone to mingle with other broods led to further doubt that rates of brood combination were constant. The weight of available evidence seemed to be that variable effects of brood mixing would have seriously weakened the validity of annual mortality indices based on the observed mean of all posthatching age classes.

Summer brood observations tended to miss the younger age classes of early-hatched broods and the older age classes of late-hatched broods. Larger broods from early in the season thus provided a disproportionately large share of the data on the size of older age classes, whereas smaller broods from later in the year contributed most of the information on the size of younger age classes. Since our brood counts differed somewhat from year to year in relation to hatching phenology, the effect of this bias was not constant. The average size of the 4- to 6-week age class was doubtlessly overestimated to a varying degree each year, but the magnitude of the error was not explored in view of other biases for which adequate correction factors could not be developed.

In conclusion, average brood sizes were influenced by so many factors in addition to juvenile mortality that we doubt they bore little more than perfunctory relationship to yearly trends in survival. Coupled with possible differences between years in the disappearance rate of entire broods, such methods were highly suspect as annual indices to juvenile mortality.

To evaluate trends in brood shrinkage as an index to seasonal mortality, it was also necessary to know whether the pattern of brood

**TABLE 30.** Annual variation in the frequency of mixed age and orphan broods

Year	Number of Broods Observed	Percent Consisting of Mixed Age Classes with Single Adult Hen*	Percent Consisting of Single Age Class with No Adult Hen**
1959	280	5	18
1960	354	1	7
1961	340	1	4
1962	350	2	11
1963	274	4	8
1964	340	5	9
1965	334	4	8

\*Difference between years in frequency of mixed age broods highly significant (chi-square with 6 = 16.83; reference value at 0.01 = 16.81).

\*\*Difference between years in frequency of orphan broods highly significant (chi-square with 6 = 48.03; reference value at 0.005 = 18.55).

**TABLE 31.** Seasonal variation in juvenile mortality based on brood shrinkage through 4 to 6 weeks of age, Waupun Study Area and Vicinity, 1959-65

Date of Hatch	Average Size at Hatching (No. Chicks/Brood)	Average at 4-6 Weeks of Age (No. Chicks/Brood)	Percent Difference
Before June 10	10.5 (58)*	7.2 (60)	31
June 10 to 24	10.2 (92)	6.1 (88)	40
After June 24	8.9 (72)	6.1 (179)	32

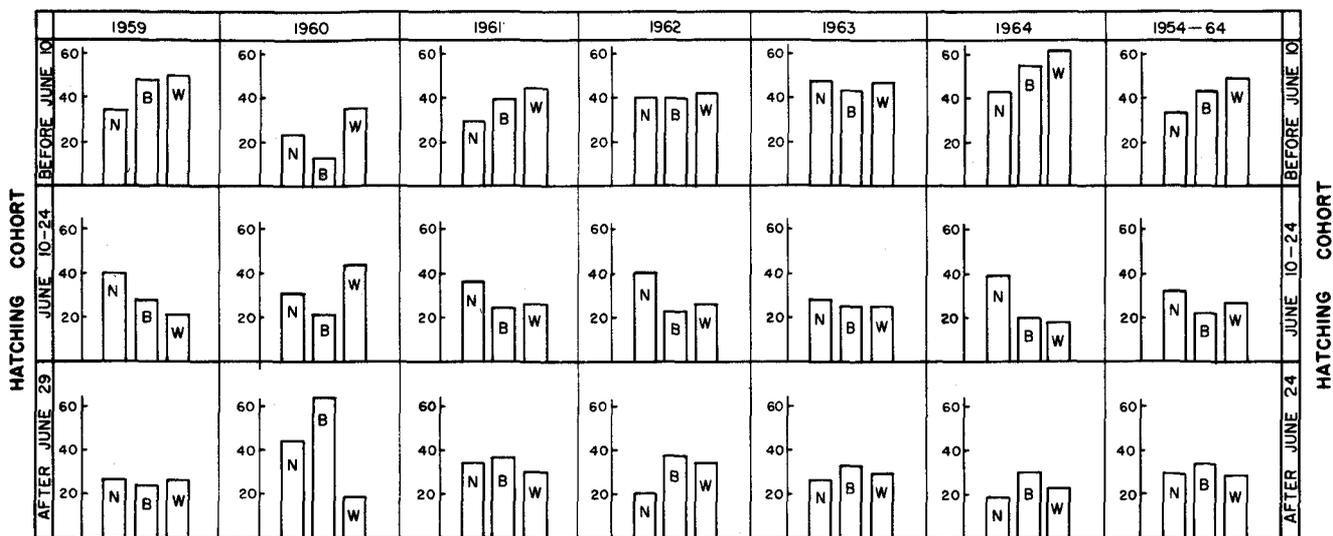
\*Sample sizes shown in parentheses. Sample sizes at hatching do not compare with totals in Figure 17 due to inclusion of undated successful clutches in the latter which could not be assigned to a particular hatching period.

combination differed within the year. Brood data from Figure 17 were divided into three hatching cohorts, and average brood size was plotted against brood age (Fig. 18). Results were similar to Wagner et al. (1965:50) and suggested a high degree of seasonal variability in brood mixing. Broods from the early stages of the hatching season showed comparatively little tendency to combine in later life, whereas those coming off later in the year demonstrated greater propensity for combination. Again, it appeared that rates of brood

shrinkage would have been unreliable as mortality indices after 6 weeks of age. Seasonal trends in juvenile mortality were therefore based on brood size at hatching versus the mean of the 4- to 6-week age groups. Because of small samples each year, comparison was necessarily restricted to combined results for all years of study.

### SEASONAL VARIATION IN JUVENILE MORTALITY

Rates of brood shrinkage over the first 6 weeks of life indicated that



**FIGURE 19.** Percentage of total brood production occurring during respective thirds of the hatching season as indicated by various methods of estimation. Legend: N = hatching dates of successful clutches; B = corrected brood

observations; and W = postjuvenile primary molts of fall-shot juvenile cocks. Ordinates of each graph represents the percentage of total brood production.

broods coming off in the middle third of the hatching season suffered relatively heavier mortality than those produced during the initial and final thirds (Table 31).

Wagner et al. (1965:49-50) segregated statewide brood observations into three hatching cohorts and then compared regressions of brood size on brood age for the first seven age groups. A significantly steeper decline in average size was observed among broods from the second third of the hatching season compared with the first. A regression coefficient was not calculated for broods produced in the final third of the season, but inspection of their graph does not suggest that the slope of the decline was materially different than that of early hatched broods. Results from both Wisconsin studies, then, suggest that brood shrinkage during the initial weeks of life tended to be fastest among broods making up the central portion of the hatching distribution.

The percentage of each year's brood production brought off during respective thirds of the hatching season is shown in Figure 19. Henceforth, broods from each of these periods will be referred to as

hatching cohorts. The relative size of a given cohort based on the actual hatching dates of successful clutches provided a starting point from which its relative survival could be successively inferred by comparison with data on corrected summer brood observations and hunting season wing molts.

Combined results for the years 1959-64 suggested differences in rates of brood disappearance between cohorts (Fig. 19). Compared with actual cohort size at hatching, brood observations revealed a substantial reduction in the relative strength of the midseason cohort. The effect was present each year of study and notably apparent 5 years out of 6.

The decline in brood number might have been attributable to brood combination, with no effect on juvenile survival, had the decrease in brood number been matched by compensatory increase in brood size. Figure 18, however, indicates that the average size of the midseason cohort increased by less than a single chick per brood after the low at 4 to 6 weeks. This was far short of the increase required to make up for the near 30 percent reduction in relative numbers indi-

cated by Figure 19.

Broods produced near the middle of the hatching season seemed to suffer disproportionately heavy posthatching mortality. Whatever mortality factors were involved obviously operated differentially against entire broods as well as individual chicks. Table 31 suggests that the effect was already evident by the age of 4 to 6 weeks.

The only mortality factors known to us which differentially affected midseason broods were hay mowing and pea harvesting. Seventy-one broods destroyed in whole or in part in mowed hay in 1959-65 averaged slightly over 2 weeks in age. Only 4 of the 71 were older than 3 weeks. Other workers have also pointed out the higher vulnerability of younger age-classes to hay harvest (Dustman 1950; Kozicky 1951).

Hay cutting at Waupun typically began in early June, peaked in mid-June, and was completed by early July (Table 9). The hatching dates of the midseason cohort fell between June 10 and June 24, and in view of the age distribution of mowing mortality noted above, it was evident that such broods bore the brunt of the juvenile losses occurring in hayfields. Broods making up

the early-hatched cohort were older, on the average, and hence less vulnerable to mowers, whereas most of the broods making up the late-hatched cohort were born too late to be exposed to mowing. Second-growth hay cutting had little effect on broods. Only two instances of juvenile mortality were encountered in second-crop hay. The small grain harvest was also of little importance in this regard; only one chick was known to have been killed by farm machinery in small grains.

Pea cutting extended from mid-June to late July and usually peaked in early July. Comparatively little brood mortality was actually documented in the cover type, probably because dead chicks became entangled in the vines which were windrowed and almost immediately trucked away or combined. Operators of pea cutting machinery however, reported that young pheasants were commonly encountered in this crop and were occasionally destroyed. Notwithstanding, juvenile mortality in peafields was considerably less than in hayfields. The pea acreage was but a fraction of the hay acreage, in addition to which mowing speeds and cover density of peafields were more conducive for escape by young pheasants.

Quantitative data on juvenile mortality were available from nest searching results in hayfields. The total number of young pheasants killed could not be calculated, since it was impossible to find all juveniles killed on study plots, but we obtained a minimum estimate of the percentage of broods from which one or more chicks were lost. As a 6-year average, some chicks from at least 10 percent of the broods produced on the two nesting study areas died as result of mowing mishaps (Table 32).

At least subjectively, it appeared from these results that hay harvest affected a sufficiently large number of broods, and with proper timing, to account for the heavier mortality suffered by midseason broods. It is also pertinent that mowing mortality affected individual chicks as well as entire broods, the latter through direct mortality of all young and indirectly through death or serious injury of adult hens caring for chicks too young to survive on their own.



*Pheasant brood killed by a haymower.*

It seemed reasonably conclusive that harvest operations were responsible for seasonal differences in juvenile mortality. This does not necessarily imply that farm machinery was the leading cause of juvenile death. Other mortality factors may well have had greater influence on brood survival, but with less tendency for seasonal variation.

### **ANNUAL VARIATION IN JUVENILE MORTALITY**

Overall rates of juvenile mortality were calculated by comparing estimates of the total number of chicks produced with the population of surviving young on October 1 (Table 33). Fall population estimates used in this comparison applied to the Waupun Study Area at large, whereas chick production figures were derived from the Alto and Mackford nesting study areas exclusively. The validity of this procedure rested on the assumption that the percentage of successful hens observed on the two smaller areas could be reliably extrapolated to the larger. On the whole, we didn't know of any good reason to question this assumption. Overall rates of hatching success on the two sample areas were similar—32 versus 29 percent, respectively (Gates 1971:834-850)—suggesting that the percentage of successful hens in a given year probably tended to be

uniform from area to area. In any event, it seemed improbable that rates of hen success on the two smaller areas would have fluctuated independently of the larger. Calculated mortality rates may have been subject to bias, but doubtlessly served as indices to mortality fluctuation from year to year.

Clear-cut differences in juvenile mortality were revealed by this analysis (Table 33). Low rates of loss, on the average 35 percent, prevailed in 1959, 1961, and 1962, compared with higher rates of loss, averaging 49 percent in 1960, 1963 and 1964. The mean rate of mortality for all years of study combined was 42 percent.

Incidence of juvenile mortality in hayfields in 1963 and 1964 was approximately twice the mean level recorded during other years of field study (Table 32). These represented two out of the three seasons of above-average overall mortality. This does not imply that heavier hayfield losses in 1963 and 1964 were the sole cause of higher juvenile death, but they were clearly a contributing factor. Reasons for heavier mowing mortality in these years were unknown. The percentage of total brood production occurring in hay in both years was lower than average (Gates 1971:834-850), and though hay cutting was early in 1964, the 1963 harvest was only slightly later than normal. Presumably the most vulnerable age classes of young were

TABLE 32. Incidence of juvenile pheasant mortality in harvested hayfields\*

Year	Acreage of Harvested Hayfields**	Broods Destroyed in Whole or in Part on Sample Plots in Harvested Hay			Projected Number of Broods Affected	Percent of Total Brood Production <sup>2</sup>
		Acres Searched	Number of Broods <sup>1</sup>	Broods Hit Per 100 Acres		
1959	699	126	2	1.6	11	8
1960	1,223	345	5	1.4	17	7
1961	1,227	355	4	1.1	14	5
1962	1,192	334	4	1.2	14	10
1963	1,100	363	9	2.5	28	14
1964	1,226	414	11	2.7	33	15

\*Based on nest searching of sample plots on the Alto Study Area in 1959 and the Alto and Mackford areas combined in 1960-64. Includes broods hit by forage choppers as well as hay mowers.

\*\*Includes pastured as well as mowed acreages, since all were sampled as a single stratum.

<sup>1</sup>Does not imply that all chicks were killed, only that one or more individuals from this number of broods were destroyed by farm machinery.

<sup>2</sup>Regarded as strictly an index to annual trends in mowing mortality.

more concentrated in hay at time of mowing, but why this should happen was unknown.

Two anomalies pervaded the 1960 brood data which may have been related to survival reduction. (1) This was the only year in which summer brood counts demonstrated a sizeable reduction in the relative size of the early-hatched cohort after hatching (Fig. 19). The average hatching date of this cohort in 1960 was May 23. Climographs reveal that May of 1960 was excessively wet, but whether these events represented cause and effect was uncertain. Chilling is known to be detrimental to chick survival (MacMullan and Eberhardt 1953; Ryser and Morrison 1954), and heavy precipitation might be expected to lower the resistance to chilling. Other writers have alluded to this possibility on strength of indirect evidence (Eklund 1942; Shick 1952; Lauckhart and McKean 1956:63; Brown and Robeson 1959), and a generalized relationship between unusually cool, wet springs and reduced production of young also has been pointed out (Allen 1947; Ginn 1948; Erickson et al. 1951). In any event, it seemed clear that some unusual sort of mortality must have befallen the early-hatched cohort in 1960, and excessive May precipitation loomed as the most likely explanation.

In 1960, two wetland clutches were successful on elevated positions on hummocks after rising water

levels had surrounded each by 4 to 6 inches of water. Both represented the early hatching cohort, which in general, consisted of broods produced mainly in wetland cover. In these two instances, it was difficult to understand how newly hatched chicks could have survived the move to higher ground. Flooding of wetland cover after nesting was underway in 1960 and probably also contributed to poorer survival of early-hatched young and overall increase in juvenile mortality.

(2) The relative strength of the late-hatched cohort from wing-molt data in 1960 was inordinately small compared with its initial size at hatching (Fig. 19). Wing molt criteria appeared to overestimate the age of late-hatched chicks and under-rated the size of the late-hatched cohort. But the size of the discrepancy in 1960 compared with other years was far too great to be explained by this bias alone. Brood numbers showed no evidence of similar reduction, nor was brood size unusually small. It was necessary, then, to postulate that late-hatched young in 1960 experienced unusually heavy mortality between summer brood observations and the time of hunting; however, we are unable to suggest mechanisms that might have accounted for this particular pattern of juvenile loss.

Juvenile mortality exhibited a substantial degree of yearly variation, which in turn could be associated with definite departures from

“normal” conditions in years when mortality rates were highest. Although evidence was largely circumstantial, and no single factor could be identified as the predominant cause of survival fluctuation, the implication was that influences in the posthatching environment were mainly responsible.

Statewide average brood sizes reported by Wagner et al. (1965:52) were inversely correlated with the average date of hatch, the latter which served as an index to nesting phenology under statewide conditions. In our area, brood size at hatching was suggestively, but not significantly higher in years of early nesting. An element of agreement, therefore, exists between Wisconsin studies that brood size tends to be larger when nesting is earlier. At Waupun, this could be attributed to smaller clutches produced by hens in late nesting years. Possibly, this also contributed to the correlation observed by Wagner et al.

Wagner et al. (1965:53) also demonstrated that rates of brood shrinkage between 1 and 7 weeks of age were higher when statewide brood data from five late nesting years were grouped and compared with five early years. The difference in mortality they observed was most pronounced between the first and fifth weeks of life, the trend in brood size thereafter being more-or-less parallel. In the previous section, it was concluded that delayed clutch production in our area was associat-

**TABLE 33.** *Estimated rates of juvenile mortality between hatching and recruitment to the fall population, Waupun Study Area*

Year	May 1 Hen Population	Percent of Hens Successful	Calculated No. of Broods Produced	Mean Brood Size at Hatching	Calculated No. of Chicks Produced	Surviving Juveniles on October 1	Percent Mortality between Hatching and October 1
1959	1,397	38	529	9.1	4,814	3,460	28
1960	1,194	59	696	9.8	6,821	3,460	49
1961	1,527	54	828	10.2	8,446	5,320	37
1962	936	41	382	9.7	3,705	2,280	38
1963	877	60	522	9.9	5,168	2,520	51
1964	986	64	614	10.8	6,631	3,540	47
1959-64					35,585	20,580	42

ed with increasingly heavy use of hayfields for initial nesting, one consequence being a sharper hatching distribution with proportionately more of the brood production concentrated during the middle stages of the hatching season. Since broods making up the central portion of the hatching curve appeared to suffer differentially heavy mortality during the early weeks of life, a faster rate of brood shrinkage, plus a reduction in overall average brood size, might well come to light in long-term comparison of brood data between early and late nesting years. Although we cannot rule out the possibility of alternative explanations, it is clear that trends in statewide brood data observed by Wagner et al. could have resulted

from the same influences affecting brood size in the present study.

### SUMMARY

Rates of brood shrinkage and the relative disappearance rate of entire broods suggested that juvenile survival was lowest among chicks produced in the middle third of the hatching season. Indirect evidence suggested that harvest operations, principally hay mowing, were responsible for the poorer survival of midseason broods. Chicks from earlier in the season were older and therefore less vulnerable to mowing, while many of the late-hatched chicks were born too late to be

exposed to mowing mortality.

Rates of juvenile mortality between hatching and October 1 varied from 28 to 51 percent and averaged 42 percent. Below-average mortality prevailed in 1959, 1961, and 1962; above-average loss prevailed in 1960, 1963, and 1964. Higher juvenile mortality in 1963 and 1964 was associated with unusually high incidence of brood mortality in hayfields. In 1960, circumstances suggested that excessive May rainfall may have contributed to increased juvenile loss. Under conditions of the present study, it was concluded that variables in the posthatching environment accounted for both seasonal and annual differences in juvenile mortality.

# ANNUAL VARIATION IN REPRODUCTIVE SUCCESS

**TABLE 34.** *Annual variation in rates of productivity and spring-to-fall gain, Waupun Study Area*

Year	Number of Juvenile Hens in Fall Population Per Hen in Spring Population		Percent Population Increase from Spring to Fall	
	From Sex and Age Structure	From Population Estimates	Hens Only	Hens and Cocks
1959	1.1	1.2	52	159
1960	1.5	1.4	92	212
1961	1.6	1.6	116	243
1962	1.2	1.2	65	167
1963	1.6	1.4	102	228
1964	1.9	1.8	124	277
1965	1.5	--	--	--
Unweighted means	1.5	1.4	92	214

## MEASURES OF SUCCESS

We defined the rate of production as the average number of young produced at hatching per breeding hen in the spring population. Juvenile survival was expressed as the percentage of total chick production alive on October 1.

Productivity was defined by Leopold (1933:22) as "...the rate at which mature breeding stock produces other mature stock, or mature removable crop," and was redefined by Hanson (1963:10) as "...ratio of sub-adult animals to adult animals." For our study, we defined productivity as the number of juvenile hens recruited to the fall population per breeding hen in the spring population.

An estimate of this ratio is theoretically obtainable from the adult sex ratio in spring and the cock age ratio in the hunting season kill. The number of young cocks per adult cock in the bag is divided by the number of hens per cock in the breeding population, giving the number of young cocks in the fall population per adult hen in spring. Assuming a 50:50 juvenile sex ratio, the same relative number of young hens will also be present. The

general procedure has been widely employed in pheasant research (Kimball 1948; Dale 1952; Stokes 1954:78-79; and others).

The method rests on two major assumptions: (1) that adult and juvenile cocks are not differentially vulnerable to hunting; and (2) that mortality of adult cocks is negligible between spring and fall. The validity of our bag-check ratios has already been substantiated (Gates and Hale 1974:7). Although the second assumption could not be met, knowledge of cock survival rates from spring to fall enables us to correct for this bias. The average survival rate of cocks between May and October (1959-64) was 68 percent and no evidence was found that survival during this interval was subject to change between years (Gates 1971:709-746). Age ratios in the bag were therefore multiplied by 0.68, and productivity rates were calculated accordingly.

An alternative measure of productivity was available by comparing the spring population estimate of breeding hens with the fall population estimate of juvenile hens. During the period 1959-64, agreement between this and the previous methods was gratifyingly close

(Table 34), leading us to place a high degree of confidence in the sex and age calculations. Because no estimate of fall population size was available in 1965, we relied completely on productivity rates calculated from sex and age structure.

Another commonly used measure of reproductive success is the rate of spring-to-fall gain, or the percentage change between spring and fall population size (Errington 1945:13; Kabat and Thompson 1963:8). In pheasants, the concept is most usefully applied to the hen segment of the population (Stokes 1954:68), since the rate of increase among cocks also depends on the sex ratio of the breeding population. Rates of gain were calculated for both sexes of the population (Table 34) to facilitate comparison with other studies in which separate calculations were not made by sex class.

The rate of gain differs from the rate of productivity in that the former integrates effects of both reproduction and adult mortality in spring-to-fall population change. While we recognize the importance of adult mortality in this context, we preferred to examine it as an independent influence on reproduction. Productivity rates were better suited for this purpose and were used as our definitive measure of reproductive success.

Agreement is general that the percentage of the hen population that ultimately succeeds in brood production is one of the principal determinants of reproductive success (Kimball et al. 1956:218; MacMullan 1960:98; Linder et al. 1960; and others). Theoretically, annual changes in this percentage should be detectable from brood observations conducted sufficiently late in summer that the majority of the hatch is already off. However, such observations apply only to hens still surviving at this season. While it is reasonable to assume that the ratio of broodless to successful hens bears some relationship to the success of surviving hens in producing young, annual changes in this statistic do

**TABLE 35.** *Late summer population characteristics based on brood observations after July 31, Waupun Study Area and vicinity*

Year	Adult Hens Seen With Broods (Percent of Total Hens)	Brood Observed Per 100 Miles*	Juveniles of Both Sexes Per Adult Hen**
1959	94 (200) <sup>1</sup>	33 (563)	6.2
1960	88 (287)	29 (1,060)	5.5
1961	86 (305)	42 (595)	5.6
1962	89 (218)	26 (1,081)	6.3
1963	90 (215)	25 (1,051)	5.8
1964	91 (221)	28 (743)	5.7
1965	92 (273)	31 (877)	6.2

\*Includes both complete and incompletely counted broods.

\*\*Based on the number of adult hens observed per 100 miles of brood observation effort related to the number of broods observed per 100 miles, the latter weighted by the average size of completely counted broods.

<sup>1</sup>Sample size shown in parentheses.

not necessarily imply corresponding variation in breeding success of the entire hen population alive in spring.

The observed percentage of hens with young in our study was restricted to observations after July 31 (Table 35). During the period 1959-64, yearly change in this statistic was unrelated to the percentage of nesting hens producing successful clutches based on actual nesting studies (Table 25) ( $r = -0.14$ ). For the 2 years of poorest productivity -- 1959 and 1961--roadside counts revealed 91 percent of the hens accompanied by broods. Five years of average or better-than-average productivity showed 89 percent of the late summer hens with young.

Other measures of reproductive performance agreed with production rates inferred from nesting studies, so it was obvious that the percentage of hens observed with young was the aberrant statistic. Despite wide variation in productivity, the percentage of the late summer hen population observed with young remained generally high and did not exhibit parallel fluctuation.

Observability differences between successful and broodless hens often have been held accountable for the unreasonably high percentage of hens observed with young (Kozicky 1951; Stokes 1954:42; and Dale 1956:34-35). At Waupun, however, another interpretation was more plausible. We found the average survival rate of hens to be 59 percent between May 1 and the approximate midpoint of summer brood observations (1959-64 data). Nesting studies revealed that the average percentage of the spring population that actually produced broods in these years was 55. If it is assumed that no hens lost entire broods, and that no unsuccessful hens pirated chicks belonging to other hens, the expected percentage of hens with broods after conclusion of nesting should have been approximately 93 ( $55 \div 59$ ). The actual percentage observed was 88 (Table 35). The general agreement be-

tween expected and observed values suggested that observability differences between successful and broodless hens were less than has previously been supposed.

Data in Table 35 therefore implied that a large and comparatively nonvariable fraction of the hen population surviving in late summer ultimately succeeded in brood production, and constituted one of several lines of evidence leading to the conclusion that reproductive success in this study depended mainly on the rate of hen mortality during nesting.

Young-per-hen ratios derived from brood observations did not agree in trend with other information on reproductive success ( $r$  with 5 df =  $-0.69$ ). Absence of a direct relationship would be expected if summer brood observations tended to sample the successful segment of the hen population and their progeny, and if productivity actually depended on the proportion of hens that survived to produce a brood of chicks.

If so, a more-or-less stable age structure would prevail each year despite major fluctuation in reproductive success. Although a certain degree of age variability was evident (Table 35), young-per-hen ratios for the years 1959-64 produced a correlation of 0.75 with annual rates of juvenile survival in Table 33. The relationship, while short of statistical significance (reference value with 4 df at 0.05 = 0.81), seemed to imply that much

of the departure from stability in late summer age composition could be attributed to yearly differences in chick survival. Although rates of productivity fluctuated widely, late summer age ratios tended toward stability, also reflecting the importance of hen survival to breeding success.

Our intensive studies revealed a substantial degree of yearly variability in productivity with a comparatively high and nonvariable fraction of the surviving hens successful in brood production. Statewide data are less conclusive in this regard (Wagner et al. 1965:58), but changes in reproductive success were not parallel by changes in the observed percentage of successful hens. On such grounds, the critical importance of adult hen mortality to reproductive success under conditions of our study may apply rather generally to Wisconsin pheasants.

Rates of productivity in the hen segment of the population at Waupun were roughly comparable to results reported elsewhere; however, spring-to-fall gains at Waupun tended to be lower than average (Table 36). Among those studies reporting rates of gain for both sexes of the population combined, spring-to-fall gains in most areas were lower than we observed, but in all non-Wisconsin studies the sex ratio in spring was also lower; hence the difference did not apply to the hen component of the population. The combination of near-normal

**TABLE 36.** *Comparison of rates of reproductive success observed on various pheasant study areas*

Area Studied and Years	Number of Juvenile Hens in Fall Population Per Hen in Spring Population	Percent Population Increase from Spring to Fall		Authority
		Hens Only	Cocks and Hens	
Pelee Island, Ont., 1947-50	1.4	120	--	Stokes 1954
No. Cent. Iowa, 1939-41, 1949-50	--	--	175	Kozicky and Hendrickson 1951
SE Penn., 1939	1.9	179	--	Randall 1940
East Cent. Mich., 1940-42	--	112	227	Shick 1952
So. Ill., 1960-61	1.7	105	--	Anderson 1964
SW Iowa, 1957-59	1.4	--	193	Klonglan 1962
No. Cent. Colo., 1948-50	--	--	183	Yeager et al. 1951
Ohio, hypothetical year	1.3	86	134	Leedy and Hicks 1945
East Cent. Wis., 1959-65	1.5	92	214	This study

productivity and reduced rates of gain in our study reflected a comparatively low rate of hen survival, but reasonably high reproductive success among survivors. Several studies outside Wisconsin also suggested that hen survival may be a critical factor affecting reproductive success (Ellis and Anderson 1963; Buss et al. 1952). In many areas, the percentage of the hen population surviving at the end of reproduction probably is a more significant variable than the ratio of broodless to successful hens among the survivors.

### MECHANISMS OF ANNUAL VARIATION

Figure 20 displays a number of annually varying influences on reproductive success.

It was evident from the correlation matrix that yearly differences in productivity depended chiefly on the number of young per hen produced at hatching. Juvenile survival exhibited a substantial degree of annual variability, but the trend was inverse to productivity and thus did not account for major change in reproductive success.

The average number of young produced at hatching depended primarily on the percentage of successful hens in the population, which in turn depended on the

average rate of nest success and the rate of hen survival during nesting. Both of the latter produced correlations with the overall rate of productivity barely short of significance. Nest success, however, behaved as essentially a random variable, controlled by a complex of interacting factors, and its relatively high correlation with productivity resulted from the unusually high rates of each which prevailed in 1964. Significant fluctuations in productivity existed during other years (Table 34) with comparatively minor variation in the percentage of nests that succeeded (Table 17).

Hen survival thus emerged as the dominant influence on productivity under conditions of our study. Rates of hen survival, in turn, were significantly correlated, or nearly so, with average clutch size, onset of nesting, hen weights in late winter, and the winter hardness index, all of which were more-or-less interrelated and also correlated with productivity. In general, more severe winters were associated with greater weight loss of hens, delayed egg laying, smaller clutches, accelerated hen mortality, and poorer reproductive success. Although correlations do not necessarily imply causality, there can be little question that variation in winter weather and resultant influence on hen condition was the primary factor responsible

for yearly changes in reproductive success that we observed.

### SUMMARY

Productivity was defined as the average number of juvenile hens recruited to the fall population per breeding hen in the spring population and was regarded as the definitive measure of reproductive success under conditions of the present study. Rates of productivity varied from a low of 1.1 in 1959 to a high of 1.9 in 1964. Despite marked variation in reproductive success from year to year, the late summer percentage of hens observed with broods and young-per-hen ratios remained generally constant, from which it was concluded that reproductive success depended chiefly on hen survival during nesting. Other Wisconsin findings were generally consistent with this conclusion.

Rates of productivity and hen survival from spring to fall were significantly correlated, or nearly so, with the average weight of hens in late winter and with indices to winter hardness. It was concluded that reproductive success was principally controlled by winter weather, through dynamics of hen condition at start of nesting and survival variation during reproduction.

5 NO. JUV HENS IN FALL PER ADULT HEN IN SPRING										
0.98	4 NO CHICKS HATCHED PER ADULT HEN IN SPRING									
-0.61	-0.65	4 % JUV SURVIVAL FROM HATCHING TO FALL								
0.80	0.78	-0.48	4 % NEST SUCCESS							
0.74	0.79	-0.75	0.35	5 % MAY 1 TO OCT 1 SURVIVAL OF ADULT HENS						
0.83	0.91	-0.46	0.60	0.80	5 AVG CLUTCH SIZE					
0.80	0.72	-0.55	0.26	0.89	0.78	4 % HENS BEGINNING CLUTCHES BY MAY 10				
-0.21	-0.26	0.57	-0.54	-0.38	-0.23	-0.05	5 NO HENS IN BREEDING POPULATION			
0.01	0.00	-0.02	0.44	0.46	-0.17	-0.39	-0.24	5 AVG DAILY TEMPERATURE APRIL 20-MAY 10		
0.73	0.85	-0.52	0.43	0.70	0.77	0.62	-0.07	-0.41	5 AVG WEIGHT OF HENS IN MARCH	
-0.85	-0.87	-0.39	-0.44	-0.75	0.95	-0.77	-0.02	0.35	-0.87	5 WINTER HARDNESS INDEX

**FIGURE 20.** Results of correlation analyses summarizing the relationship between individual factors affecting reproduction and eventual rates of productivity in terms of the number of juvenile hens recruited to the fall population per hen in the spring population. Numerals next to each heading indicate degrees of freedom; to establish the significance of each correlation coefficient, refer to the smaller of the two as the appropriate number of degrees of freedom for comparison with reference values (reference values at 0.05 with 5 df = 0.75; with 4 df = 0.81). Variables showing 4 degrees of freedom based on 1959-64 data; those with 5 degrees of freedom based on 1959-65 data.

## APPENDIX A: Scientific Names of Animals and Plants Used in Text

Crow, *Corvus brachyrhynchos*

Raccoon, *Procyon lotor*

Red fox, *Vulpes fulva*

Skunk, *Mephitis mephitis*

Thirteen-lined ground squirrel,  
*Citellus tridecemlineatus*

Bull snake, *Pituophis melanoleucus*

Fox snake, *Elaphe vulpina*

American hazel, *Corylus americana*

Aster, *Aster* spp.

Blackberry, *Rubus*, spp.

Black cherry, *Prunus serotina*

Bluegrass, *Poa* spp.

Bluejoint grass, *Calamagrostis canadensis*

Boxelder, *Acer negundo*

Bromegrass, *Bromus inermis*

Burdock, *Arctium minus*

Canary grass, *Phalaris arundinacea*

Cattail, *Typha latifolia*

Common milkweed, *Asclepias syriaca*

Cordgrass, *Spartina pectinata*

Elderberry, *Sambucus canadensis*

Giant ragweed, *Ambrosia trifida*

Goldenrod, *Solidago* spp.

Gray dogwood, *Cornus racemosa*

Lesser ragweed, *Ambrosia artemisiifolia*

Locust, *Robinia pseudo-acacia*

Marsh milkweed, *Asclepias incarnata*

Meadow rue, *Thalictrum dasycarpum*

Mint, *Mentha arvensis*

Nettle, *Urtica dioica*

Plum, *Prunus americana*

Quackgrass, *Agropyron repens*

Red-osier dogwood, *Cornus stolonifera*

Redtop grass, *Agrostis gigantea*

Reed-canary grass, *Phalaris arundinacea*

Sedge, *Carex* spp.

Silky dogwood, *Cornus obliqua*

Smartweed, *Polygonum* spp.

Spiraea, *Spiraea alba*

Sunflower, *Helianthus grosseserratus*

Thistle, *Cirsium* spp.

Wild parsnip, *Pastinaca sativa*

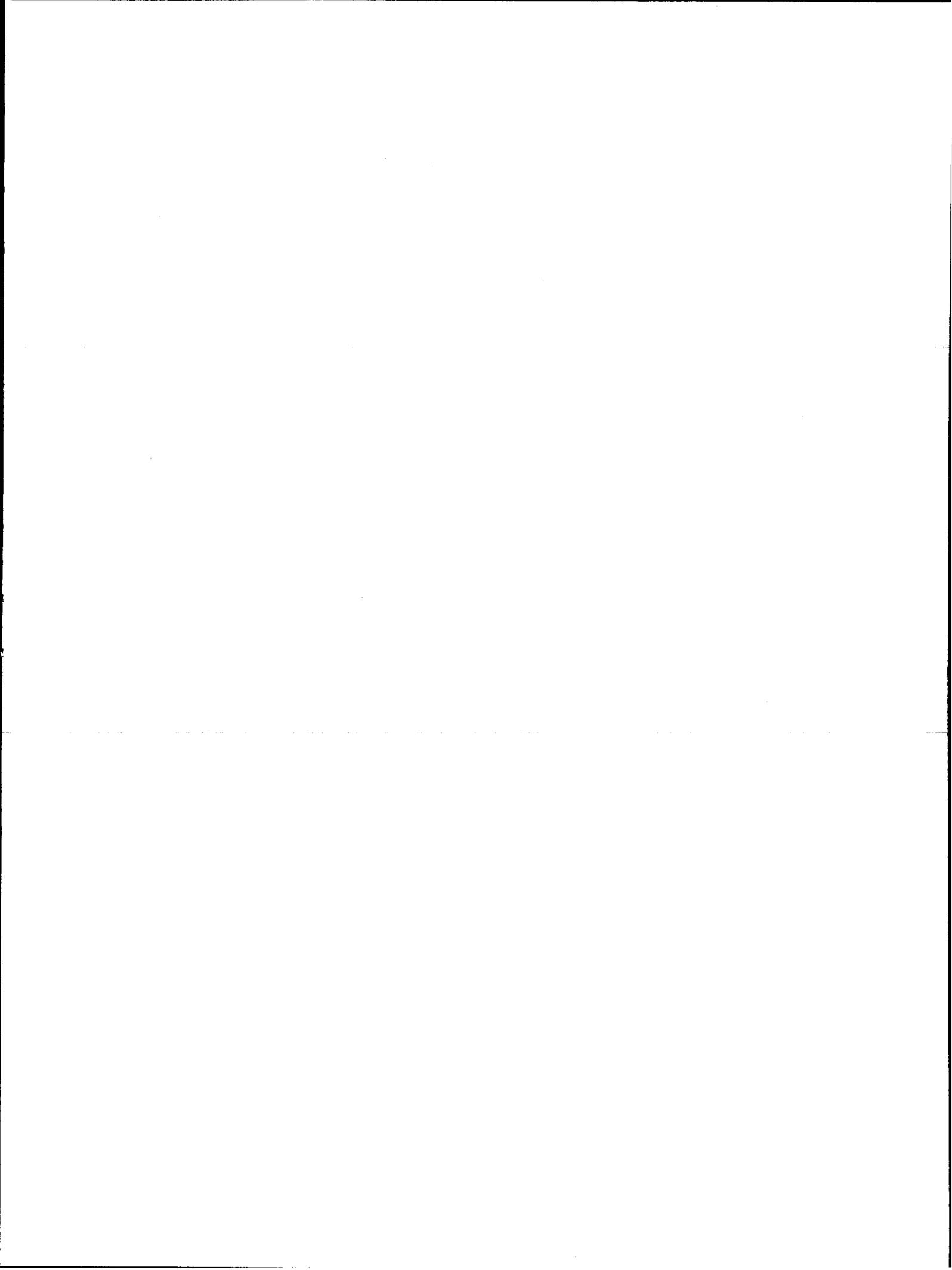
Willow, *Salix* spp.

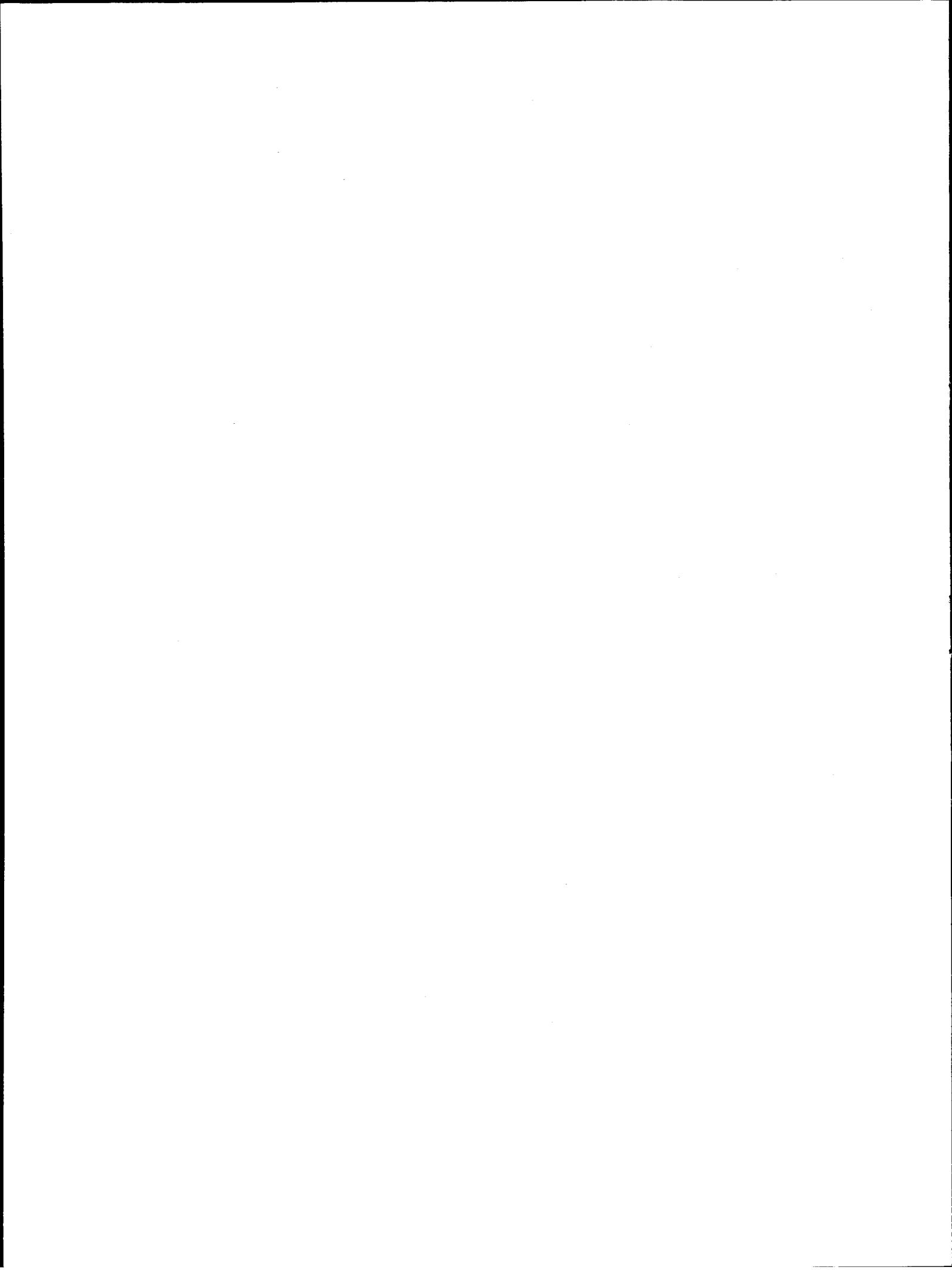
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